VKM Report 2022:15

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Scientific Opinion of the Panel on Alien Organisms and Trade in Endangered species (CITES) of the Norwegian Scientific Committee for Food and Environment

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Preparation of the opinion

The Norwegian Scientific Committee for Food and Environment (Vitenskapskomiteen for mat og miljø, VKM) appointed a project group to draft the opinion. The project group consisted of four VKM members, two VKM staff and seven external experts. Two referees commented on and reviewed the draft opinion. The Panel on Alien Organisms and Trade in Endangered Species (CITES) supplemented with a member of the Panel on Plant Health, evaluated and approved the final report.

Author contributions

All authors have contributed to the report in a way that fulfills the authorship principles of VKM (VKM, 2019). The principles reflect the collaborative nature of the work, and the authors have contributed as members of the project group and/or the VKM Panel on Alien Organisms and Trade in Endangered Species (CITES) or the VKM Panel on Plant Health.

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Competence of VKM experts

Persons working for VKM, either as appointed members of the Committee or as external experts, do this by virtue of their scientific expertise, not as representatives for their employers or third-party interests. The Civil Services Act instructions on legal competence apply for all work prepared by VKM.

Table of Contents

1.1 A Guide to the Reader

In this report, we summarize the current state of knowledge and best estimates of how climate change is expected to impact Norwegian forest ecosystems from now to the year 2100. As the topic of the report is extensive, we here present a summary of the structure and content of the report.

Chapter 1 consists of this guide, and an executive summary presenting the essence of our findings and conclusions with reference to the Terms of Reference (ToR), as well as an abstract in Norwegian. The chapter also includes a glossary of terminology, a list of abbreviations, and a list of key species and species groups to connect common English, scientific, and Norwegian names unambiguously. The chapter ends with the background for the assignment and the ToR as provided by the Norwegian Environment Agency.

Chapter 2 provides background information on the past and present boreal forest biome, subdivided into three main sections. Section 2.1 provides relevant information on the past and present distribution, ecology, biodiversity, climate zones, carbon cycle and pressures on the boreal forests of the world. Section 2.2 presents global climate change with regards to the boreal biome. Section 2.3 provides relevant information on the Norwegian parts of the boreal forests specifically, including how they have been managed and the natural history of key species. Section 2.4 gives an overview of previous assessments of the impact of climate change and other global drivers changing the ecological condition of Norwegian forests.

Chapter 3 presents the materials and methods used for this report. Section 3.1 describes how we interpret and operationalize the ToR with respect to the specific questions posed regarding Norwegian Ecological Condition Framework; relevant Nature in Norway forest types; main sources for climate factors and climate projections; treatment of pests, diseases, and alien species; specific impacts on tree species stand ages and regions; thresholds, resilience (*q.v.*), robustness and vulnerability; forest management and adaptation; and national biodiversity targets. Section 3.2 describes reasons for the climate scenario selection, climate data, and projections used. Section 3.3. describes our literature searches and methods for knowledge synthesis to address the different aspects of the ToR.

Chapter 4 the main results chapter, presents and summarizes the evidence base retrieved by the report. Section 4.1 presents our findings pertaining to projected changes in climate and climate-related drivers, including both gradual changes and changes in climate-related extremes and disturbances. Section 4.2 presents the evidence for impacts of these changes on abundances, demographic rates, and distributions of key boreal forest species and functional groups (*q.v.*) across all trophic levels (primary producers, herbivores, pollinators, omnivores, insectivores, carnivores, mutualists, and decomposers), including information on climate impacts on physiology via population to species and functional groups. Section 4.3 summarizes impacts on invasive alien and native pests, pathogens and parasites. Section 4.4

summarizes community-level impacts on plants, vertebrates, forest invertebrates, insects, decomposers and mutualists, and habitat specialists, along with biodiversity and ecosystem-level impacts. Section 4.5 delves into the complexities of how plants and animals respond to climate change: why and how adaptive responses such as range shifts often lag behind changes in climate, and the disruptions in ecological interactions that then arise (such as loss of synchronization between plants and their pollinators or natural enemies). Section 4.6 summarizes information specifically related to managed versus natural forests, and 4.7 summarizes information on red-listed species and habitats.

Chapter 5 then synthesizes the knowledge from Chapter 4 with respect to the specific questions posed in the ToR. Section 5.1 summarizes evidence for impacts of climate change and climate-related variables on each of the seven characteristics of ecological condition in boreal forests. Section 5.2 summarizes the role of native and alien pest and pathogen species in climate change impacts on boreal forests. Section 5.3 summarizes the results for key tree and shrub species, different stand ages, and regions, where available. Section 5.4 discusses factors that confer resilience, resistance, and vulnerability to climate change: that is, what determines how well boreal forests can tolerate disruptions related to changes in climate. Section 5.5 summarizes the vulnerability of managed and natural forests to climate change. Section 5.6 summarizes the consequences for Norway's ability to reach its biodiversity goals regarding ecological condition and red-listed species (national biodiversity targets 1.1 and 1.2).

Chapter 6 focuses on the main knowledge gaps and uncertainties, starting with Section 6.1 that summarizes knowledge gaps that should be given priority. Section 6.2 summarizes knowledge gaps in forest models and studies, Section 6.3 summarizes gaps in climate models and uncertainties, and 6.4 summarizes uncertainties in assessing ecological condition. And section 6.5 lists further knowledge gaps.

Chapter 7 summarizes how this report relates and compares to the IPCC sixth assessment report, especially its Working Group II report on impacts and vulnerability which was published as this report was being finalized.

Appendices provide additional tables and information.

1.2 Executive summary

1.2.1 Background

The Norwegian Environment Agency tasked the Norwegian Scientific Committee for Food and Environment (VKM) to "provide an overview of the knowledge status about how the forest in Norway will develop in a changing climate". The assessment should be based on the Norwegian Ecological Condition Framework (NECF), focusing especially on impacts on functionally important groups and species, landscape ecological patterns, and biological diversity. The review should assess how these aspects of ecological condition will be directly affected by climatic factors (changes in temperature, precipitation, wind, extreme weather events, snow and ice), and indirectly, through climate-related increases in pests, diseases, or invasive species. As far as knowledge permits, the report should differentiate between tree species, stand ages, habitat types, and geographical regions. The overarching goal is to provide updated and useful scientific information for management and other stakeholders. The report should also consider properties that can contribute resilience to climate change or confer vulnerability with respect to reaching the national biodiversity targets 1.1 -that ecosystems should be 'in good condition' and 1.2 -that no species and habitats should be eradicated and the development of endangered and near endangered species should be improved.

The assessment should be based on climate projections from the Norwegian Centre for Climate Services (NCCS), which provide fine-scaled climate predictions for Norway based on the global models and emission scenarios used by the Intergovernmental Panel on Climate Change (IPCC), as well as historical data. The NCCS projection data run until the year 2100, and this forms the time horizon of the report.

1.2.2 Methods

A working group with expertise in forest ecology, climate change, and the ecological impacts of climate change was established. The group assessed foreseeable climate effects on the seven "characteristics" [C] used in the Norwegian Ecological Condition Framework to cover key aspects of ecological condition: [C1] primary production, [C2] distribution of biomass across trophic levels, [C3] functional composition within trophic levels, [C4] functionally important species and biophysical structures, [C5] landscape ecological patterns, [C6] biological diversity, and [C7] abiotic factors. The working group reviewed the international scientific literature and management reports, supplemented by original analyses and visualizations where data were available. Expert knowledge was used to identify relevant literature, giving priority to recent publications over older, and to geographically close and similar systems over more distant or dissimilar, and to seek out studies reporting weight of evidence and being open about uncertainties and knowledge gaps. Relevant functional groups of organisms were identified in the process of aggregating data. Impacts on rare and threatened species and habitats were assessed by analysing information in the national red lists provided by the Norwegian Biodiversity Information Center.

1.2.3 Changing conditions

The IPCC and NCCS predict different climate outcomes depending on greenhouse gas (GHG) emission scenarios. Considering the precautionary principle and current emission trajectories, we disregarded both the most optimistic and worst case scenarios. Given the uncertainty about what climate outcome a given GHG concentration will entail, we consider the space between the IPCC Fifth Assessment Report scenarios RCP4.5 and RCP8.5 a "cone of plausible futures" (see Figure S1).

Until about 2050, all IPCC scenarios make roughly similar predictions, as ongoing changes over the next two to three decades are mostly dependent on emissions from the late last century to the present. After 2050, the scenarios diverge depending on ongoing and future emissions.

The median annual temperature in Norway in 2070-2100 is expected to be between 2.7 and 4.5 ºC above the average for 1971-2000. Accounting for uncertainties broadens this range to between 1.6 and 6.0 ºC, with natural between-year variation in annual temperatures coming in addition. The increase in temperature will be stronger further away from the coast and further north, and stronger during winter than in summer.

Increased rainfall, particularly in winter, and a shorter period of snow cover, combined with increased evaporation, especially in summer, are expected to create wetter winters and more variable summer conditions, with more extreme rainfall events and more frequent heatwaves and droughts. Wind and storms may increase in strength or frequency but projections are uncertain. Lightning activity at higher latitudes is expected to keep increasing and become more similar to the global mean. Fire activity is thus expected to increase, but not evenly due to the strong bioclimatic gradients in Norway.

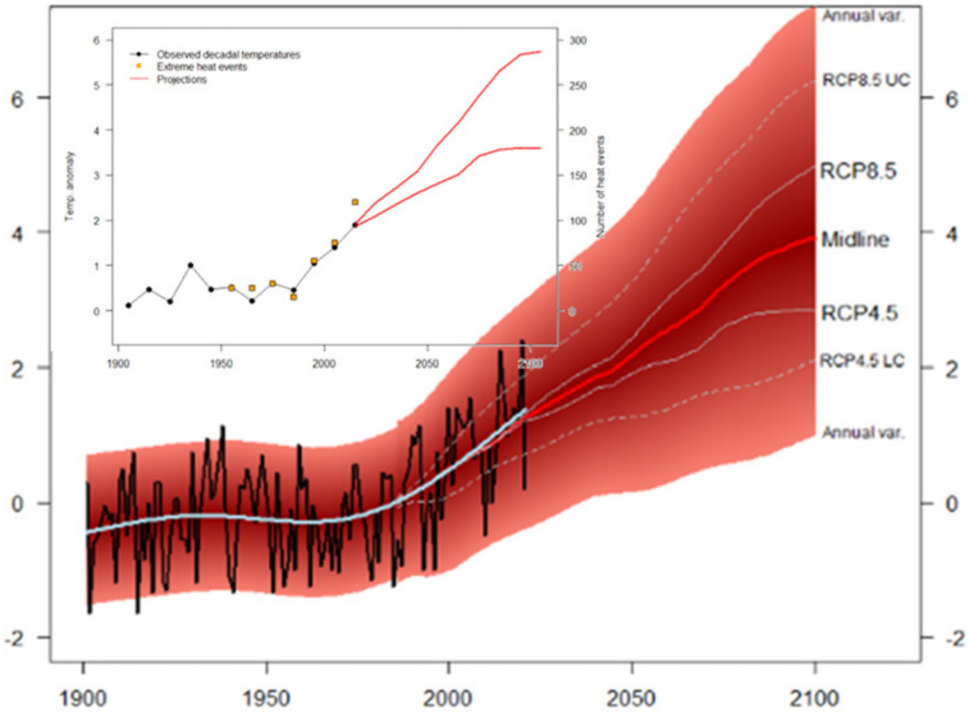


Figure S1. Summary of median annual temperature anomalies in mainland Norway from the year 1900 to 2021 (black line) with a smoothed historical mean (light blue). The red and white lines indicate the projected means from 2022 to 2100. RCP8.5 and RCP4.5 are IPCC climate scenarios denoting little or fairly effective emission control over the next fifty years, respectively. The dotted lines marked RCP4.5 LC (lower consensus) and RCP8.5 UC (upper consensus) mark the outer boundaries of the interval containing at least 80% of the mean annual temperatures predicted by an ensemble of climate models for the respective scenarios. These consensus intervals largely overlap, meaning that an RCP4.5 scenario where climate responded a little bit stronger than expected is indistinguishable from an RCP8.5 scenario where climate responded a little less to emissions than expected. A solid red line marks the middle of the scenarios. The red shading shows the extent of natural between-year variation when the variation is kept at the same level as in the historical (i.e., observed) data. For instance, a period around 2100 where mean temperatures have followed the RCP8.5UC would see cold years with mean temperatures around 5ºC and warm years with mean temperatures around 7ºC. **Insert**: The observed relation between extreme events (heatwaves) and annual mean temperature. Red lines mark extrapolations for RCP4.5 and RCP8.5 respectively.

1.2.4 Impact of climate change on the ecological conditions of forests

Climate change and climate-related factors can have both positive and negative impacts on the seven characteristics of ecological condition in forests (Figure S2). Overall, warming and general climate change are the main causes of the positive impacts for each ecosystem characteristic (i.e., >60%); for negative impacts, a much wider range of drivers are documented, and in particular weather extremes and climate-related disturbances play a larger role (Figure S2).

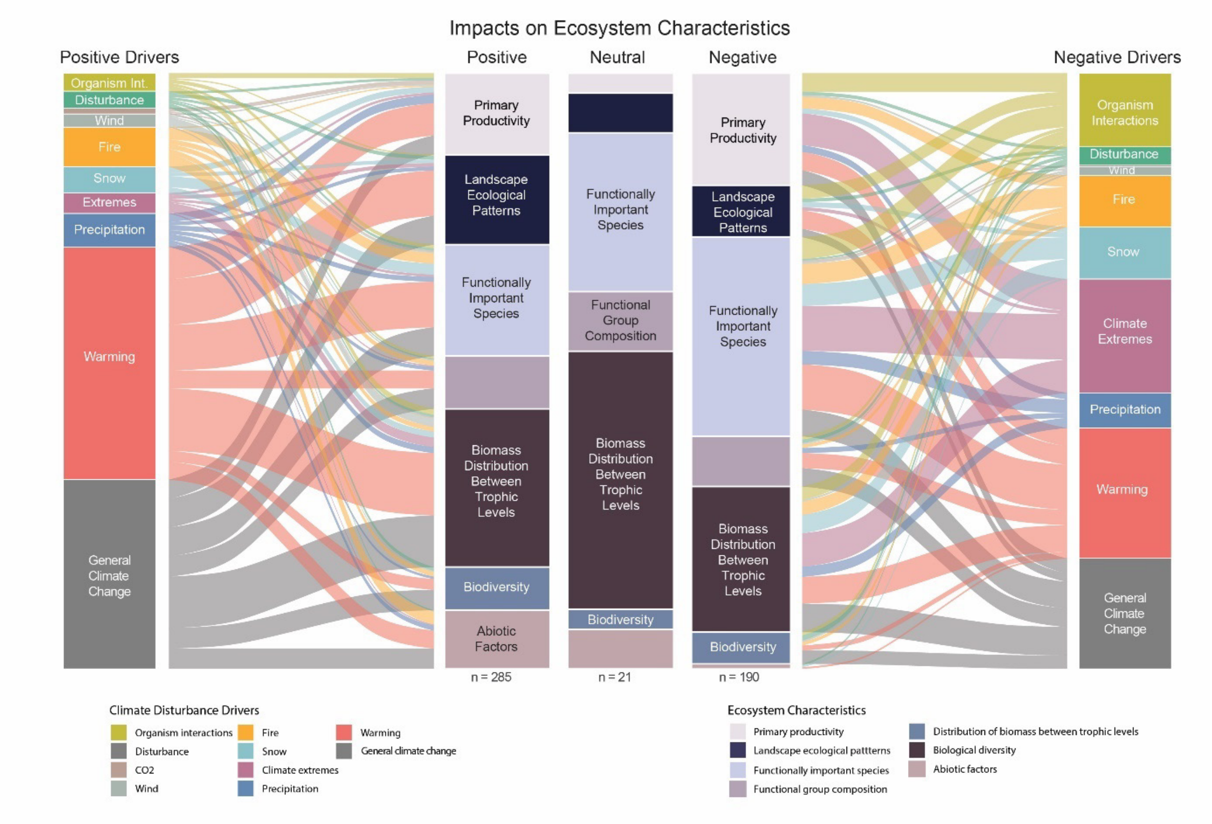


Figure S2 A summary of the amount of evidence for positive (left) and negative (right) impacts of climate change-related drivers on the ecological condition of Norwegian boreal forests. Ecological conditions are represented by the seven ecosystem characteristics of the Norwegian Ecological Conditions Framework. Climate change-related drivers are aggregated into nine major classes reflecting gradual climate change, corresponding frequencies of extreme weather events, and climate-related disturbances. The height of each driver class or ecosystem characteristic within the respective bars represents the relative weight of evidence from the reviewed scientific literature that is related to that specific driver class or ecosystem characteristic. The flows represent the relative strength of evidence for a specific climate driver class having a positive or negative influence on a specific ecosystem characteristic. Note that positive, negative, and neutral impacts were evaluated separately in this figure. Sample sizes under each ecosystem characteristic bar plot represent the overall weight of evidence within the report. Alien species are not included.

The report finds that current and projected climate change is likely to impact **primary productivity in forests [C1]** in complex ways (Figure S2). In the near term (until 2050), increases in mean temperatures and growing season length will likely increase the growth of trees and understory plants. However, these positive effects are counteracted to some extent by increased risks from climatic extremes (drought, heat extremes, and winter warm spells), disturbances (fire and possibly wind), and from tree pest outbreaks and diseases. The effects of CO_2 fertilisation are contradictory and any positive effects are unlikely to persist beyond those for young plants. In the longer term (until 2100), climate warming is projected to reach levels where growth and range sizes of the dominant boreal trees (pine, spruce, and birch) will be reduced for most of the current boreal zone in Norway (e.g., Figure S3). Meanwhile, the negative impacts of climatic extremes, disturbances, pests, diseases and herbivores will become more pronounced, causing significant reductions in the growth of trees and understory plants with negative impacts on forest productivity and the ability of tree species to track their climatic ranges. The net impact on primary production is likely to vary over time and between species. Spruce-dominated forests are likely to experience the greatest negative impacts from fire, even though pine-dominated habitats have higher fire risks. Broadleaf-dominated forests are less at risk. No clear prediction exists for changes in or responses to windthrows, due to uncertain predictions as to how climate change will affect the frequencies and strengths of storms.

Focusing on the **functionally important species [C4]** (Figure S2), boreal trees and local forest growth, survival, and recruitment are likely to benefit from warming in the short term, however this will likely be reduced or reversed as warming proceeds (until 2100). Negative impacts of climate change-related extremes and of biotic and abiotic disturbances will increase over time, suggesting that the net climate change effects will reduce forest growth and survival in the longer term. In the forest understory, ericaceous dwarf shrubs may have reduced survival due to declining snow cover, whereas many bryophytes and lichens may suffer from increased temperatures or worse fires. Many boreal birds and rodents are poorly adapted to climate warming, whereas invertebrate herbivores and more southern-distributed ungulates, such as roe deer and red deer, may benefit. Small carnivores specialised on rodent prey may decline under climate change due to cascade effects (*q.v.*) from decreased prey populations and disrupted population cycles. Negative impacts of warming and increased weather extremes on plants may translate into positive impacts on saprophyte and decomposer communities, although the evidence is limited.

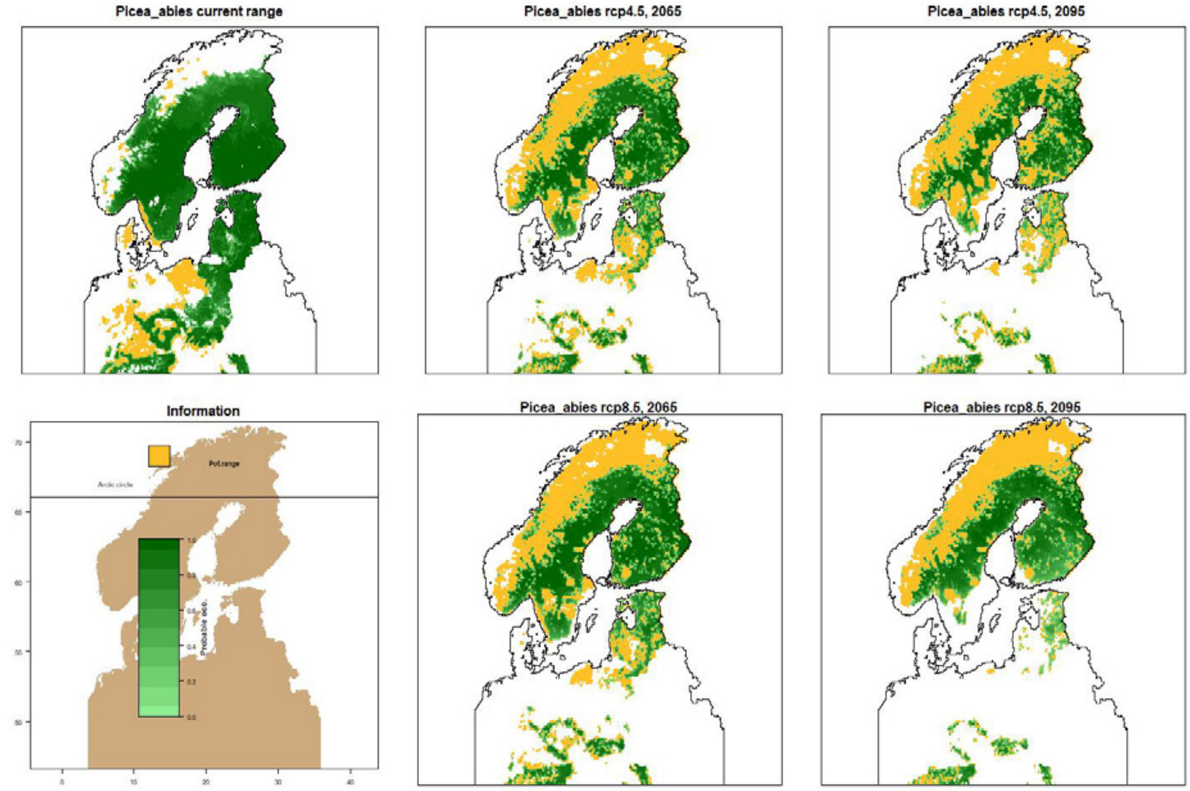


Figure S3. Current and future distributions of spruce (*Picea abies*) in Europe, estimated for RCP4.5 and RCP8.5 mean scenarios. The analyses are based on the same EURO-CORDEX climate models used by the NCCS, and are coupled with tree distributions, climate, soil and landuse data to develop a data set of 67 European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers in 2022. Tree dispersal capacity has been explicitly modeled. The green color scale shows probability of the species occurring (from 0 to 1, approximately 10 x 10 km resolution), yellow shows potential distribution. The current range (upper left) shows where spruce is found today, with yellow showing where conditions would have permitted it but it is currently not observed. The lower left panel shows color scales and longitude-latitude. The four right panels show estimates for two future time points for the two climate scenarios. We see that while spruce as a forest-building species is expected to retreat from the south, new climate zones are opening up for potential colonization, but actual colonization at the leading edges happens too slowly to compensate for the loss of range at the trailing edges of the distribution. Hence, spruce range contracts.

Forestry practices, complex topography, and the wide geographic distribution of the boreal biome (*q.v.*) render Norwegian boreal forests and forest biota spatially fragmented, despite the high forest cover in Norway (37%). Under climate warming, species distributions tracking the movements of their climate zones across the landscape is the major projected **landscape ecological process [C5]** for boreal biota (Figures S3, S4, S2). Such range dynamics are widely documented, including for trees, birds and bats, ungulate and rodent grazers, bumblebees, moths, other invertebrate groups, and for viruses and fungi. However, current range shifts are generally not keeping up with the changing climate, and climate-related disturbances, pests, and diseases may hamper range shifts of some tree species. Climate change is likely to benefit pests and other species prone to sudden population bursts (outbreaks), negatively impacting trees and forest communities. Deciduous trees, and in some habitats pine, as well as disturbance specialists and early succession species are likely to expand in range. They will however be limited by available habitat unless actively assisted by forest management. Important factors that limit tree establishment and slow down their range expansion via tracking climate zones include herbivores consuming young plants, poor landscape connectivity, and disrupted synchrony with mutualistic or symbiont species, such as pollinators or mycorrhizal fungi.

Climate-change-related changes in **biodiversity [C6]** (Figure S2) will entail increased richness of trees, understory species, small mammals and other vertebrate communities, saproxylic communities and other forest insects, soil invertebrate and fungal communities, whereas insectivorous bats, pollinating insects, mutualistic fungi, and specialized northern species across other taxonomic groups are expected to decline. The replacement of boreal and cold-adapted species with more warm-adapted species ("nemoralization": Figure S5) is expected to result in increased local species richness among trees, small mammals and other vertebrates, saproxylic forest insects, soil invertebrates, and fungal communities, because nemoral forests *(q.v.)* are often more diverse in these taxonomic groups than are boreal communities (e.g., Figure S5). However, this replacement may result in a loss of specialised boreal biota (see biodiversity goals below). Increased incidence of pests and diseases may lead to loss of tree and bird biodiversity. For species dependent on mature forests, including insectivorous bats, food-hoarding birds and rodents, and saproxylic insects, negative impacts of disturbances and climate change may appear. The evidence for climate-change-related biodiversity change in forest is limited, especially given the high biodiversity and many specialized organismal groups found here.

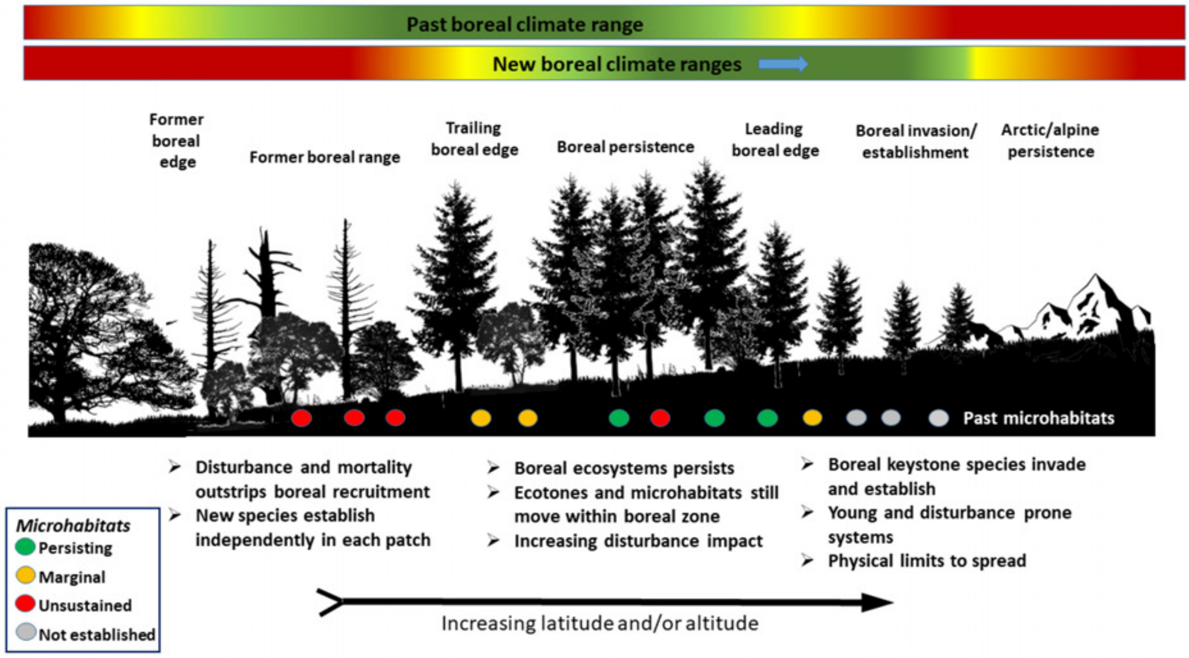


Figure S4. Range expansion by habitat-building species must occur before the remaining forest community can establish. For instance, large trees need an accumulation of topsoil and to be buffered against wind and drought. Also, microhabitats associated with mature or old growth forests (q.v.) require one or more centuries to establish at expanding northern or upper elevation forest edges before other species can colonise. In contrast, habitats can be removed by drought, fire, or forestry in just one summer at the southern or lower elevation edges. Old forest takes centuries to develop and hours to destroy. This mismatch of rates makes species associated with old growth forests particularly vulnerable to local extinctions when biomes move.

A recurring pattern across many organismal groups is thus a replacement of boreal biota by species adapted to warmer climates. This is generally expected to result in faster carbon capture and carbon cycling through the ecosystems. Substantial and asynchronous time-lags in **functional composition within trophic levels** (*q.v.*) **[C3]** (Figure S2) may create temporal mismatches (*q.v.*), for example between plants and their pollinators or birds and their insect prey, and cause feedbacks, decreasing resilience, and increasing vulnerability of the forest ecosystem as climate changes proceed.

These climate-driven but variable changes across forest biota may change the **trophic structure [C2]** (Figure S2) of the boreal forests. These effects may be exacerbated by climatic extremes (drought, heat extremes, winter warm spells), disturbances (fire, wind), and tree pests and diseases, and feedbacks and trophic cascades may add variability and uncertainty. In the longer term, we may see a trophic restructuring of the boreal forest ecosystems, with an overall decline in vertebrate herbivores, birds, bats, and to some extent carnivores accompanied by an increase in invertebrates, tree pests, and diseases.

Climate change is predicted to enhance rates of ecosystem nutrient cycling **[part of abiotic factors, C7]** (Figure S2). Specifically, the literature suggests increased and more easily decomposable carbon and nutrient inputs to boreal forest soils via increased litter from trees under warming, along with faster litter decomposition and nutrient cycling in warmer soils leading to increased carbon loss to the atmosphere. Decomposers are also expected to increase in abundance and efficiency, further enhancing nutrient cycling. Combined with changes in the soil microbial community and less frozen ground, increased soil respiration and decreasing soil carbon storage are likely consequences. Further ecosystem carbon loss may result from increases in climate-related disturbances. Droughts may result in reallocation of biomass and phosphorus from leaves to roots, and increased rain-on-snow events may increase nutrient leaching. Climate-related increases in fire risk may impact soil and ecosystem carbon and nutrient dynamics via feedback from cascade effects starting with treelayer damage.

1.2.5 Pests, pathogens, and outbreaks

Native and alien pests and pathogens are more often positively than negatively impacted by climate change. Increased disturbances and weakened hosts often result in increasing ranges and abundances, greater invasiveness, and more persistence, leading to more volatile population dynamics and more variable outbreak risks on the time scales we consider. Impacts of warming and general climate change are most frequently documented, but pests and pathogens are influenced by a range of climate drivers, including increased disturbance frequency, windfelling, decreasing frosts, increased precipitation but also increased heat extremes and droughts. Warmer, drier summers and milder winters with less extreme cold and frost will likely lead to more frequent and more extensive outbreaks of native forest pests and pathogens, and increase the overall area in which invasive alien species can establish viable populations. Fungal disease risk increases under cold periods in otherwise warm areas, whereas bacterial disease risk increases under warm periods in cold areas. Among parasites, helminths benefit more from warming than other groups. Viral infections show less obvious relationships with climate change, although vector-borne viruses may be an exception as they follow the response of their vectors and hosts. Local outbreaks might be partly controlled by corresponding (climate-related) increases in parasite or predator populations, mixed forest tree species, and limited regrowth of spruce. For herbivorous invertebrates, increased mean temperatures are likely to cause an increase in abundances and in population growth rates. Some herbivorous forest insects and plant and wildlife diseases may be negatively impacted by climate change, mostly in relation to extreme weather events.

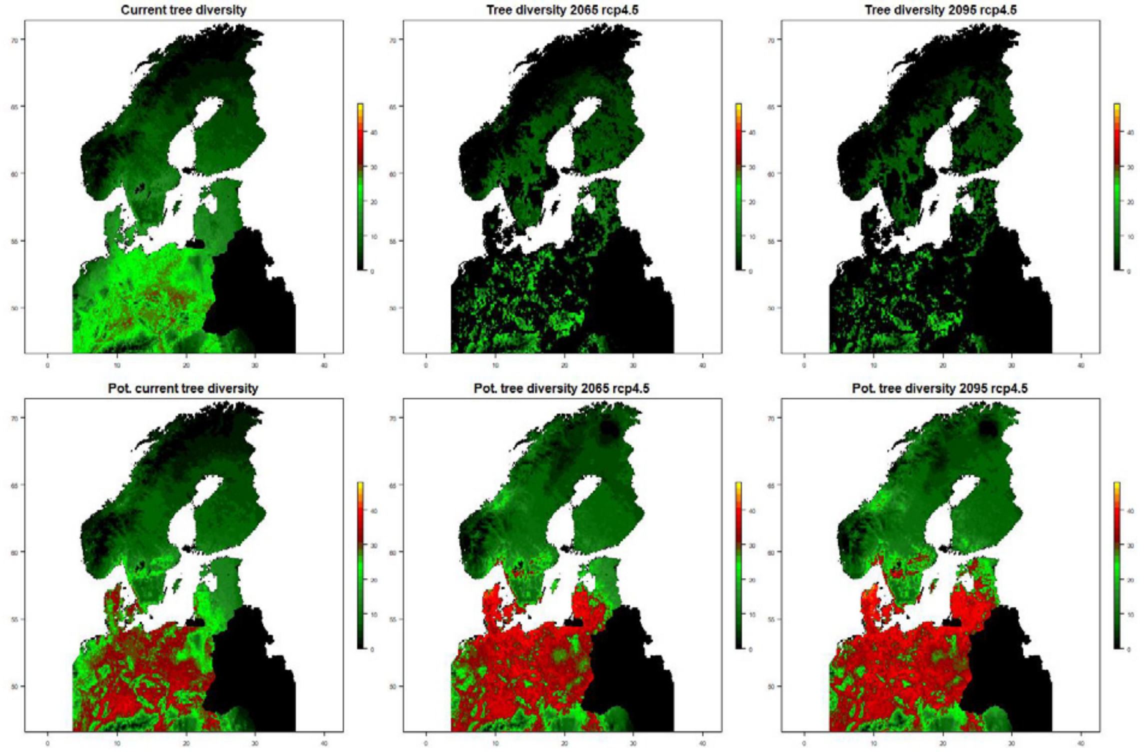


Figure S5a

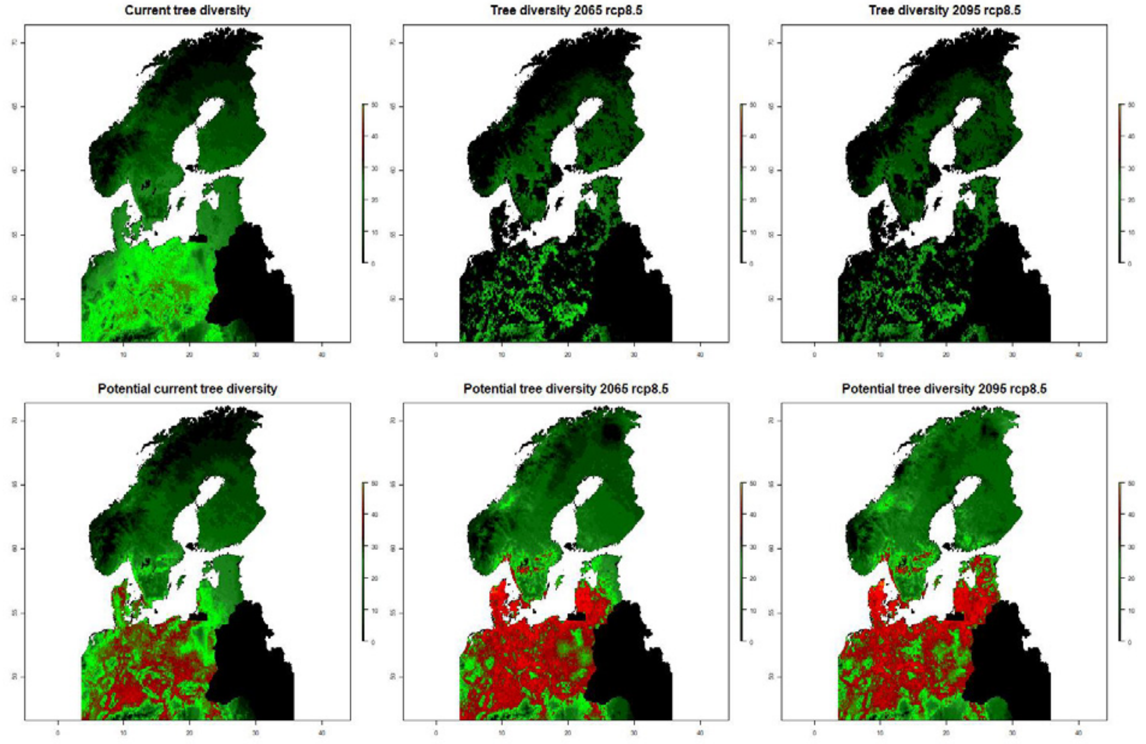


Figure S5b

Figure S5. Changes in potential tree community and likely realized composition for RCP4.5 (**a**) and RCP8.5 (**b**). An effect shared by many tree species modeled by Mauri et al. (2022) (see S3) is that while they are directly impacted to varying degrees, any negative impacts on the trees happen faster on the vulnerable "trailing edges" (usually more southern, or lower altitudes) than the range expansions at the "leading edge" (more northern, higher altitudes) can compensate (spruce being a typical example, as shown in S3). This effect is intuitive considering the rate of ongoing climate change relative to the long life spans, persistence and often limited dispersal capabilities of habitat-forming tree species, and seems likely to have important but hard-to-predict effects on community structure and biodiversity in periods with quick changes in average weather conditions. Judging from the models of Mauri et al., most northern areas will get climate zones where more potential distributions overlap–signaling higher diversity–but with the realized distributions being smaller and less overlapping–signaling less diversity and possibly less forest cover until the climate stabilizes at some level long enough for forests to catch up.

1.2.6 Biodiversity goals, red listed species, and habitat types

In the near term, climate warming is likely to have some positive effects on the ecological conditions of boreal forests (Figure S2), including increased primary productivity, enhanced abundances of many functionally important species, and range expansions of many species towards higher elevations and latitudes (Figures S3, S4, S5). In contrast, climate change related increases in the frequency and severity of extreme weather events (including drought, temperature, and freeze-thaw cycles) and climate-associated disturbances (fire, wind, snow, outbreaks) are likely to drive negative responses in forest condition (Figure S2). Specifically, these extremes and disturbances will likely lead to reduced primary productivity via decreased plant growth and increased mortality [C1], loss of many functionally important species [C4], and changes in biomass distribution across trophic levels (*q.v.*) [C2]. Increased fire risk and fire intensity under climate change also enhance nutrient cycling [C7], but otherwise have predominantly negative impacts, especially on biodiversity [C6, Figure S2].

These findings imply that gradual climate changes, such as warming or increased precipitation, are not likely to cause immediate threats to boreal forest ecosystem structure, functioning, and biodiversity; they may result in a net increase in forest productivity in the near term. In contrast, the increased frequency and intensity of weather extremes and climate-related disturbances (like fires and pest outbreaks) are likely to incur negative impacts that are often system-wide and lead to at least short-term losses of ecosystem functioning and resilience (*q.v.*). The risks and uncertainties regarding net effects of climate change on forest biodiversity and ecosystem functioning over time are exacerbated by the limits to our knowledge about how climate impacts interact with time lags, asynchrony, trophic interactions and ecological cascades.

Considering the national biodiversity target 1.2, climate change is presently identified as a specific threat to only 38 of 2083 forest-associated species on the Norwegian red list for species. A common theme for these 38 species is that climate change is only one among several threats, that the specific climate change driver responsible is not given, and that the Norwegian populations make up a small fraction of a species' global distribution. We do not know if these species are threatened throughout their range. Risks may be exacerbated because suitable habitats for many threatened forest species are often highly fragmented due either to the habitat being rare, or to changes in land use zoning or in agricultural or forestry practices that lead to loss or degradation of habitats. In addition, range limit contractions starting in the south or at lower altitudes are projected for all boreal taxa, including trees. The contractions may lead to local extinctions in boreal and northern species not currently classified as directly climate impacted or red-listed.

1.2.7 Resilience, vulnerability, and mitigation

The rugged topography of Norway fragments the forest landscape, making it less likely that disturbances and extreme events, like pest outbreaks, droughts, storms, and forest fires, exert large-scale effects over very large areas. The strong climate gradients and rugged topography can mean that species do not always need to relocate over long distances to find conditions that are within their climate envelopes. However, this also implies that local habitats and ecosystems could be displaced relatively rapidly, exacerbating risks that cold-adapted species can "run out of habitat" regionally as climate change proceeds. Rates of change are generally difficult to predict, because both the time lags for each individual species as well as the compound effects of moving multiple species dependent on each other are likely common, but rarely known.

Generally, the boreal forest biome is expected to be least resilient to climate change at its bioclimatic margins. This means that the ecotones with alpine and arctic tundra or with nemoral forest are likely to be the regions experiencing the greatest rate of change initially. The profound vegetation state changes due to the recent spread of insect pest outbreaks across the birch forest–arctic tundra transition zone in eastern Finnmark are consistent with these expectations.

Mature spruce trees are relatively resilient to drought under present climatic conditions in Norway. However, increased mortality has been observed and is expected in the future after extreme events and on some soil types. Mature pine is considered highly resilient to drought under Norwegian conditions, and typically occupies drier sites, although extreme drought years may limit recruitment and establishment. The functionally important dwarf shrubs are vulnerable to a suite of climate change factors, especially reduced snow cover and frost-drought (*q.v.*) during winter. Reduced productivity of palatable dwarf shrubs is expected to have cascading impacts in the food web, because several boreal rodents, grouse and ungulates are dependent on these plants.

In a warmer climate more frequent and extreme drought events, increased fire frequencies and burnt-over areas are expected. Pine and deciduous trees are more resilient to fire than spruce, and it is difficult to predict whether Norwegian forests will be more vulnerable, less vulnerable, or resilient to fire in the future. Spruce is susceptible to windfellings because of its shallow root system and its tendency to form dense patches of trees, while pine has a deeper anchoring and is considered to be relatively resistant. Spruce forests may therefore be more vulnerable and less resilient to an increase in the frequency or strength of weather extremes.

Most conifer forests in Norway are managed for timber production, though the intensity of management is highly variable. Management systems greatly affect how forests react to disturbances. Functional and structural diversity play an important role in forest resilience and in resistance to droughts and pest outbreaks. Dense and homogeneous forests are more vulnerable to storms, snow-load, and pest attacks. Most studies find that forests that are heterogeneous (in terms of age, size, and species composition), relatively open, and only lightly managed are more drought and pest resistant than homogeneous, dense, and heavily managed forests. Management strategies mimicking key natural processes have been proposed, as a way of introducing more heterogeneity to managed forests. However, current uneven-aged management practices result in forest structure that only to a limited degree resemble those of natural forests. Forest management systems that focus in part on preserving or increasing biodiversity promote leaving portions of forests to develop freely. Our report finds that increasing the amount of protected forest has positive consequences for forest health and biodiversity. For example, increasing the amount of timberland removed from harvest eventually increases the resilience of the wood decomposer community to environmental perturbations and thus makes the diverse invertebrate and fungal decomposer communities less vulnerable to climate change.

Thus, management for increased resilience involves balancing multiple strategies. (1) Conservation of species-rich habitats of varying size, both in sheltered localities in the trailing edge where boreal, spruce-dominated forests are weakened and disappearing and in regions with stable presence of boreal climate, to minimize species loss and help species migrate. (2) Maintaining habitat connectivity to allow species migration while at the same time hindering establishment of invasive species as much as possible. (3) Facilitating diversity and range expansion of broadleaf trees that are better suited to emerging climate conditions; broadleaf trees contribute to resistance through creating mixed, diverse stands that are less prone to large-scale disturbances and more capable of maintaining diverse and functioning forest cover, and that start building habitats capable of receiving migrating communities.

1.2.8 Uncertainties and knowledge gaps

A good number of studies have assessed specific impacts of climate warming, both near term and long term, on forest ecology. The studies cover a wide range of organisms, ecological characteristics, and climate factors (Figure S6, S2). There is relatively good coverage of studies that assess abiotic and biotic climate-change factors for trees and forest habitats, and to some extent, try to address climate effects at the ecosystem level. However, the amount of knowledge differs widely between combinations of climate change organism groups. Across organismal groups, we find that the majority of the evidence is related to impacts on abundances, range shifts and the main demographic rates of dominant species (their survival, growth, and recruitment), with much less evidence for effects on biodiversity, biotic interactions, and species and ecosystem functioning (Figure S6). This limits our collective understanding and ability to predict and mitigate threats to forest ecosystem resilience and to manage for reduced forest vulnerability in a changing climate.

There is a lack of knowledge about how climate change, and especially changes in climate extremes, will impact the ecosystem carbon balance. In particular, we lack understanding of how climate change impacts the contributions and interactions between the primary producers (trees) and the soil decomposer and mycorrhizal symbiont communities in controlling the net ecosystem carbon uptake and emissions. For clear practical reasons there is a general lack of knowledge about forest transition and succession on the scales and time frames we are foreseeing. There is also a lack of knowledge about insects, especially considering their diverse roles in Norwegian forest ecosystems, and to what degree and how the ongoing global loss of insect biodiversity and biomass also occurs in Norwegian forests.

There is also a lack of knowledge of animal and plant diseases that do not affect humans or economically important species. Fungal pathogens in plants are much more studied than bacteria (including phytoplasmas), water molds (oomycetes), nematodes, and viruses. The evidence for climate change impacts on the ecological condition of forest collated for this report covered a wide range of organisms, ecological characteristics, and climate change-related factors, however, some systems remain relatively understudied (Figure S2).

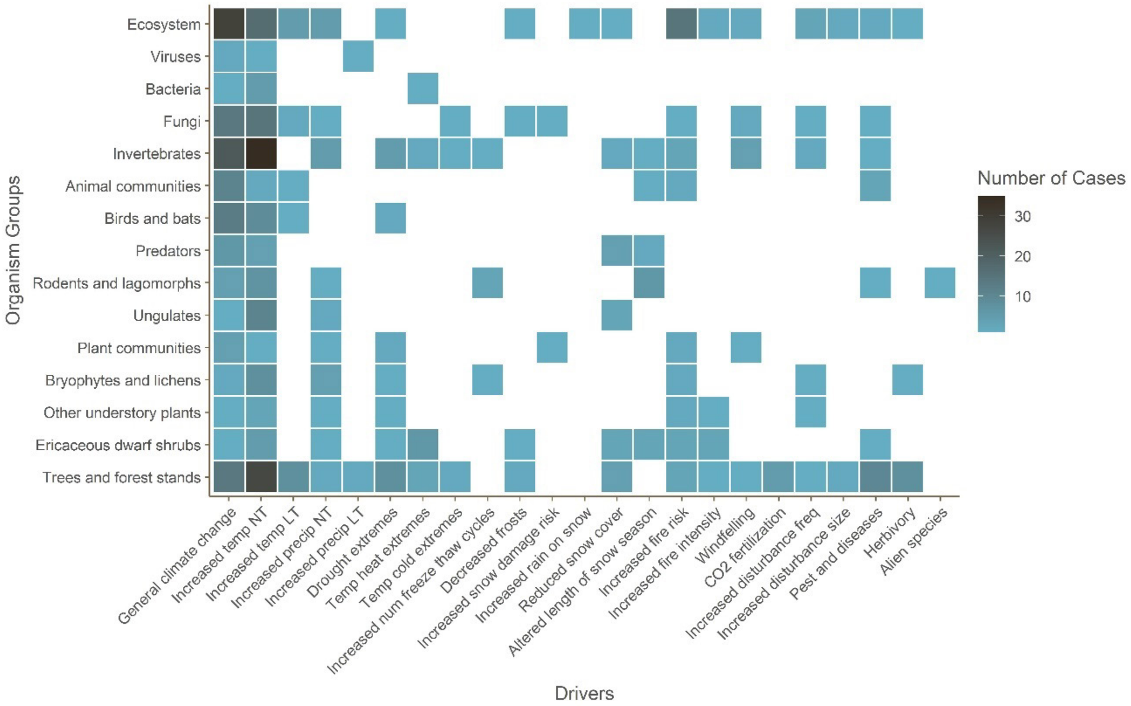


Figure S6. The weight of evidence in this report, given as the number of cases from the literature in which a relationship between a specific climate change related driver and the response of a specific organismal group was recorded. The drivers include climatic changes and climate change-related disturbances and biotic factors, as reported in the literature. Note that each cell may include information on a broad range of response types of the organismal group to the specific driver (such as changes in growth, demographic rates, biodiversity, or functioning), and that the total cases per cell includes both positive, negative, and neutral response of the particular organismal group to the specific driver. A given research paper may include information on one or more driver-response cases. Empty cells (or low number of cases) are indicative of knowledge gaps in the reviewed literature. Temp" = temperature. "precip" = Precipitation, "NT" = Near-term changes (until year 2050). "LT" = long-term changes (until year 2100).

1.2.9 Concluding remarks

In a historical perspective, the speed and magnitude of climate change that is expected for all but the strongest mitigation scenarios (the "best case" scenarios) are without precedent. Prehistoric climate shifts have been followed by forest distribution changes lagging at least several centuries behind the climate change. Range shifts northwards and to higher altitudes are a commonly predicted consequence of climate change. By 2070-2100, being in the warmer half of the "cone of plausible futures" (Figure S1), would mean that most of the boreal forests we know today—in Norway and globally—will be outside of the climate zone where such forests are currently occurring naturally. These future boreal forests will then be living under climates that today are found in more southern climate zones (see Figure S7) where deciduous trees and hardwoods are dominant. While this report finds that range shifts will be a major consequence of climate change, it also stresses that the 78 years remaining until 2100 is less than the time from planting to expected logging (forestry rotation time)– and much less than the natural lifespan–of most Norwegian forest trees. The normal pace of forest succession will not be able to keep up with the rate at which climate regimes change, and Norwegian forests are likely to be increasingly unstable and changing in the coming decades. It is also clear that climate stress affects multiple, interacting ecosystems simultaneously, with likely consequences for vulnerability and for mitigation strategies. New forestry strategies taking the rate and magnitude of change into account are urgently needed to manage forests in this period of rapid ecological transitions.

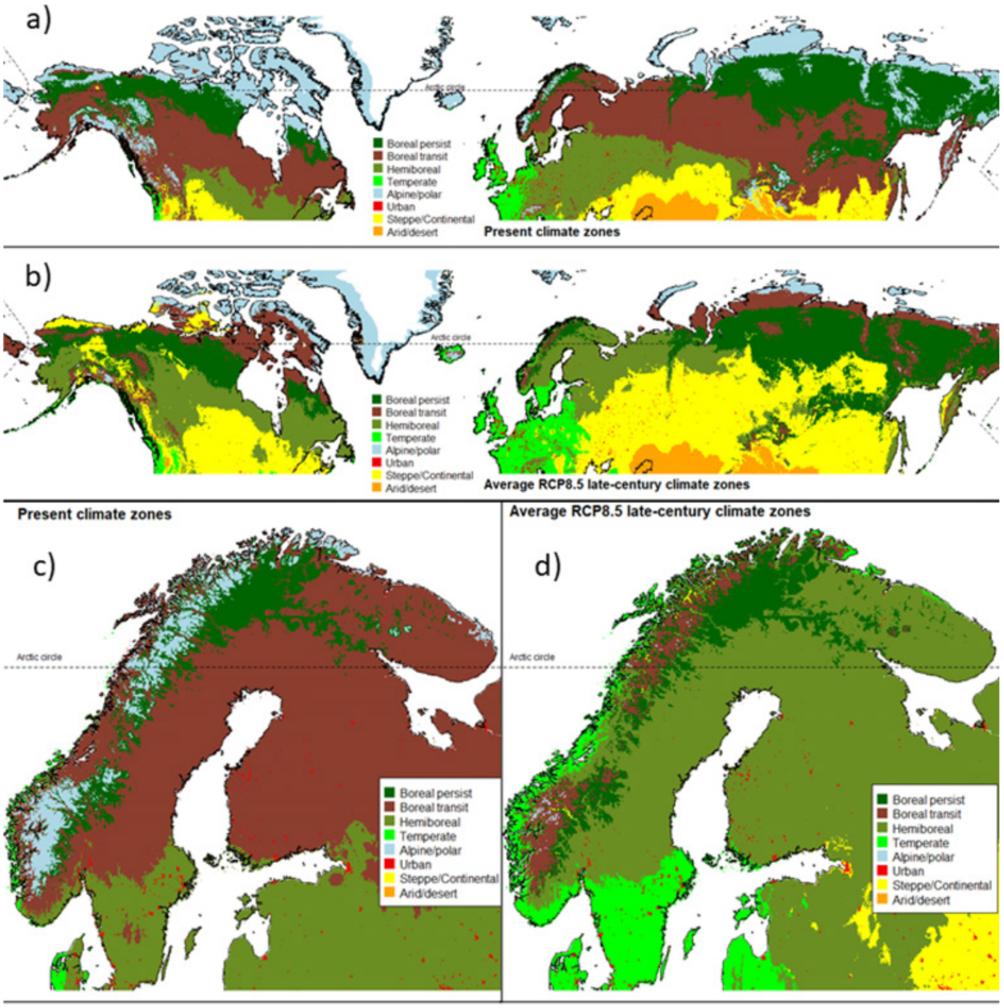


Figure S7. The climate zones associated with major vegetation types today (**a**, **c**) and 2070-2100 (**b**, **d**). The Norwegian forest as we know it today, dominated by spruce, pine and in some places birch, is a product of the boreal zone (dark green and brown). Boreal forests, often called taiga, are currently found in a broad belt across the northern hemisphere (**a**, **b**), including Fennoscandia (**c**, **d**), mostly bordering tundra to the north and hemiboreal, temperate, or steppe zones to the south. Towards the end of the century (**b**, **d**), under a future climate around the mean estimate for the RCP8.5 (see Figure S1), most of the current boreal belt will be outside the climate zone that shaped the biome. Only the areas marked dark green are persistently boreal both in the present and 2071-2100. The part of the boreal zone marked brown in the early period (**a**, **c**) will have transitioned into a hemiboreal climate by the end of the century (**b**, **d**). Similarly, the boreal areas marked brown in the latter period (**b**, **d**) will have transitioned from the arctic or alpine climates that they are in in the present. Note, though, that a change in climate zone does not mean that the vegetation types will have had time to change correspondingly. Based on data from Beck et al. (2018) (see 3.2.3).

1.3 Norsk sammendrag

Bakgrunn

Boreal skog er en viktig naturtype i Norge, som dekker 37% av det norske landarealet. Disse skogene er en del av det boreale barskogbeltet som strekker seg fra Fennoskandia gjennom Sibir, Alaska og Canada og utgjør ca. ⅓ av verdens skogareal. Disse skogene er formet av det klimaet de vokser i, og utsettes i dag for raske klimaendringer.

Miljødirektoratet har derfor bedt Vitenskapskomiteen for mat og miljø (VKM) om å vurdere og sammenfatte tilgjengelig kunnskap om hvordan klimaendringer vil påvirke økologisk tilstand i norsk skog, og hvilke faktorer som gjør skogøkosystemene mer sårbare eller resistente mot klimaendringer. Denne vurderingen er blitt gjort på grunnlag av en omfattende gjennomgang av vitenskapelige studier som dekker de fleste aspekter ved skogøkosystemets struktur (bl.a. biologisk mangfold) og funksjon (f.eks. primærproduksjon og karbonlagring).

Resultater

Rapporten fokuserer på effekter av klimaendringer, og ikke av andre menneskelige påvirkninger, som skogbruk. Vi ser på fremtidsscenarioer som ligger mellom moderat optimistisk og moderat pessimistisk når det gjelder hvor sterke klimaendringene blir frem mot år 2100, som er endepunktet for de fleste klimamodellene. I et skogperspektiv er år 2100 ikke langt unna, ettersom 80 år er betydelig kortere enn de boreale treslagenes naturlige levealder, og i nærheten av skogbrukets omløpstid fra planting til hogst. Det betyr at klimaendringer i denne perioden vil møtes av allerede etablert skog, og at treslagene har begrensede muligheter til å tilpasse seg nye klimaforhold gjennom å spre seg i samme takt som klimaet endrer seg. Siden trærne bestemmer habitat for mange andre skogsarter, påvirker trærnes spredningsevne og tilpasning i stor grad skogens struktur og funksjon.

Basert på den kunnskapen vi har i dag, finner VKM at norske skoger vil bli moderat til sterkt påvirket av klimaendringer frem mot utgangen av århundret, avhengig av i hvilken grad klimagassutslippene fortsetter å øke, stabiliseres, eller reduseres over de neste tiårene. En god del treslag forventes å nyte godt av økte temperaturer og lengre vekstsesong, særlig i nordlige og alpine deler av utbredelsesområdene. Gitt nok tid vil boreale treslag derfor kunne forventes å spre seg inn i dagens arktiske og alpine soner.

Klimaendringene innebærer imidlertid også økt risiko for ekstremvær (tørke, snøfall, brann og storm), noe som skulle tilsi økt dødelighet blant flere av de dominerende treslagene. Dette vil igjen kunne medføre redusert produktivitet, tap av biologisk mangfold, og generelt økt sårbarhet. Mildere og våtere vintre gir lengre vekstsesong, men også bedre overlevelse for mange insekter og patogener som tidligere har vært begrenset av vinteroverlevelse. Dette vil føre til økt risiko og nedsatt motstandskraft mot klimaendringer og ekstremvær hos de viktige boreale treslagene, både på kort og lengre sikt. Det forventes også at en rekke funksjonelt viktige dyre- og plantearter, som er tilpasset et borealt klima med lange og stabilt kalde vintere, går tilbake. Dette gjelder i varierende grad andre treslag, og til dels alle andre organismer, fra fugl og pattedyr til sopp og mikrober.

Gran er spesielt sårbar for klimapåvirkninger, særlig for tørke, hetebølger, skogbrann, og stormfelling. Gran er også utsatt for en rekke insekter og soppsykdommer som forventes å øke i omfang. Vi må derfor regne med økende skader på norsk granskog i sørlige og lavereliggende strøk, slik man allerede har sett på det europeiske kontinentet, i Sibir og i Nord-Amerika.

På lang sikt forventes høyere temperatur, høyere årsnedbør og høyere CO_2 -innhold i atmosfæren å kunne gi økt primærproduksjon og biologisk mangfold ettersom dagens vekstsoner for en rekke europeiske treslag og skogøkosystemer tilsier at disse skulle kunne vokse i Norge i framtida. Flere sørlige arter er på vei nordover og inn i Norge, mens andre arter trekker høyere opp mot fjellet. Når klimaendringer skjer raskt, vil mange arter miste deler av sitt opprinnelige utbredelsesområde raskere enn nye områder koloniseres. Arealbruk og landskapsstruktur påvirker artenes mulighet til å møte klimaendringene. Når artene må spre seg hurtig gjennom fragmentert terreng for å følge sine klimasoner, må man forvente tap av biologisk mangfold, og forringelse av økologisk tilstand og økosystemfunksjoner. Dette vil redusere mulighetene til å opprettholde robuste og produktive skoger på det nåværende skogarealet i Norge. Det er også sannsynlig at skogøkosystemets evne til å lagre karbon svekkes ettersom nedbrytingen av de store mengdene med organisk materiale som finnes i det boreale jordsmonnet vil gå raskere i et varmere klima.

Et sentralt tema for skogforvaltningen vil bli å legge til rette for å redusere skogens sårbarhet og øke motstandskraften mot klimaendringer. Mangfold på alle trofiske nivåer, inkludert struktur og funksjon, og sammenhengende funksjonsarealer for arter og naturtyper, er viktige faktorer for å redusere sårbarhet og understøtte skogens motstandskraft.

Konklusjon

Frem mot 2030 - 2050 vil positive og negative effekter av klimaendringene på skogøkosystemet sannsynligvis oppveie hverandre. Følgelig vil ikke klimaendringene føre til vesentlig endring av norske skoger og deres økologiske tilstand og funksjoner i denne perioden. Fra 2050–2100 forventes de negative effektene, og særlig effekter av ekstremvær og skadegjørere, å bli mer fremtredende, med økt risiko for skogdød, tap av biologisk mangfold og nedsatt økologisk tilstand. Pionérvekster forventes å spre seg raskere enn arter med saktere vekst og etablering. Arter som er avhengige av gammel skog vil ha spesielt store problemer når leveområdene deres ødelegges og forringes. Siden det tar tid for klimasystemet å komme i likevekt, må det selv med rask begrensning av klimagassutslipp forventes at en god del av norske skoger kommer utenfor sine klimatiske tålegrenser mot midten og slutten av århundret, med potensielt store konsekvenser for skogens økologiske tilstand.

1.4 Glossary and terminology

Term	Definition	Norwegian
Abiotic	The non-living chemical and physical components of the environment.	Abiotisk
Abundance	The number of discrete units of an organism within a site: for non-clonal organisms, the number of individuals of a given taxon; for clonal organisms, the number of clonal fragments (ramets).	Abundans, antall individer, forekomst
Albedo	The ability of a surface to reflect sunlight as light rather than heat. Light-coloured surfaces return a large part of the sun rays back to the atmosphere (high albedo) and thus contribute less to warming than dark surfaces that absorb the rays from the sun (low albedo) and radiate heat.	Albedo
Anthropogenic	Caused by human activity.	Antropogen, menneskeskapt
Average	Throughout the report, unless otherwise stated, averages are provided with the relevant range of confidence in brackets (e.g., 25 [15,30])	Gjennomsnitt, intervalll

Biodiversity	Measures of the number of different species, or genotypes within a species, or the abundances of species or genotypes *within* a spatial unit (*alpha diversity*) or *across* spatial units (*beta diversity*). Also includes diversity of habitats, nature types and ecosystems.	Biodiversitet, biologisk mangfold, naturmangfold
Biome	A large naturally occurring community of flora, fauna and fungi occupying a major habitat, such as boreal forest or tundra.	Biom
Biotic	Associated with, or derived from, living organisms.	Biotisk
Boreal	The boreal climate zone is defined by cold winters with some snow cover, a short summer, and low to moderate annual precipitation. The boreal forest is the dominant land cover type. The term "subarctic" is sometimes used interchangeably, but here we use "boreal" consistently. See section 2.1.1 for details.	Boreal
Boreonemoral	The ecotone, or transition zone, between the boreal forests dominated by conifers and the nemoral, also called temperate, forest zones dominated by broadleaved deciduous trees.	Boreonemoral
Cascade effects	In ecology cascade effects are secondary (indirect) effects triggered by changes in the abundance or behavior of one key species. Trophic cascades occur when such change at one trophic level (*q.v.*) leads to changes in other trophic levels. Trophic cascades can be top-down, such as when removal of predators releases herbivore populations to the extent that the abundance of their food plant becomes reduced, bottom-up when altered primary production affects all higher trophic levels, or subsidiary when triggered by supplements (subsidies) from outside the system.	Kaskadeeffekter
Climate debt, climatic debt	The degree to which a plant or animal community is not yet adapted to recent changes in climate; hence, the extent to which biodiversity changes lag behind current climate change. The inertia of long-lived organisms such as trees persisting despite increasingly unfavorable climate makes forest ecosystems prone to climate debt.	Ingen etablert terminologi

Climate forcing	The physical process of affecting the climate through some mechanism. Examples include: variations in solar radiation, volcanic eruptions, changing albedo, and changing levels of greenhouse gasses in the atmosphere. Forcing effects are usually given as the increase in heat energy per square meter, or, more loosely, as a certain net contribution to rise in global mean temperature.	Klimapådriv, klimapådrag
Downscaling	The procedures for using large-scale climate models to make predictions at finer temporal and spatial scales, thus being able to consider local variables like elevation, exposure, land cover etc. to make more fine-grained predictions and analyses.	Nedskalering
Drought	Droughts are defined as a prolonged deficit of water over a larger area, and may have implications for agriculture, forestry, irrigation needs, and intensity and frequency of forest fires.	Tørke
Ecosystem	An area with all organisms, and the processes that regulate biotic relations among organisms, as well as between organisms and the abiotic environment (whether natural or shaped by human activities)	Økosystem
Ectotherm	An organism that can only regulate body temperature behaviourally, not physiologically. Body temperature usually follows immediate surroundings, and can be regulated by moving to warmer or colder places.	Vekselvarm (tidl. kaldblodig)
Environmental gradient	Continuous variable that expresses gradual variation in an observable environmental characteristic	Miljøgradient
Explanatory variable	A variable which, when used as a predictor in a statistical model, accounts for some of the variation in the model's response variable	Forklaringsvariabel
Forest	Forests are defined as wooded areas on solid land where more than 10% of the ground tends to be covered by the tree canopy. Clear-cuts are included in the forest land cover type if replanted or naturally regenerated without significant delay. See section 3.1.2 for more on forestcategories as defined in this report.	Skog (NiN: Fastmarks-skogsmark og Flomskogsmark)

Frost-drought	Also known as frost dessication. Low or freezing temperatures during winter can cause plants to dry out, if water lost by transpiration is inadequately replaced by uptake of water.	vintertørke
Functional group	A functional group is a set of ecologically similar species which interact similarly with the environment–they have similar ecological niches and perform similar functions in the ecosystem. Examples inlude "trees", "pollinators", and "pathogens" (see section 3.3.2 for a fuller list of examples).	Funksjonell gruppe
Land-cover type	Dominant vegetation, material or biome covering the Earth's surface. Different classification schemes use different classes and spatial scales.	Naturtype, arealdekke
Life history	Refers to the timing of events related to reproduction and survival. Life history traits include among others body size, age at first reproduction, fecundity, whether an organism reproduces once or many times, and how and when an organism invests in maintenance and survival.	Livshistorie
Natural	For the purpose of brevity, the term "natural" is sometimes used as shorthand to describe a forest or biome that has been relatively unaffected by human activities. While humans are clearly part of nature, this usage seems to be readily understood and improves readability.	Naturlig; i skogskontekst, naturskog
Nature in Norway (NiN)	Classification system for the ecological variation found in Norway. First version published by the Norwegian Biodiversity Information Centre (*Artsdatabanken*) in 2009, and later revised according to increasing knowledge and user needs in cooperation with other scientific institutions with expertise in this field. "Forest" in this report follows NiN nomenclature and is defined as nature types T4 Forest (*Fastmarksskogsmark*) and T30 Riparian forest (*Flomskogsmark*) in the NiN system.	Natur i Norge (NiN)
Nemoral	The temperate zone biome of deciduous trees.	Nemoral

Old growth forest, mature production forest, primeval forest	Old growth forest in a Norwegian context is defined as forest >160 years old. This is not to be confused with primeval forest (old forest largely unaffected by human activity) or mature, sometimes called old, production forest in Stand class V (see below), but shades into the latter when used about "biologically old forest". Old growth forests are late-successional communities that often have quite different ecological features and support unique biodiversity compared to earlier successional stages and intensively managed forest.	Gammelskog vs. hogstmoden skog og urskog
Phenological match or mismatch	The degree to which the timing of key events in the life of an organism is optimal in its current environment. Flowering that is not syncronized with pollinator availability is an example of phenological mismatch.	Fenologisk tilpasning/ mistilpasning
Phenology	Refers to the timing of key events in the life of an organism, usually with respect to season, such as the timing of when plants grow, leaf out, flower, fruit, or go dormant, or the timing of when animals are active, disperse, become mature sexually, mate, or go dormant. Such events may be triggered by cues such as temperature, rainfall, day length, night length, or in some cases by specific combinations of these. Typically, organisms uses an external cue such as day (or night) length or temperature to initiate such life history events such as flowering or hibernation.	Fenologi
q.v.	*Quod vide,* "which see", used for internal cross-referencing in a text—in this report, to indicate that a term can be looked up in the Glossary.	*q.v.*
RCP, SSP	These are the acronyms used by the Intergovernmental Panel on Climate Change (IPCC) to denote different trajectories of atmospheric greenhouse gas concentrations for future scenario climate projection in the IPCC framework. Representative Concentration Pathways (RCP) have been used since the Fifth Assessment Report (AR5) in 2014, while Shared Socioeconomic Pathways (SSP) were introduced in 2021 with AR6. Since most	RCP, SSP

	studies are still only available in the RCP framework we mostly refer to that in this report.	
Resilience	In this report, the ability of an ecosystem to return to its original or desired state following disturbance. When quantified, resilience is the speed at which the system returns to the initial state.	Resiliens/ elastisitet
Riparian forest	Riparian forest includes periodically flooded, non-wetland forest (see below for definition of forest) on banks of rivers and lakes, impacted by water-mediated disturbance.	Flomskogmark
Robustness, resistance	The capacity of a system to maintain a desired state despite fluctuations in its component parts or its environment.	Robusthet, resistens
Saprotrophic	Saprotrophic organisms feed on nonliving organic matter, known as detritus: fungi that decompose fallen leaves and twigs (leaf litter) are saprotrophic.	Nedbryter
Saproxylic	Organisms that for part or all of its life cycle are dependent upon dead or dying wood, upon wood-inhabiting fungi, or upon the presence of other saproxylic organisms. Related terms include saprophytes (plants, fungi or microorganisms growing on dead matter) and saprotrophs (organisms eating dead matter).	Saprofyttisk
Site index	A widely used measure of forest site productivity and quality, as it can be estimated from direct measurements of height and age of dominant trees at certain ages. Used as a key predictor of volume growth and yield.	Bonitet
Stand class/ cutting class	Forestry classification system: Class I: Bare ground to be replanted or rejuvenated Class II: Young forest of adequate density Class III: Young productive forest with some useable trees Class IV: Mature productive forest with high growth Class V: Older productive forest with slower growth	Hogstklasse
Snow water equivalent	Hydrological indicator of the amount of liquid water contained within the snowpack.	Snøens vannekvivalent

Trees	Formally, trees are woody plants capable of growing more than 5 m tall under favorable conditions, and more than 2 m under growth-reducing conditions.	Trær
Trophic level	The trophic level of an organism is the role it plays in a food web. Trophic levels include primary producers, herbivores, pollinators, omnivores, insectivores, carnivores, mutualists, and decomposers.	Trofiske nivåer
Trophic structure	How biomass is distributed among the trophic levels of a food web.	Trofisk struktur
Voltinism	The time that is required to complete a life cycle before conditions become unfavorable for reproduction often locks organisms with short life cycles into an integer number of generations per year. A univoltine population has one generation per year, while multivoltine populations can complete multiple generations in a single year and a semivoltine population can only complete part of a generation in the first year of life.	Voltinisme
Vulnerability	The state of susceptibility to harm from exposure to stresses associated with environmental (including human-caused) change and from the absence of capacity to adapt.	Sårbarhet

Confidence terms used in the knowledge syntheses in Chapter 5		
Established	High quantity and quality of evidence, high level of agreement. Confidence term for knowledge synthesis,	Etablert
Established but incomplete	Low quantity and quality of evidence, high level of agreement. Confidence term for knowledge synthesis,	Etablert men ufullstendig
Unresolved	High quantity and quality of evidence, low level of agreement. Confidence term for knowledge synthesis,	Uavklart
Inconclusive	Low quantity and quality of evidence, low level of agreement. Confidence term for knowledge synthesis,	Ufyllestgjørende

1.5 Key species mentioned in text, by organism group.

Organism group	English	Scientific	Norwegian
ANIMALS			
spider	[Ground spider, no Eng. name]	*Zelotes puritanus Chamberlin*	Amerikasvartedderkopp
Tick (pest)	Sheep tick	*Ixodes ricinus*	Skogflåtten
Insect	[Paper wasp, no Eng. name]	*Polistes biglumis*	Mørk papirveps
Insect (non-native, potential pest)	Bronze birch borer	*Agrilus anxius* (Gory)	Amerikansk bjørkepraktbille
Insect (non-native, potential pest)	Two-lined chestnut borer	*Agrilus bilineatus* (Weber)	[uten offisielt norsk navn]
Insect (non-native, potential pest)	Emerald ash borer	*Agrilus planipennis* (Fairmaire)	Asiatisk askepraktbille
Insect (non-native, potential pest)	Common Willow Agrilus	*Agrilus politus* (Say)	[uten offisielt norsk navn]
Insect (non-native, potential pest)	Asian longhorned beetle	*Anoplophora glabripennis* (Motschulsky)	Asiatisk løvtrebukk
Insect (non-native, potential pest)	Mountain pine beetle	*Dendroctonus ponderosae* Hopkins	[Barkbille uten offisielt norsk navn]

Insect (non-native, potential pest)	Spruce beetle	*Dendroctonus rufipennis* Kirby	[Barkbille uten offisielt norsk navn]
Insect (pest)	The pine weevil	*Hylobius abietis* (Linnaeus)	Gransnutebillen
Insect (pest)	European spruce bark beetle	*Ips typographus* L.	Stor granbarkbille
Insect (potential pest)	Scarce umber	*Agriopis aurantiaria* (Hübner)	Gul frostmåler
Insect (potential pest)	Pine looper	*Bupalus piniaria* (L.)	Furumåler
Insect (potential pest)	[Flea beetle, no Eng. name]	*Crepidodera lamina*	[Bladbille uten norsk navn]
Insect (potential pest)	Pine lappet	*Dendrolimus pini* (L.)	Furuspinner
Insect (potential pest)	Conifer sawfly	*Diprion pini* (L)	Vanlig furubarveps
Insect (potential pest)	Autumnal moth	*Epirrita autumnata* (Borkhausen)	Fjellbjørkemåler
Insect (potential pest)	Eight-toothed spruce bark beetle	*Ips acuminatus* Wood & Bright	Skarptannete barkbille
Insect (potential pest)	European pine sawfly	*Neodiprion sertifer* (Geoffroy*)*	Rød furubarveps
Insect (potential pest)	Winter moth	*Operophtera brumata* (Linnaeus)	Brun høstmåler
Insect (potential pest)	Pine beauty	*Panolis flammea* (Denis & Schiffermüller)	Furufly

Insect (potential pest)	Elm bark beetle	*Scolytus laevis* Chapuis	Almesplintborer
Bird	Little bunting	*Emberiza pusilla*	Dvergspurv
Bird	Eurasian pygmy owl	*Glaucidium passerinum*	Spurveugle
Bird	Willow ptarmigan	*Lagopus lagopus* (Linnaeus)	Lirype
Bird	Two-barred crossbill	*Loxia leucoptera*	Båndkorsnebb
Bird	Parrot crossbill	*Loxia pytyopsittacus*	Furukorsnebb
Bird	Red-throated bluethroat	*Luscinia svecica*	Blåstrupe
Bird	Black grouse	*Lyrurus tetrix* (L.)	Orrfugl
Bird	Coal tit	*Periparus ater*	Svartmeis
Bird	*Siberian jay*	*Perisoreus infaustus*	Lavskrike
Bird	Common redstart	*Phoenicurus phoenicurus*	Rødstjert
Bird	Three-toed woodpecker	*Picoides tridactylus*	Tretåspett
Bird	Pine grosbeak	*Pinicola enucleator*	Konglebit
Bird	Siberian tit	*Poecile cinctus*	Lappmeis
Bird	Willow tit	*Poecile montanus*	Granmeis
Bird	Goldcrest	*Regulus regulus*	Fuglekonge
Bird	Great grey owl	*Strix nebulosa* J. R. Forster	Lappugle

Bird	Northern hawk owl	*Surnia ulula* (Linnaeus)	Haukugle
Bird	Eurasian capercaillie	*Tetrao urogallus* Linnaeus	Storfugl
Bird	Common cuckoo	*Cuculus canorus* L.	Gjøk
Bird	Pied flycatcher	*Ficedula hypoleuca* (Pallas)	Svarthvit fluesnapper
Mammal	Eurasian moose	*Alces alces* (L.)	Elg
Mammal	Gray wolf	*Canis lupus* L.	Ulv
Mammal	European roe deer	*Capreolus capreolus* (L.)	Rådyr
Mammal	Eurasian beaver	*Castor fiber* L.	Bever
Mammal	Red deer	*Cervus elaphus* L.	Hjort
Mammal	Wolverine	*Gulo gulo* (Linnaeus)	Jerv
Mammal	Norway lemming	*Lemmus lemmus*	Lemen
Mammal	Brown hare	*Lepus europaeus*	Sørhare
Mammal	Mountain hare	*Lepus timidus*	Hare
Mammal	Eurasian lynx	*Lynx lynx* (Linnaeus)	Gaupe
Mammal	European pine marten	*Martes martes*	Mår
Mammal	Stoat	*Mustela erminea*	Røyskatt
Mammal	Least weasel	*Mustela nivalis*	Snømus
Mammal	Bank vole	*Myodes glareolus* (Schreber)	Klatremus

Mammal	Grey red-backed vole	*Myodes rufocanus* (Sundevall)	Gråsidemus
Mammal	Wood lemming	*Myopus schisticolor* (Lilljeborg)	Skoglemen
Mammal	White-tailed deer	*Odocoileus virginianus* (Zimmermann)	Hvithalehjort
Mammal	Eurasian wild boar	*Sus scrofa Linnaeus*	Villsvin
Mammal	Brown bear	*Ursus arctos*	Brunbjørn
Mammal	Red fox	*Vulpes vulpes* (Linnaeus)	Rødrev
FUNGI			
Wood-decomposer fungus	Red-banded polypore	*Fomitopsis pinicola* (Sw.) P.Karst.	Rødrandkjuke
Wood-decomposer fungus	[Polypore fungus, no Engl. name]	*Fomitopsis rosea* (Alb. & Schwein. : Fr.) P. Karst.	Rosenkjuke
LICHENS			
Lichen	Tube Lichen	*Hypogymnia physodes* (L.) Nyl.	Vanlig kvistlav
Lichen	[Lichen, no Engl. name]	*Melanelia olivacea*	Snømållav
Lichen	[Lichen, no Engl. name]	*Peltigera retifoveata*	Huldrenever
PLANTS			
Plant, moss	Mountain fern moss	*Hylocomium splendens* W. P. Schimper	Etasjemose

Plant, moss	Red-stemmed feathermoss	*Pleurozium schreberi* Mitten	Furumose
Plant, moss	Lanky moss	*Rhytidiadelphus loreus* Warnstorf	Kystkransmose
Plant, moss	[Moss, no Engl. name]	*Tayloria acuminata* Hornsch.	Spisstrompetmose
Plant, shrub	Arctic bell-heath*er*	*Cassiope tetragona*	Kantlyng
Plant, shrub	Mountain avens	*Dryas octopetala*	Reinrose
Plant, shrub	Black crowberry	*Empetrum nigrum*	Krekling
Plant, shrub	Dwarf juniper	*Juniperus communis* L.	Einer
Plant, shrub	Lapland rosebay	*Rhododendron lapponicum*	Lapprose
Plant, shrub	Bilberry	*Vaccinium myrtillus* L.	Blåbær
Plant, shrub	Lingonberry	*Vaccinium vitis*	Tyttebær
Plant, tree	Gray alder	*Alnus incana* (L.) Moench	Gråor
Plant, tree	European white birch	*Betula pendula* Roth	Hengebjørk
Plant, tree	Downy birch	*Betula pubescens* Ehrh.	Bjørk
Plant, tree	European beech	*Fagus sylvatica* L.	Bøk
Plant, tree	European ash	*Fraxinus excelsior* L.	Ask
Plant, tree	Norway spruce	*Picea abies* (L.) Karst	Gran
Plant, tree	Scots pine	*Pinus sylvestris* L.	Furu

Plant, tree	European aspen	*Populus tremula* L.	Osp
Plant, tree	English oak	*Quercus robur L.*	Sommereik
Plant, tree	White willow	*Salix alba L.*	Hvitpil
Plant, tree	Goat willow	*Salix caprea L.*	Selje
Plant, tree	Rowan	*Sorbus aucuparia* L.	Rogn
Plant, tree	Wych elm	*Ulmus glabra* Huds.	Alm
Plant, tree (non-native)	Siberian larch	*Larix sibirica* Ledeb.	Sibirlerk
Plant, tree (non-native)	Quaking aspen	*Populus tremuloides*	*Amerikaosp*
Plant, tree (non-native)	Silver fir	*Abies alba*	Vanlig edelgran
DISEASES			
Pathogen, bacterium	Anthrax	*Bacillus anthracis*	Miltbrann/ anthrax
Pathogen, bacterium	Tularemia	*Francisella tularensis*	harepest
Pathogen, bacterium	Potato blackleg	*Pectobacterium atrosepticum*	Stengel- og bløtråte
Pathogen, fungus	Scleroderris canker	*Gremmeniella abietina*	Granas topptørke
Pathogen, fungus	Root Rot	*Heterobasidion annosum* (Fr.) Bref.	Fururotkjuke

Pathogen, fungus	Heterobasidion root rot	*Heterobasidion parviporum* Niemelä & Korhonen	Granrotkjuke
Pathogen, fungus	Ash dieback	*Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, Hosoya, comb. n*ov.*	Askeskuddbeger
Pathogen, fungus	Needle cast	*Lophodermium seditiosum* Minter, Staley & Millar	
Pathogen, fungus	Dothistroma blight	*Mycosphaerella pini* Rostr.	Rødbandsjuke
Pathogen, fungus	Dutch elm disease	*Ophiostoma ulmi* (Buisman) Nannf.	
Pathogen, fungus	Pine pitch canker disease	*Fusarium circinatum*	[Uten norsk navn]
Pathogen, nematode	Pine Wilt Nematode	*Bursaphelenchus xylophilus Steiner & Buhrer*	Furuvednematode
Pathogen, single-celled parasite	Avian malaria	*Plasmodium relictum*	Malaria
Pathogen, water mould	Phytophthora disease of alder	*Phytophthora alni* Brasier & S. A. Kirk	Phytophthora-råte
Pathogen, water mould	Root and crown rot	*Phytophthora cinnamomi* Rands	Rotråte

1.6 Frequently used acronyms

Acronym	Definition
BP	Before Present (by convention years before 1950, in historical context)
GCM	Global Climate Model
IPCC	Intergovernmental Panel on Climate Change
NFI	National Forest Inventory (Nor. Landsskogtakseringen)
NIBIO	Norwegian Institute of Bioeconomy Research
NiN	Nature in Norway classification system for ecological variation
RCM	Regional Climate Model
RCP	Representative Concentration Pathway
SSP	Shared Socio-economic Pathway

1.7 Background as provided by the Norwegian Environment Agency

Climate change will affect biodiversity and ecosystem functions and services in the forest. On behalf of the Norwegian Environment Agency, NINA prepared a report in 2015 that compiled knowledge about the effects of climate change on Norwegian nature, from species level to habitat types and ecosystems (Forsgren et al. 2015). In this report, the forest was one of many ecosystems treated.

In 2017, a report was made on a system for assessing ecological condition, which discusses seven properties that describe ecological status in an ecosystem (Nybø et al. 2017). These properties include structural and functional aspects of ecosystems. The system for assessing ecological conditions will provide a basis for setting management goals across various societal interests and will be an important basis for nature management (incl. forests) in the future.

There is a need for an update of the knowledge base on the impacts of climate change on the main forest ecosystems for Norwegian conditions, linked to the properties discussed in

Nybø et al. (2017) and about the international development of both the knowledge base and framework for ecological status.

The knowledge base about which factors can contribute to ecosystems being resilient and robust in the face of climate change is developing rapidly. This is essential knowledge for nature management, and there is a need for an updated compilation of this knowledge base for forests. There is also a need for an overall assessment of the forest ecosystems' vulnerability to climate change and the impacts of climate change on forests in Norway.

Forests produce several natural goods and ecosystem services, and there have been formulated many objectives within a wide range of policy areas, as a basis for policies that govern the use and protection of forests. This assignment focuses on biodiversity and on the ecological condition of forests–and how climate change will affect opportunities to achieve two of the national biodiversity targets: 1) that the ecosystems should be in good condition (national biodiversity target 1.1) and 2) that no species and habitats should be eradicated and the development of endangered and near endangered species should be improved (national biodiversity target 1.2).

The purpose of the knowledge acquisition is also to shed light on how climate change will affect ecosystem services from forests and to provide knowledge that can help formulate new strategies for adapting to climate change.

1.8 The Terms of reference provided by the Norwegian Environment Agency

The assignment is to provide an overview of knowledge status about how the forest in Norway will develop in a changing climate. Forests in this context are defined as wooded areas on solid land. This includes the nature types T4 Fastmarksskogsmark and T30 Flomskogsmark in NiN (Nature types in Norway). Nybø et al. (2017) discuss seven properties that describe the ecological condition of an ecosystem. VKM should make an assessment on how climate change will affect these 7 properties in Norwegian forest ecosystems. If there is a need to delimit the assignment, one should focus on 4 of the properties:

- No. 3: Functional groups–functional composition within trophic levels
- No. 4: Functionally important species, habitat-building species and biophysical structures (in the assignment, biophysical structures can be downgraded)
- No. 5: Landscape ecological patterns
- No. 6: Biological diversity–represented by the genetic diversity of ecosystems, species composition, and species exchange.

A review should be made of how climate factors (e.g. temperature, precipitation, wind, extreme weather) and other influencing factors that may be related to climate change (e.g. pests and diseases, establishment/increased spread of harmful alien species) are directly and indirectly expected to affect these properties in Norwegian forest ecosystems.

If there is available knowledge of differences in the effects for different tree species, stand ages, or geographical regions, these differences should be clarified.

To the extent possible, an overall discussion should also be made of what kind of significance the expected effects may have for endangered and near endangered habitat types or habitat types with central ecosystem functions in forests, based on the list in attachment 1. Attachment 1 provides an overview of nature types in forests in accordance with the mapping instructions by the Norwegian Environment Agency, but VKM is asked to assess at what level of categorization the assessments can be made (within the NiN system).

The assessment should be based on climate projections from the Norwegian Centre for Climate Services based on emission scenarios from the IPCC, and results should be related to these. If there is available knowledge of threshold values for when climate change can or will trigger changes in biological diversity or the other properties, these should be presented.

Furthermore, the VKM should make a summary of factors that can contribute to resilience to climate change, linked to the same seven properties from Nybø et al. (2017). An overall assessment should also be made of the vulnerability to climate change in Norwegian forest ecosystems with regard to achieving the national biodiversity targets 1.1 and 1.2. We request that a review be made of knowledge deficiencies, with an assessment of which knowledge gaps should be given the highest priority in the years to come.

2 Background

Overview: Here we present background on the ecology and development of boreal forests in general (2.1) and Norwegian forests in particular (2.2), followed by an introduction to global climate change and its manifestation in the boreal zone (2.3). We end the chapter by presenting the main conclusion from a selection of previous assessments of the impact of climate change on Norwegian forests (2.4).

2.1 The boreal forest – a circumpolar biome under pressure

2.1.1 Delineation of the biome

The boreal forest (*q.v.*; also referred to as the taiga) is the world's largest vegetation zone (Figure 1). This biome (*q.v.*) covers around 18.9 million km^2 across northern Eurasia and North America with conifer-dominated forests. Boreal forests make up about one third of the global forest area and more than 10% of the world's total land surface (Gauthier et al. 2015) (Figure 1).

The boreal (also called subarctic) climate zone is currently found roughly between 45°N and 70°N, between the July 13 °C and July 18 °C isotherms (Brandt et al. 2013, Stocks et al. 2001). Summers last no more than three months, at least one month has a 24-hour average temperature of at least 10 °C, and below-zero temperatures may occur for six to eight months of the year, with at least one month averaging below freezing. Being in high latitudes, the boreal climate zone is also subject to a strong annual cycle in day length.

Most boreal forests are dominated by continental climate types, meaning they have large seasonal temperature variations and modest precipitation, most of which falls during summer. The majority of the area has, or has had until recently, an active layer of permafrost of varying depth and dynamics (Körner 2012, Brandt et al. 2013, Price et al. 2013, Helbig et al. 2016). The Norwegian boreal forests are somewhat atypical, as the proximity to warm currents of the Atlantic Ocean gives relatively mild winters and little to no permafrost (Christiansen et al. 2010). This makes them to some extent suitable for agriculture. Similar conditions are found on the southern taiga border and the Pacific coasts.

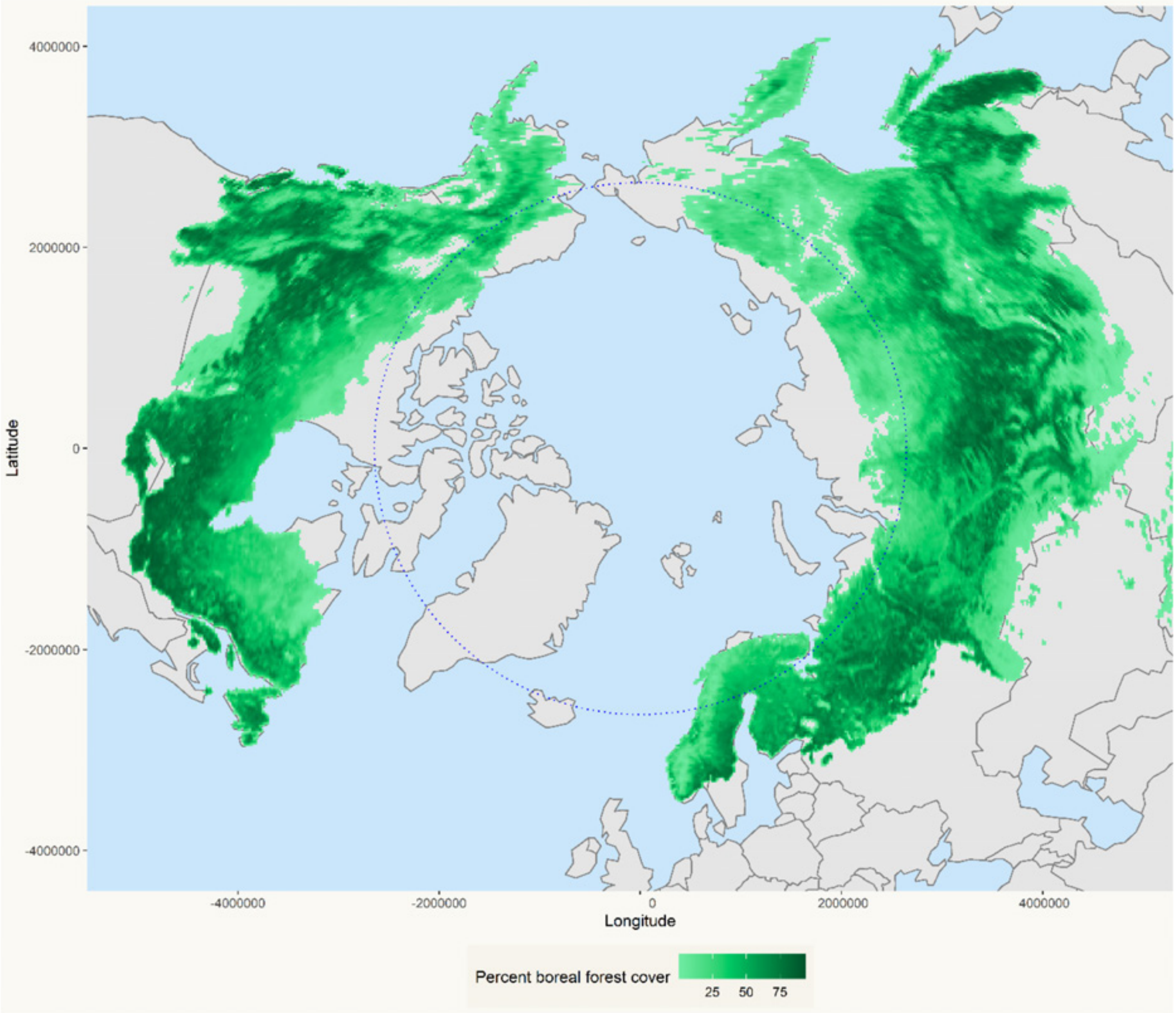


Figure 1. Crown cover (%) in the boreal forest biome in the year 2000. Map based on data from Potapov et al. (2008).

2.1.1.1 The boreal climate classification

The most used biological definition and classification systems for global climate zones are based on broad similarities of vegetation. Named after a pioneer in the field, the Köppen climate classification is the most widely used empirical climate classification system, and corresponds to the globe's major vegetation zones including the boreal forest biome. It divides terrestrial climates into five major types, A to E, defined primarily by temperature criteria (see Figure 2). Climate subtypes are designated based on seasonality and water availability defined by the relationship between precipitation and evaporative loss. The boreal climate zones are variants of the continental (D) and consist of the subtypes Dfc, Dwc, Dsc, Dfd, Dwd and Dsd (Figure 2). The Köppen system classifies most of Norway (including almost all forested area) as Dfc (boreal), with E (tundra) in the north and at high altitudes.

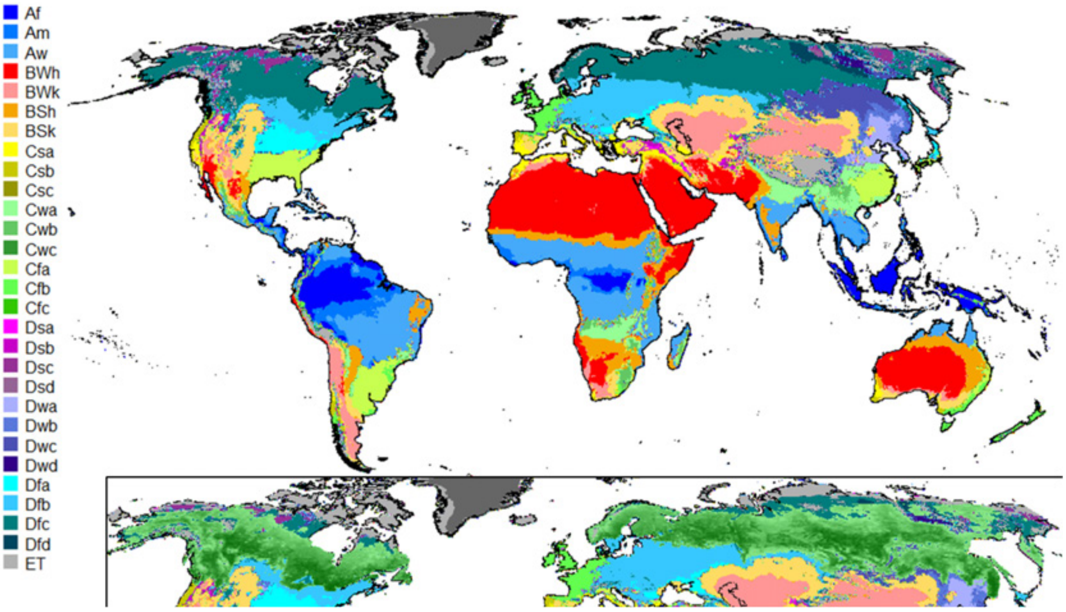


Figure 2. Current global distribution of climate zones (Data from Beck et al. 2018). **Insert map:** The distribution of boreal forest cover (Figure 1) over the boreal climate zones (main map).

2.1.2 Origin, biota, and habitat-forming communities

Despite their great expanse and ecological importance the circumpolar boreal forests are geologically recent in their current form. Today's boreal forests emerged over the past 12,000 years of the Holocene, covering what was once mammoth steppe and Scandinavian and Laurentide ice sheets during the last ice age. Because of this recent formation - in combination with low insolation and seasonal variation putting a premium on migration - the boreal biome does not contain any of the planet's major biodiversity hotspots (Hu et al. 2021, Myers et al. 2000).

The boreal forest biome is dominated by spruce, pine, larch, and fir conifers in the genera *Picea, Pinus, Larix, and Abies,* mixed to varying degrees with deciduous hardwoods such as birches, aspens, alders, rowans, and willows in the genera *Betula, Populus, Alnus, Sorbus,* and *Salix*. Other aspects of ecosystem structure and dynamics vary geographically. The understory in the more oceanic parts of Fennoscandia is typically dominated by low-growing woody ericaceous dwarf shrubs including species of *Vaccinium* and *Empetrum*. In contrast, tall deciduous shrubs (e.g., *Betula* spp. and *Salix spp.*) dominate the understory in continental areas of Siberia and North America (Boonstra et al. 2016). Mosses and lichens are common throughout the boreal zone and peat-forming mosses can build up substantial peat layers over extensive areas.

The boreal ecosystem includes a variety of large and mid-sized mammals (Leroux et al. 2020), as well as a considerable richness of small mammals. While 3- to 4-year vole–mustelid cycles characterize the food web dynamics in European boreal forests, 10-year snowshoe hare–lynx cycles are typical of the North American boreal forests (Boonstra et al. 2016). Boreal forests also hold a diverse avifauna that accounts for more than 70% of the vertebrate species in these ecosystems (Niemi et al. 1998, Grinde and Niemi 2016).

A considerable yet incompletely known diversity of invertebrates of all major groups fills key ecological roles in boreal forests. A wide variety of herbivorous and detritivorous insects from many taxonomic groups contribute to key ecosystem functions. Despite the dominance of mostly wind-pollinated conifers in boreal forests, insect pollination is important, especially for plants in the forest understory (Kevan et al. 1993, Nielsen and Totland, 2014).

Fungal and microbial communities play key roles in forest ecosystems, including as decomposers, mutualists, and pathogens. These communities thus shape ecological interactions in the forest ecosystem, from nutrient uptake to carbon sequestration (Clemmensen et al. 2021, Kim et al. 2021), and are in turn shaped by plant species composition, geology, climate, seasonality, and disturbance regimes (Cutler et al. 2017). Most forest-forming trees engage in ectomycorrhizal symbiosis, while Ericaceous dwarf shrubs form ericoid mycorrhiza. Both types of symbiose are crucial for the nutrient uptake of plants in boreal forests and play important and complex roles in the carbon cycle (Baskaran et al. 2017, Lindahl et al. 2021). While mycorrhizal fungi predominate deeper in the boreal soil, the upper litter layer is dominated by a diversity of decomposer fungi. Both groups are likely important for the vast carbon stores found in high-latitude soils globally (Crowther et al. 2019).

The boreal biome thus holds a substantial biota over a vast range, and conservation of boreal forests is a necessary and effective part of simultaneously conserving biodiversity and carbon sequestration (Jung et al. 2021).

2.1.3 Disturbance regimes

The natural (see Glossary) biotic and abiotic disturbance regimes of boreal forests are important and integral to ecosystem functioning, dynamics, and biodiversity (Bonan and Shugart 1989, Seidl et al. 2017, Pausas and Bond 2019, Seidl et al. 2020). Important disturbance types range in scale from small-gap dynamics affecting individual trees to stand-replacing events and even-aged dynamics affecting whole landscapes, such as storm windthrows, forest fires, snow breakage, and outbreaks of insects and diseases.

Small-scale disturbances are part of the common natural dynamics of boreal forest ecosystems; the death of single trees or groups of trees gives rise to small-gap dynamics, which is the most common type of forest dynamic in Fennoscandian boreal forests (Shorohova et al. 2011, Kuuluvainen and Aakala 2011). Larger-scale disturbances dominate in the continental parts of Siberia and Canada (Shorohova et al. 2011). Small-scale disturbances play an important role in moist and wet forest types where large-scale (stand-replacing) fire disturbances are rare or virtually absent (Hörnberg et al. 1995, Ohlson et al. 2011). Small-scale disturbances create light gaps and expose and turn over soil, and are typically caused by increased mortality risks of older trees due to windfall or pathogens and pests, as well as by grazing and browsing by rodents and wild and domestic ungulates (Austrheim and Eriksson 2001, Rydgren et al. 2007).

Globally, more than 100,000 km^2 of boreal forest burn during a normal year, mostly in Siberia, Canada, and Alaska (Flannigan et al. 2009). A few large-scale fires are responsible for most of the burned area. The ecological impact of fires is determined by how often they occur (frequency), how hot they burn (intensity), and how large area they burn over (magnitude) (Driscoll et al. 2010, Seidl et al. 2011). The boreal fire regime, defined by fire frequency, intensity, and magnitude, is driven by climate, landscape, and biotic features (Wardle et al. 2003), but is to a large extent modified by forest management strategies. Humans have contributed to boreal forest fire dynamics throughout history, mostly through agricultural and forestry practices. These practices include land clearance and slash-and-burn farming, as well as more recent active fire control that has become more and more effective (Wieckowska-Lüth 2017, Hjelle et al. 2018, Aasetre and Bele 2009, Breidenbach 2020). Disturbance regimes alter niche spaces within forest habitats, allowing for the processes of succession and natural selection to occur, altering community composition and function (Lorentzen et al. 2018, Sitters et al. 2019), and more generally they affect landscape structure, connectivity, and redistribution of nutrients (Barthelemy et al. 2015).

Localised disturbance may arise from autumn and winter storms, which often cause extensive windthrows, particularly in waterlogged sites (Stokes, 2002) where stands are dominated by shallow-rooted trees, such as spruce (Peterson, 2007), or by early succession shade-intolerant species (Rich et al. 2007). Disturbances may also arise from insect outbreaks and diseases (section 2.3.6) which can cause large-scale disturbances and diebacks; examples include outbreaks of the European spruce bark beetle (*Ips typographus* L.) in spruce forests and of geometrid moths (*Epirrita autumnata* and *Operopthera brumata*) in northern boreal birch forests (Hlásny et al. 2021, Jepsen et al. 2008, Netherer and Schopf, 2010). Disturbances are often linked, as major wind throws, droughts or other disturbances cause a surplus of dead or weakened trees that increase the likelihood of outbreaks of insects, which also can be major vectors of diseases (Seidl et al. 2017). These dynamics are described in Norwegian forests in chapter 2.3, and integral to the assessment of climate change impacts on Norwegian boreal forests in chapters 4, 5, and 6.

Major human contributions to forest disturbance regimes, now and in the past, include logging, soil scarification, grazing, hunting, ditching, and fire suppression. There is regional variation in the mode, intensity, and historic development of disturbances depending on accessibility and strategies for use and management of forests (Pohjanmies et al. 2017). These issues are described in detail for Norwegian forests in chapter 2.3, and considered when relevant for climate change impacts on Norwegian boreal forests in chapters 4, 5, and 6.

2.1.4 Current pressures

The boreal forest biome contains some of the world's last sizeable wilderness areas, but nearly two-thirds of boreal forests are managed, largely for commercial wood production (35-40% in Canada (Burton et al. 2010), 58% in Russia (Gauthier et al. 2015), and 90% in Fennoscandia (Burton et al. 2010, Venier et al. 2014). While current rates of boreal deforestation globally are variable, boreal forests are currently under pressure from multiple stressors (Johnson and Miyanishi 2012, Gauthier et al. 2015, Allan et al. 2017). Major disturbance factors include deforestation (the transformation of forests into arable and urban areas), forestry, infrastructure for transport and energy, climate change, and the increasing scale of fires and insect outbreaks driven by the interplay between climate change and natural and human-induced disturbances (Seidl et al. 2017, Grantham et al. 2020).

Over the course of the 21st century, the boreal biome is expected to experience the largest temperature increase of all forest biomes (Gauthier et al. 2015, IPCC 2022), and unprecedented climatic extremes are already occurring. For example, in June 2021, readings from the Copernicus Sentinel-3A and -3B satellites showed that the land surface temperature in Siberia was above 35°C, with a peak of 48°C in the Sakha Republic (Yakutia). Siberian heat waves coincide with exceptionally active boreal and arctic fire seasons. Some of the larger fires burned into carbon-rich peat soils (Zhao et al. 2021), suggesting that the climate impact of the longer and more intense boreal fire seasons may be larger than what the burnt forest area alone suggests.

Large-scale clearcutting forestry has affected large areas across the boreal zone since World War II (Belousova 2021, Burton et al. 2010). Old-growth, and in particular primeval (see glossary) forests, have thus become increasingly rare, currently making up a small and decreasing proportion of standing biomass throughout the boreal biome. In some areas, older and mature production forests have increased in proportion over the last decades. The post-Soviet trends of the Siberian forests are contested but are likely impacted by poorly regulated clearcuts and unofficial forest roads (Schepaschenko et al. 2021, Belousova 2021, Light 2021). In Canada and Fennoscandia, the situation has been more stable, with the amount of young boreal forest increasing. Some sizeable areas of old-growth forest remain in the Canadian Northeast, while very little old-growth forest remains in Fennoscandia

(Kuuluvainen and Gauthier 2018). In all areas, the increasing road network, from highways to local logging roads, increases fire frequency and aids firefighting efforts, while adding to noise and other direct disturbances, roadkill, erosion, and more generally increasing forest ecosystem vulnerability to climate changes, including climate extremes and related stress factors (Kuklina et al. 2021).

Long-range transported atmospheric pollution and acidification is another stress factor for boreal and nemoral forests (Dirnböck et al. 2018, Austnes et al. 2018), but the extent and severity vary. Nitrogen deposition from fossil fuel combustion often has negative effects on e.g. biodiversity but may have positive effect on primary productivity through a fertilization effect. However, the rate of nitrogen deposition in Fennoscandia has been declining and no strong effect of further decline nor interaction with climate is expected (Schmitz et al. 2019). Maps of acid sensitive areas and acid deposition suggest that surface water acidification occurs also in regions and countries for which no data or reports were available for the current assessment (Austnes et al. 2018). Other types of pollutants from transport, industry, and agriculture affect the boreal forest and, in some areas, add up to significant stress (Maynard et al. 2014, Gauthier et al. 2015). However, except when known interactions exist with the carbon cycle or climate change, effects of non-greenhouse gas pollution will not be discussed in this report.

2.1.5 Role in the global carbon cycle

Boreal forests are key components of the terrestrial carbon cycle as they absorb and store about a quarter of all terrestrial carbon globally. This makes the boreal region one of the largest and most carbon-dense terrestrial carbon sinks on Earth (Kayler et al. 2017, Crowther et al. 2019). In a recent study of the global distribution of biodiversity, water, and carbon, large swaths of the boreal zone are consistently ranked as being of very high priority for conservation efforts to safeguard global terrestrial carbon stores (Jung et al. 2021; Noon et al. 2021). Up to 80% of the boreal carbon stock is stored below ground in the forest soil (IPCC 2001; IPCC 2022; Scharlemann et al. 2014, Astrup et al. 2018, Søgaard et al. 2019) because of high accumulation of organic soil and large allocation to belowground plant-parts and microbial communities.

While plants regulate the rate of CO_2 sequestration from the atmosphere via photosynthesis (Figure 3), the subsequent fate of the organically bound carbon is regulated by complex ecosystem processes involving plant symbionts, decomposers, and other soil organisms, as well as herbivores (Basile-Doelsch et al. 2020). Boreal forest soils have slow carbon cycling due to a combination of cool temperatures, a precipitation surplus, a dominance of evergreen species with relatively recalcitrant litter both in the canopy (conifers) and the understory (*Ericaceae*), and slow cycling fungi, bacteria, and fauna in the carbon-rich boreal forest soils (Nilsson and Wardle 2005, Thurner et al. 2019, Crowther et al. 2019, Jeong et al. 2018).

Saprotrophic fungi (*q.v.)* living in litter and wood are the main decomposers of plant organic matter in boreal forests (Figure 3). Their activity is mainly regulated by temperature and nitrogen availability and by access to other macro- and micronutrients. The effectiveness of these organisms in decomposing plant litter, relative to litter accumulation rates, largely regulates how much carbon is sequestered in the soil. Mycorrhizal fungi (fungi living in symbiosis with plant roots) also regulate belowground carbon dynamics (Smith and Read 2008). Some mycorrhizal fungi can, as saprotrophic fungi, decompose organic matter and extract nitrogen (Lindahl and Tunlid 2015). The presence of certain mycorrhizal fungi may predict how much carbon is being stored below ground, by regulating carbon turnover through competitive relationships with saprotrophic fungi and through other mechanisms (Fernandez and Kennedy 2016, Lindahl et al. 2021). Not only dead plant litter, but also dead mycelium contribute to the build-up of soil organic matter (Wang et al. 2021), and melanized mycelia, which are more common in colder climates (Krah et al. 2019), have a slower turnover and longer retention time compared to non-melanized mycelia (Fernandez and Koide 2014). The organic layer in boreal forest soils is thus to a large extent built up from below, by dead fungal mycelia and plant roots, and not only from above (Clemmensen et al. 2013).

Another important but often neglected aspect of the carbon dynamics of the boreal forest is the role of dissolved organic carbon (DOC; Figure 3). The boreal forest contains more surface freshwater than any other terrestrial biome (Burton et al. 2010, Gauthier et al. 2015), facilitating transport and metabolization of DOC to CO_2 and methane (CH_4) (Battin et al. 2009). However, this is beyond the scope of this report and is thus not further considered here.

Carbon sequestered in soil and biomass may be released through forest fires (Figure 3). Fires can release large amounts of carbon from standing biomass and organic topsoil layers, to the point where the fire magnitude may shift boreal forests from carbon sinks to carbon sources (Walker et al. 2019, Köster et al. 2018). Natural disturbances other than fire also contribute to reduced uptake and increased release of carbon from the ecosystem by causing tree mortality. However, large-dimension dead wood decomposes slowly in boreal forests and hence stores its carbon for long periods (decades to centuries), contributing to the accumulation of soil carbon stocks. Clear-cutting, however, especially if followed by site preparation (Sundqvist et al. 2014, Vestin et al. 2020), causes loss of carbon from the ecosystem in the form of both extracted timber and increased carbon emissions from the soil and logging residues.

The carbon cycle of the boreal forests plays an important role in producing and removing carbon-based greenhouse gasses (e.g. CO_2, CH_4) from the atmosphere. In addition they regulate water (H_20) vapor and heat reflection (albedo, *q.v.*). The net result on climate is complex, including multiple feedback mechanisms between climate and biological activity. Boreal forests may switch between being important sources and sinks for greenhouse gasses depending on season, forest age, logging status, soil moisture, temperature, disturbances, and other factors (Thom et al. 2016, Chi et al. 2020, Siljanen et al. 2020, Vestin et al. 2020).

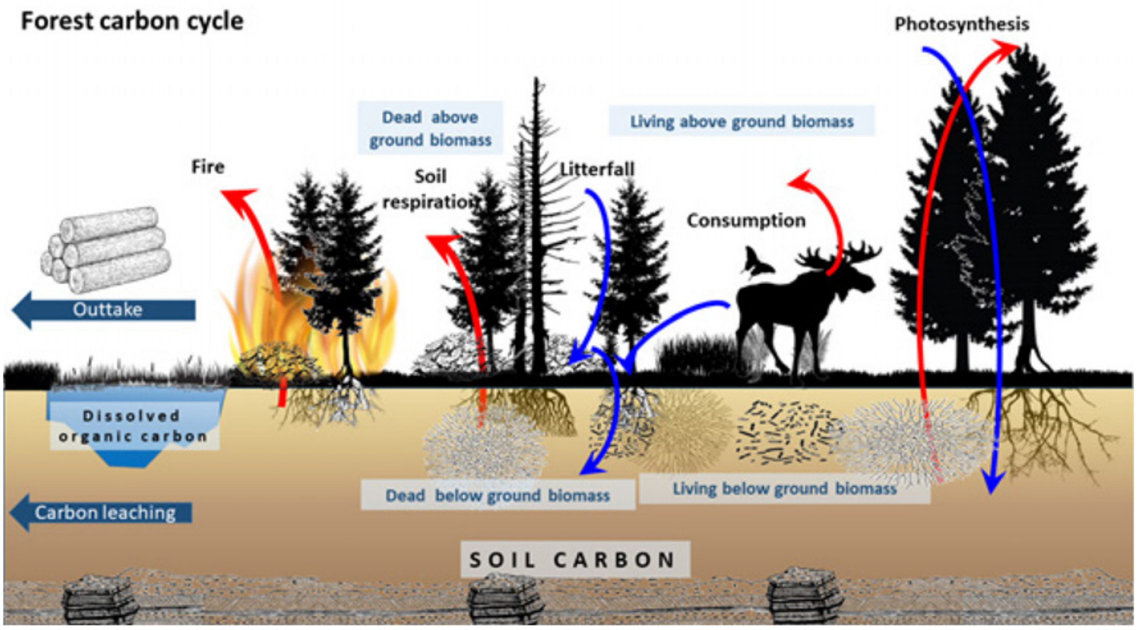


Figure 3. The fluctuating carbon balance of boreal forest systems. Carbon is removed from the atmosphere by photosynthesis and is sequestered in living and dead biomass, soil carbon accumulation, and carbon mineralisation (blue arrows). Release of carbon as greenhouse gasses (red arrows) happens through fires, animal and plant respiration, and soil respiration by heterotrophic microorganisms (primarily fungal and bacterial decomposers), soil animals and plant roots. Carbon may also leave the system through removal of timber, soil, animals, or other forest products, as well as through leaching of dissolved inorganic carbon.

2.2 Global climate change and the boreal zone

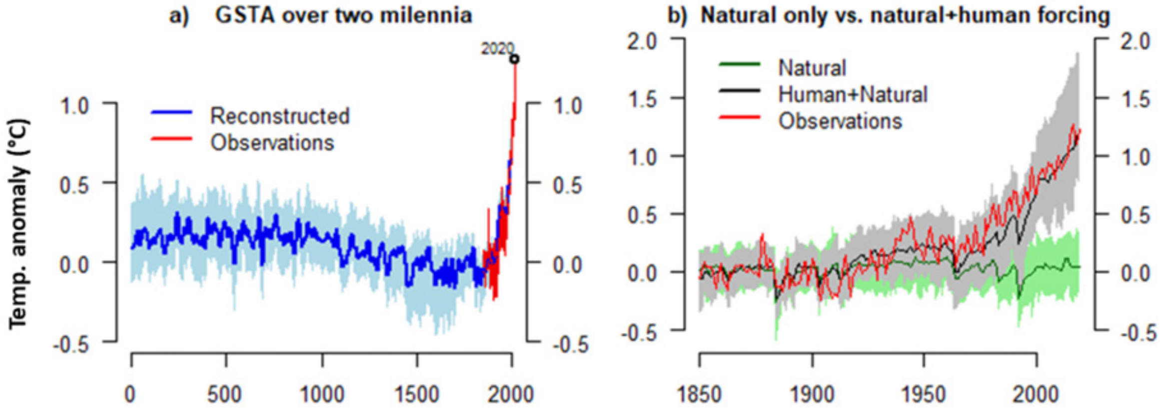
Climate change refers to long-term shifts in temperatures and weather patterns. Climate variation occurs naturally, for instance throughout the approximately 11-year solar activity cycle, the multi millennial orbital Milankovitch cycles, volcano emissions of greenhouse gasses and sun-blocking particles, and long-term geological effects (Iles et al. 2015, Szarka et al. 2021, Schuur et al. 2015, IPCC 2021). Because of industrialization, however, human activities have been the main driver of climate change since the late 1800s. The burning of fossil fuels adds more carbon than what is taken up, leading to an accumulation and rise in the concentration of CO_2 and other greenhouse gasses in the atmosphere and dissolved in water. As greenhouse gasses redirect heat that is radiating back into space, earth surface temperature not only increases, but the increased energy in the atmosphere and ocean, where most of the accumulated energy is stored (Cheng et al. 2022).

Due to their complexity, most global climate models have to be run on coarser scales than needed for examining local climate effects. *Downscaling* (*q.v.*) is a procedure for using large-scale climate models to make predictions at finer temporal and spatial scales, thus being able to incorporate local variables like elevation, exposure, land cover etc. to make more fine-grained predictions. As computing power is increasing, the resolution possible for both global and downscaled models keeps improving.

The Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR6 WG1) was published in 2021 (IPPC 2021). According to this report, human activities have already caused approximately +1.0°C [0.8, 1.2] of global warming above pre-industrial levels, making the past decade (2011-2020) the warmest on record. Warming is likely to reach +1.5°C [1.2, 1.9] before 2040 from effects that are already influencing the climate (climate forcing, *q.v.*), irrespective of what greenhouse gas emission pathway (RCP/SSP, see section 3.2.1) is followed from today onwards. Emissions and climate policies over the coming decades will determine whether climate change stabilizes at a global temperature increase of +1.3°C after the year 2040 (low end of an optimistic scenario) or at +5.7°C or more (high end of a pessimistic scenario) towards the end of the century (Figure 4).

Climate change is not uniform. In general, the temperature increase is strongest over land and is greatest in the Arctic. The boreal zone, with its high latitudes and largely continental climate, is expected to experience the largest change in temperature regime of all forest biomes over the course of the 21st century. While the western parts of Norway are strongly influenced by the ocean, the eastern and northern parts of the country are drier and more continental, and thus more similar to the boreal belt globally (Ketzler et al. 2021, Hanssen-Bauer et al. 2015). Accordingly, for all scenarios, warming is projected to be greatest for continental parts of northern Norway, and to be smallest for western Norway.

Mean annual temperature increases of 1-1.5°C are estimated to already have occurred over the boreal zone, with large variation between areas and between years. For instance, in 2020 annual mean temperatures exceeding +6°C over certain areas of Siberia were reported, or +4.3°C above the 1981–2010 normal if averaging over the whole Siberian Arctic (the previous record was +2.5°C above annual average in 2016). Most of the boreal zone is projected to experience a warming of at least 1.5 times that of the global average. Thus, under a globally averaged projection of +3.0°C by 2090, boreal regions would be expected to experience temperature increases from 4.5°C to over 5°C. The expected increase in precipitation is considerably less than the warming-induced water loss from increased evaporation, which ultimately is expected to result in more drought resistant ecosystems. In the +3°C scenario, shrubland might be favored in large parts of the current boreal zone (Gauthier et al. 2015, Christensen et al. 2007). The transformative potential of temperature and related ecological cascades, is evident for the fact that large parts of the boreal forests presently have a range of annual precipitation averages that greatly overlap with those of semi-arid scrublands (Bahn et al. 2010). An example is shown in Figure 5 by comparing the climate profiles and pictures of contrasting sites found in central Siberia and Namibia bordering the Kalahari.



a) GSTA over two milennia

b) Natural only vs. natural+human forcing

c) Global Surface Temperature Anomalies (GSTA) relative to 1850-1900

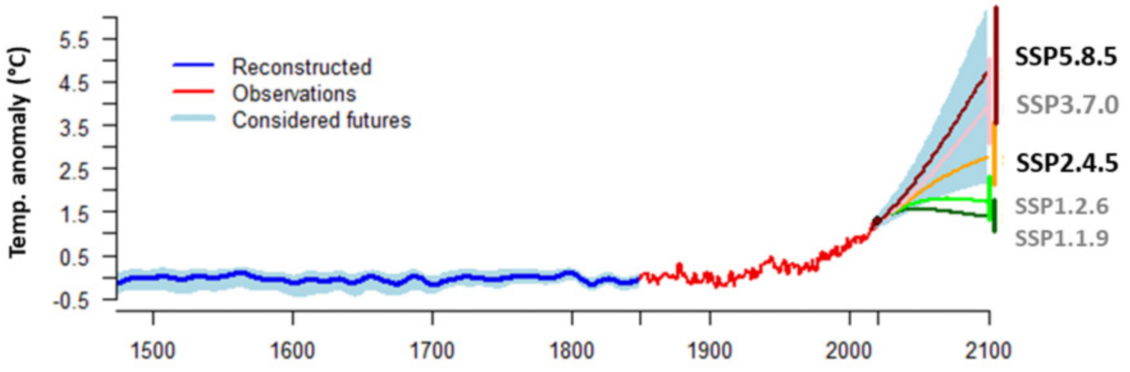


Figure 4. Global surface mean temperature anomalies (GSTA) relative to 1850-1900, as given in the IPCC AR6 (2021). Note differences in y-axes between panels. (**a**) Reconstructed temperatures over the last two millennia. The climate has varied markedly, but the contemporary warming period is already unprecedented on this time scale. (**b**) Averages of many representative models (often called model ensembles) using only natural mechanisms affecting climate (climate forcing) vs. the same models when also including human-induced (anthropogenic) effects on climate. Only the latter explains observed temperatures. (**c**) Long-term climate fluctuations shown in (a) dwarfed by observed warming and future projections. The intervals within which 95% of the models agree are shown for the different SSPs, and the "probable futures" corresponding roughly to scenarios considered in this report are shown as a light blue polygon. The figure is based on updated data from AR6 SPM data archive (IPCC 2021), where the data point for 2020 is from Rohde (2020).

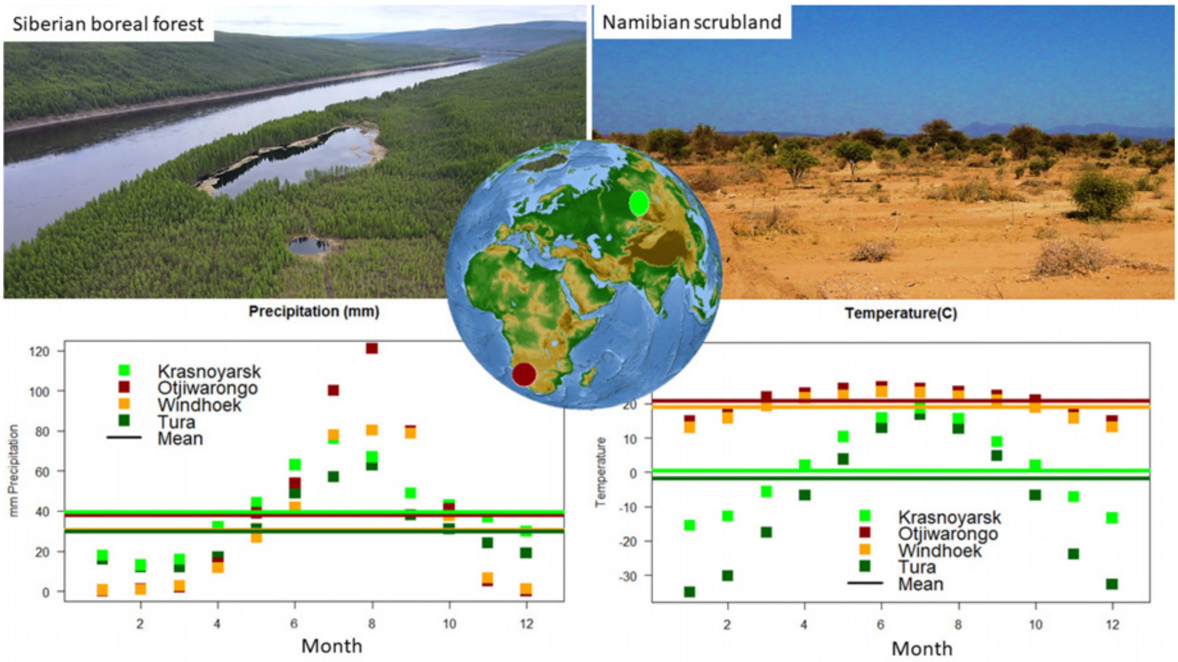


Figure 5. Interactive effects of temperature and precipitation on the world's biomes. The dry scrub and bushweld surrounding the Namibian towns of Windhoek and Otjiwarongo (upper left) and the densely forested, marshy Siberian taiga of Krasnoyarsk and Tura (upper right) experience very similar total annual rainfall (lower left), but very different temperature (lower right) and thus evapotranspiration. Months for Namibia are shifted by six months to reflect southern vs. northern seasonality. Annual mean values are shown with horizontal lines, monthly means as colored points (Data: https://en.climate-data.org/, Photo courtesies of Alberto Arzac, Siberian Federal University, and Hannah Schønhaug, ARCRA).

2.3 The Norwegian boreal forests past and present

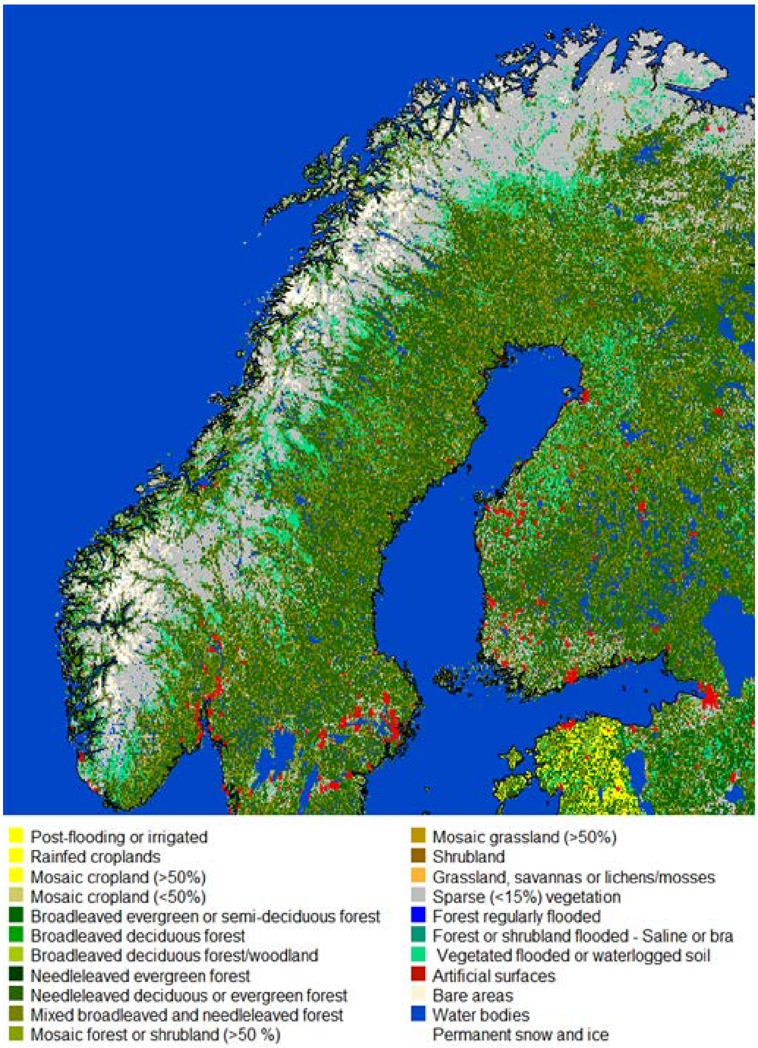


Figure 6 Overview of Fennoscandian land cover at the onset of the 21th century, showing the main distribution of Norwegian forests. Map based on data from ESA 2010 and UCLouvain http://due.esrin.esa.int/page_globcover.php

2.3.1 Origins and responses to historical changes

The first forests to establish in Norway after the last glaciation around 10 000 to 9500 before present (BP) were open birch and pine forests. Soil accumulation in combination with continued warming until the Holocene thermal maximum occurred about 7500 to 6500 BP (Warden et al. 2017; Velle et al. 2005; Velle et al. 2010), allowing forests to expand northwards and upwards. At the same time, forests in the most climatically favorable locations transformed into closed and mixed temperate deciduous forests with oak, elm, ash, and linden. The tree line during the thermal maximum extended significantly higher than at present. While some estimate a 170-210 m higher treeline and 1 to 1.3 ºC higher summer temperatures (Paus and Haugeland 2016), megafossil finds at even higher altitudes implies treelines up to 600-700 m higher in altitude than in the early 2000s, suggesting up to 3.6 ºC higher summer temperatures (Kullman 2017a, Kullman 2017b). With cooling temperatures, pine increased in abundance, and spruce became common in pollen records towards the early Scandinavian iron age (around 2500 BP). At that point, the northwestern European climate was cool and wet, and spruce and pine invaded Scandinavia from the east (Büntgen et al. 2011, Mauri et al. 2015, Warden et al. 2017, Hannon et al. 2018). The spruce-dominated forests that have been common in parts of Norway for the last 2000 years were thus largely established from genotypes originating in Siberia and Central Europe (Alps and Carpathians) (Fagernäs 2017; Šeirienė et al. 2021).

Recent research combining genetics and fossil finds suggests a complex post-glacial history where some spruce and pine may have survived the glaciation in Scandinavian refugia (Parducci et al. 2012; Paus et al. 2006, see also Alsos et al. 2020), or at least may have been present intermittently from as early as 16 800-13 000 BP along with birch, rowan*,* aspen and grey alder as shown by finds in thawing glaciers (Kullman 2017). Out of all the conifer trees of the taiga, only a single spruce species (Norway spruce; *Picea abies*) and a single pine species (Scots pine; *Pinus sylvestris*) currently have natural distributions as forest forming trees in Norway (in addition to some *Juniper* and *Taxus* species usually seen as shrubs), although Siberian larch (*Larix sibirica*) was present in earlier interglacial periods (Kullman 2017). The present composition of the Norwegian boreal forest is thus a product of a complex process of migrations and admixtures (Seppä et al. 2009). This seeming contradiction between current abundance and time since establishment suggests an explanation involving climate shifts and competition, in addition to spread and expansion.

2.3.1.1 From first clearings to industrialization

In southern Norway, there is evidence of animal husbandry and cereal cultivation from before 5500 BP, but large-scale anthropogenic changes to the biome remain sparse until intensifying animal husbandry, cereal cultivation and farming economies take hold in the late Bronze Age/ early iron age from approx. 2500 BP-2200 BP, bringing extensive forest clearance and local fires from crop cultivation in permanent fields and open pastures (Wieckowska-Lüth 2017; ter Schure et al. 2021; Hjelle et al. 2018). Since then, the species assemblages in the Norwegian forests have developed in interaction with human subsistence of gradually increasing impact.

Despite challenging topography and relatively low human population density, Norwegian boreal forests have been commercially harvested for timber for a long time. Norwegian round timber was supplied to Iceland by 900 CE, mast timbers sold to England in the 1000s, and by the 1300s timber export, particularly to Britain and the Netherlands, had become a major income source (Myking et al. 2016). Through the Middle Ages and into the Renaissance, forests were harvested domestically as fuel for cooking and heating, farming and related cottage industries, raw material for fencing, bridging, toolmaking, boat building, house building, charcoal and tar, for mining, salt production and metalworking, and countless other purposes in rural and increasingly urban societies. In combination with grazing, browsing, and harvesting of fodder, bark, and firewood for summer farming in the sub-alpine zone, human impact limited regional rejuvenation and lowered the tree line in many areas (Aasetre and Bele, 2009). As elsewhere, human contributions to fire dynamics in Norway include agricultural and forestry practices, including land-clearance, slash-and-burn, and active fire control.

With the introduction of the hydro powered sash sawmill in the 1500's, trade and export experienced a further substantial increase to supply building materials and charcoal to growing cities, merchant and military ships, mining and other industries. Selective logging and diameter-limit cutting (cutting all trees above a given size) including increasingly smaller trees, resulted in a gradual, and eventually accelerating, loss of production and trees of profitable size ranges from accessible areas from the 1600s. By the end of the 1800s, the Norwegian forests had become sparsely stocked by generally small trees (Øyen and Nygaard 2020). Following a seminal publication by prof. Agnar Barth in "Tidskrift for Skogbruk" in 1916 where he warned of a collapse of Norwegian forestry, the Norwegian Parliament established the National Forest Inventory (*Landskogtakseringen* – NFI) in 1919. The inventory is still ongoing and has generated a century worth of data on Norwegian forests (Aasetre and Bele, 2009, Breidenbach et al. 2020).

2.3.1.2 Stand-based forestry

Stand-based forestry practices, based on clearcutting, were developed gradually from the 1700s in Europe and introduced to Norway from Germany and Sweden between World War I and World War II to become the prevailing form of forestry in the 1950s. The aim was to build up a rotation of relatively even-aged stands to be re-planted or systematically rejuvenated from seed trees after felling. These forestry practices include auxiliary measures, such as soil scarification to promote seedling growth and survival, removal of deciduous trees, thinning, and fertilization to promote timber production. In combination with the internal combustion engines becoming more common after World War II, the mechanization of agriculture and forestry facilitated stand management on larger scales and in less accessible areas.

In stand-based forestry, biological differences between the two dominating forest tree species in Norway resulted in different silvicultural strategies. While spruce is regenerated by planting after clear-cutting, pine is most often naturally regenerated by leaving seed trees (3-15 seed trees per 1000 m^2) after cutting. The scattered pine seed trees are cut when the regeneration has succeeded, and both strategies therefore tend to result in relatively even-aged, single species stands and structurally homogeneous landscapes. Since World War II, most spruce-dominated areas have been intensively utilized, and multi-aged forests have been transformed into timber-rich clearcut stand managed forests. During the period 1950-2000, 35-42% of the total spruce forest area in Norway was clear cut and replanted with spruce, mostly in the most productive forest areas (Nygaard and Øyen 2020).

With the increased production efficiency of stand-based forestry, combined with less local use of forest products for domestic and subsistence use due to new material technology, the annual increase in tree biomass from growth has exceeded the timber harvest since monitoring started in the early 1900s. The volume of standing trees is estimated to have tripled from about 323 million m^3 in 1933 to about 987 million m^3 in 2021, with about 10 million m^3 being felled each year (SSB 2021, Breidenbach et al. 2020, Tomter and Dalen 2018).

The current stand-based forestry practices have resulted in a gradual increase in the average age and size of trees in a national perspective as the trees have recovered volume from overharvesting in the previous century (Stokland et al. 2021). The practices have also limited the maximum age and tree size by stand harvesting well below the biologically maximum age (Figure 7). Only a negligible fraction of productive forests is resembling primeval, i.e. with no clear sign of human impact, and only a small fraction of the forest areas is old-growth. About 3.6% of today's productive forests are older than 160 years, and almost all of the old-growth forests are in the less productive areas (site index <8). Less than 1.4% of the more productive forest (site index >11) is >160 years old (Framstad et al. 2014; Stokland et al. 2021; Tomter and Dalen 2018). This is partially due to differences in stand ages and tree species and partially due to the greater incentive for harvesting the most productive areas. Continuous habitat is a related issue, as of 2018 less than 12% of Norwegian land area was further than 5 km away from major buildings or infrastructure (Miljøstatus for Norge 2021). The continuous areas of truly old-growth forests still seem to be declining. Consequently, there is a gradual loss of very large living and dead trees and of coarse woody debris in widely different decay classes (e.g. Berg et al. 1994; Ohlson et al. 1997; Lie et al. 2009; Stokland 2012, Mikusinski et al. 2021). Currently, 48% (1330 out of 2752) of the species classified as critically endangered, endangered, or vulnerable in the Norwegian red list are associated with forests, of which a majority (84%) with old-growth forests (Artsdatabanken 2021). So while the proportion of endangered species in forests is only a third higher than the overall proportion of Norwegian land area covered by forest (37.4% in 2021 according to SSB), old-growth forests are clear diversity hotspots. The loss of old-growth forest habitats is especially dire for the more productive forest types, as the remaining old-growth forests are concentrated in low-productivity forest regions bordering the high-altitude alpine or high-latitude arctic tundra zones (Miljøstatus for Norge 2021). As of January 2022, about 5.2% of the Norwegian forests are protected, which translates into 3.8% of the productive forest and 8.4% of the non-productive forest area (Miljøstatus i Norge 2022).

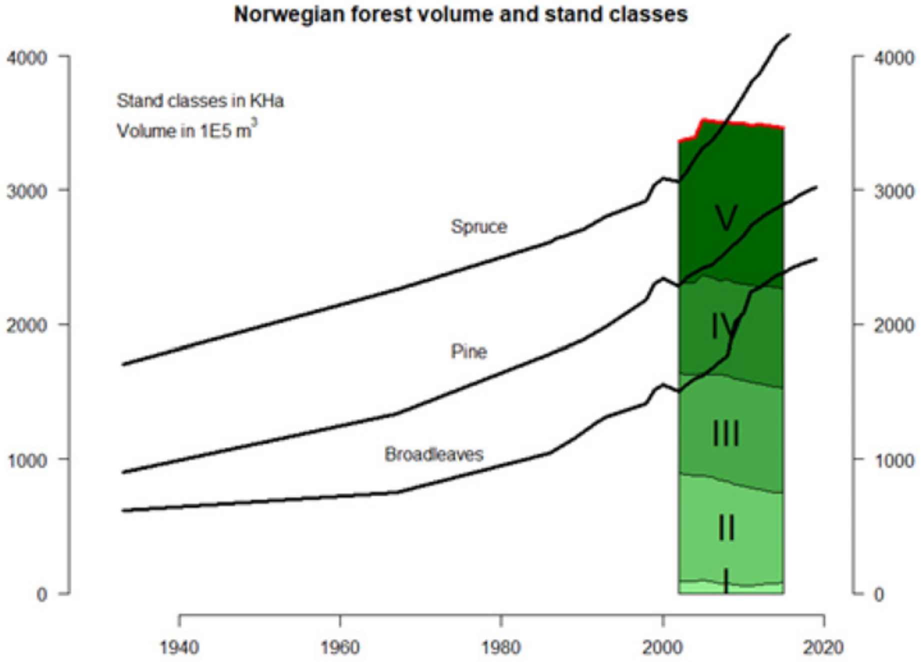


Figure 7. 10^5 cubic meters standing trees in Norway 1933-2019 as estimated by the National Forest Inventory. Green-shaded areas indicate 10^3 standing hectares of different stand classes (see glossary) from class I (replanting), II (juvenile trees), III (young harvestable forest), IV (productive forest), V (mature productive forest) and old-growth/primeval productive forest (<1.5%, in red) 2006-2019 in Norwegian forests (https://www.ssb.no/lst).

2.3.2 *Variability and bioclimatic gradients*

A distinctive feature of Norwegian forests is their sharp bioclimatic gradients, where annual average values for both temperature and precipitation can vary greatly over short distances due to rain shadows and to changes in altitude, oceanic influence, and solar exposure. The

NiN classification system (see 3.1.2) used to describe landscape types in Norway therefore is based on a set of complex gradients.

Lush and species-rich deciduous forests dominated by ash, oak, linden, hazel, and black alder are typical of low altitude areas in southern and western parts of Norway, regions that include pockets of boreal rain forest. Slow-growing and less species-rich coniferous forests dominated by spruce and pine dominate further to the north and east, and at higher altitudes. Sparsely stocked forests dominated by birch cover large areas in regions with a short growing season in the northernmost parts of Norway and in sub-alpine areas of southern Norway (see Tomter and Dalen 2018).

All Norwegian forests are classified as part of the boreal forest biome (Halvorsen 2016). However, there is substantial local variation in features such as drought risk and limestone richness, giving rise to a large number of (minor) forest types that vary in dominance along the regional bioclimatic gradients. Due to the large variation in both bioclimatic and local environmental conditions, Norwegian forests provide a great variety of habitats and microhabitats for a large number of species that are adapted to the conditions and dynamics of their ecosystem and long-term climatic conditions, with a range of ecological strategies.

2.3.3 Atypical disturbance regimes

The Norwegian forest is susceptible to the range of disturbance types seen elsewhere in the boreal biome (see 2.1.3). However, the boreal areas in oceanic regions like Norway experience significantly smaller annual temperature amplitudes, milder climates, and relatively more precipitation, especially during autumn and winter, than the more continental regions that dominate the boreal zone globally (MET Norway: www.met.no/, Shorohova et al. 2011).

Large-scale forest fires are not common in Norway. This is a result of generally moderate temperatures and abundant rainfall combined with heterogeneous landscapes as described above (Tomter and Dalen 2018). Thus, many stands of Norwegian forest may not have burned during the Holocene (Ohlson et al. 2009, 2011). Fires still occur with a frequency that seems to increase from coastal to inland continental climates and warmer summers, as suggested by densities of charcoal in forest soils (Ohlson et al. 2009, Vandvik et al. 2014).

Current Norwegian policy entails allowing only small and controlled fires, to avoid damages to forest resources, habitats, and human installations (Rolstad 2018), and is made possible by extensive access points and a well-established fire-fighting system. Over the last 100 years, Norway has thus experienced on average one large-scale fire (area >1 km^2) per decade, and the frequency has been relatively stable over this period (Hanssen et al. 2019) However, warm summers are positively associated with fire frequencies over centuries (Wallenius 2011, Rolstad et al. 2017; see Section 4.1.7). Lightning is the most common natural ignition source, and many recent fires have been caused by human activity after long-lasting warm and dry weather, but all were limited and controlled within one to four days.

Overall though, Norwegian forests have tended to be more affected by disturbances caused by wind or snow than by fire, similar to much of European forests (Seidl et al. 2014). Wind felling is therefore a relatively more important disturbance factor in Norwegian forest due to its vicinity to the Atlantic Ocean and varied topography. Forest insurance payouts may give an indication of the relative importance of the various disturbance factors in Norwegian forest: 77% were due to wind damage, 13% were due to snow breakage, 5% were due to fire and 4% were due to rodents from 2011 to 2020 (Finansnorge.no 2020).

The period 1971-81 saw severe outbreaks of the spruce bark beetle (*Ips typographus*) following a series of windthrows and droughts in southern Norway Trees equivalent to 5 million m^3 of timber were damaged (Bakke 1989). No large-scale outbreaks have occurred since, but smaller-scale outbreaks and a clear connection between beetle dynamics, killed trees, and drought stressed trees is evident, not the least following the summer drought of 2018 (Økland et al. 2021).

Changes in disturbance regimes are expected to be important consequences of climate change, and as such recurring themes in the results and discussions in this report.

2.3.4 Forest diversity and threatened species

Norwegian forests consist of about 30 tree species, of which only a few are dominating and stand-forming (see separate sections below). Norwegian forest ecosystems are rich in biodiversity. Out of 43,705 species documented and 60,000 estimated to exist in Norway, over half are thought to be associated with forest habitats (Framstad et al. 2018). The arthropods are the group of multicellular organisms with the most documented species in Norway; 22,695. Many species of unknown fungi, protists, other microeukaryotes and prokaryotes are likely to exist. The post-WWII changes in forest structure and connectivity imposed by human influence have had great impact on a wide range of forest-dwelling species (Berg et al. 1994; Gjerde et al. 2010, Nordén et al. 2018, Breidenbach et al. 2020, Framstad et al. 2021, Moor et al. 2021), and 48% (1,330 species) of the known threatened species in Norway live in forests including 387 fungi, 232 beetles, 167 lichens and 137 flies (Diptera), with a majority in the southern parts of the country (Artsdatabanken 2021). However, the distribution and abundance of many species are not sufficiently known, suggesting that the number of threatened or rare species is likely to be higher.

2.3.5 Key organisms in the Norwegian boreal forests

In this section, we provide background information on important organism groups found in Norwegian forests, which are relevant for the results chapter (Chapter 4). Due to space limitations, we limit ecological background information to a few key groups. For recent assessments of the ecological condition of Norwegian forests and their biodiversity, we refer to the assessment by Framstad et al. (2021; see section 2.5.3), Nature index for Norway (Jakobsson and Pedersen 2020), and the Norwegian Red List (Artsdatabanken 2021).

2.3.5.1 Spruce

Norway spruce, *Picea abies*, covers 27% of Norway's forested area, and is estimated to represent about 43% of the standing forest volume (SSB, 2020). Spruce is a dominating tree species in eastern and middle parts of Norway. Occasional stands are found north of Saltfjellet and in smaller pockets in eastern parts of Troms and Finnmark, as well as in inner parts of western Norway (Skrøppa and Fjellstad 2020, Øyen and Nygaard 2020). In the middle parts of Norway, spruce forms coastal forests, while in eastern Norway it often forms the treeline when this is not formed by birch. European forestry is adapted to and strongly dependent on the use of the straight-growing spruce, which makes up 23% of the growing tree stock in the EU (FOREST EUROPE, 2020). Spruce has therefore been planted far outside its natural distribution in Europe (Solberg 2004; Seidl et al. 2017). This is to some extent true also for Norway, where planted spruce have replaced pine forests, deciduous forests, grasslands, and heathlands in southern, western, and northern parts of the country.

Spruce is a shade tolerant species that grows best on nutrient rich, deep, and humid soils, but it may also be found on clay and moraine. The relatively dark, cool, and moist environment of the spruce forest is important for many lichens, fungi, and birds. Its relatively shallow root system makes it susceptible to windthrow and drought (Caudullo et al. 2016).

2.3.5.2 Pine

Scots pine, *Pinus sylvestris*, is a common tree species all over Norway, including in coastal areas, along the alpine treeline, and the world's northernmost pine forests in Finnmark. Pine forests are estimated to make up 31% of the standing volume of Norwegian forests (SSB, 2020), and pine accounts for the largest growing stock of European forests (30%) (FOREST EUROPE, 2020). After spruce, pine is the most important commercial tree species in Norway and is thus actively managed. In contrast to the other Nordic countries, pine in Norway is largely naturally regenerated from seed trees left after clear-cutting, but planting and sowing of pine are increasingly common.

Pine can grow on almost any kind of soil and from very dry to wet conditions. It is often outcompeted by spruce on humid and nutrient-rich soils, especially in eastern and central

Norway. Because of its solid root system, pine can grow on shallow soils and is well-anchored against windfelling. The thick bark and high crown allow larger trees to survive fires. Pine can colonize recently disturbed sites if grazing pressure is low and if site conditions are sufficiently nutrient poor or water stressed so as not to favor more fast-growing species. Pine requires winter chilling to break autumn dormancy. Pine is an important feed source for many forest animals, including wood-decaying organisms, red squirrels, crossbills, woodpeckers, capercaillie, moose and red deer that feed on seeds, shoots, and bark.

2.3.5.3 Birch

Birch, *Betula* species, is the most common type of tree by number (41% of forest trees) and represent 16% of the volume in Norwegian forests (SSB 2022, Framstad et al. 2020). Two naturally occurring species grow as trees, including *Betula pendula* Roth (Norw. *hengebjørk*) and *B. pubescens* (Norw. *bjørk*, includes *fjellbjørk*), both hereafter referred to as "birch". Birch is found all over Norway where trees grow, and form both the polar treeline in the north and the alpine treeline many places in the south. It is a typical light-dependent pioneer species and establishes fast on recently cleared localities. In the forest, it is usually found as single trees or small groups intermixed with spruce. However, birch acts as a late-successional forest-forming species in some places in western and in most of northern Norway. Norwegian mountain birch forests are extensive and contain much genetic and ecotypic variation (Wielgolaski et al. 2001).

Parts of the mountain birch forests are rich in nutrients and can have a high diversity of flowering plants, bryophytes, lichens, insects, and birds. Commercial use is largely for firewood, and only a few local sawmills trade in birch products in Norway today. Accordingly, there is little active planting and management of birch, except for removing birch from spruce or pine plantations where it may compete with seedlings or saplings of these commercially more important tree species.

2.3.5.4 Rowan, aspen, and willows

Collectively, rowan (*Sorbus*), aspen (*Populus*), and willows (*Salix*) are important for both herbivores and mutualists such as pollinating insects.

Rowans are mostly small deciduous trees in the genus *Sorbus*. Their small red fruits are important food for some birds and Lepidoptera, and the seeds are dispersed by birds such as thrushes. *Sorbus aucuparia* occurs from the south coast all the way to Vardø in Arctic Norway. Numerous hybrids between rowans and related *Sorbus* species reproduce asexually and thus act as true species that are endemic to Norway (NIBIO, 2022).

Aspens are resistant to drought and to cold and can reproduce clonally through offshoots. Recent research, however, has found such "clonal" aspen stands to often have a mix of genetically different individuals from seeds intermixing. Seeds are wind-transported and germinate soon after landing as they do not survive to make seed banks. Aspens grow best where there are good light conditions, and they can compete with spruce on favorable sites. Both old and young aspen stands are associated with a high diversity of red listed species in Norway, especially beetles, snails, and earthworms; this is in part due to the high pH associated with aspen debris. Recruitment of aspens seems to be particularly vulnerable to moose browsing (NIBIO, 2022).

Willows are common and an important source of food for browsers, particularly in arctic and alpine areas. Willows are hosts for many fungi, and they are also important for early-season insects because most species flower early. All willows are dioecious (each plant being either male or female) and as hybrids form frequently the exact species is often hard to determine. Seeds are transported by wind and, to some extent, by water. Willows exhibit flexible growth responses to environmental conditions, browsing, and management. Willows grow fast, some forming trees 20-30 m tall, others forming bushes or small trees, and are short-lived (NIBIO, 2022).

2.3.5.5 Understory vascular plants

The dominance of evergreen and deciduous ericaceous dwarf shrubs is a distinctive characteristic of boreal forests in Europe, in contrast to boreal forests in North America and parts of Siberia where taller deciduous shrubs often dominate the understory (Boonstra et al. 2016). Dwarf shrubs are woody perennials, typically only 25-50 cm in canopy height (c-Dombois and Ellenberg 1967). Their unique growth forms, physiology, ecology, and trophic interactions allow them to play dominant functional roles across several major biomes.

Dwarf shrub-dominated boreal forests cover >26% of the land area of mainland Norway (Bryn et al. 2018). Dwarf shrubs are often clonal and can form dense monocultures. While some are deciduous, the majority are evergreen with long-lived flat or needle-shaped leaves rich in phenolics (Díaz et al. 2016). Some dwarf shrubs exhibit allelopathic effects and can suppress seed recruitment of other species, including trees (Nilsson et al. 1993). The low, dense sward limits light penetration, air flow, and evapotranspiration, which decouples the ecosystem microclimate from the regional climate (Monson and Baldocchi 2014, Campbell and Norman 1998) and creates habitat for specialized ground layer and soil organisms. Many dominant dwarf shrub species, including *Vaccinium, Empetrum,* and *Calluna,* are in the Ericaceae and hence associated with ericoid mycorrhizal symbionts (see below).

The dwarf shrub understory influences the population dynamics of herbivores, such as vole, grouse, and many invertebrate herbivores (Boonstra et al. 2016). Bilberry (*Vaccinium* *myrtillus*, Norw. *blåbær*) and lingonberry (*Vaccinium vitis-idaea*, Norw. *tyttebær*) are important components of forest food webs as they interact throughout the year with a wide array of pollinators, frugivores, herbivores, and omnivores including humans (Lilleeng et al. 2021, Nilsson et al. 1993).

Other forest understory vascular plants include grasses, forbs and shrubs, which may have a role in forest biodiversity and trophic structure (e.g., by supporting insect communities) and may also have a role in successional processes (Halvorsen, 2016).

2.3.5.6 Bryophytes and lichens

A well-developed bryophyte layer is an important and characteristic feature of boreal forests, especially in oceanic regions like Norway (Økland 1996). Bryophytes (mosses and liverworts) play important functional roles and contribute to a substantial proportion of the total biomass production (Gundale et al. 2013; Lindo and Gonzalez 2010, Lindo et al. 2013). For example, bryophytes can account for more than half of the annual production of organic matter in some types of boreal forests (Kumar et al. 2018). Changes in bryophyte abundance and species composition in the understory vegetation thus have the potential to significantly affect the cycling and storage of both carbon and nitrogen.

Similarly, lichens are ubiquitous in the boreal forest and can cover substantial areas of forest soil, tree trunks, and stones. They play significant roles in biogeochemical and ecological processes, and offer resources to other species (Asplund and Wardle 2017). Lichen species associated with living or dead wood are sensitive to changes in microclimate, light conditions as well as density and connectivity of the host trees and consequently sensitive to both climate change and forest management (Gauslaa et al. 2008, Lie et al. 2009, Lommi et al. 2010, Belinchón et al. 2017, Ylisirniö and Hallikainen 2017, Klein et al. 2021).

A fundamental and functionally important difference between bryophytes and lichens compared with vascular plants (trees, shrubs, and herbs) is that the biological activity of bryophytes and lichens is *not* regulated by day length. Unlike higher plants, bryophytes and lichens grow actively even when light is available only for short periods and their growth is mainly limited by moisture and temperature (Demmig-Adams et al. 1990, Proctor 2000).

Boreal forest bryophytes and lichens are adapted to relatively cool climatic conditions, as indicated by their low temperature optimum for photosynthesis (Skre and Oechel 1981). Widespread and abundant forest bryophytes such as red-stemmed feathermoss (*Pleurozium schreberi*) and stairstep moss (*Hylocomium splendens*) can even have positive net carbon uptake at temperatures below 0° C (Stålfelt 1937). Many lichen species tolerate cold or drought stress better than plants (Asplund and Wardle 2017). Thus, the growth conditions for understory bryophytes and lichens can be near optimal in late autumn because of moist soil conditions and reduced shading by deciduous trees and other understory plants (Økland 1995).

2.3.5.7 Vertebrates

2.3.5.7.1 Birds

Birds comprise 70% of the vertebrate species in the boreal forest biome (Niemi et al. 1998, Grinde and Niemi 2016). Boreal bird assemblages undergo strong seasonal fluctuations, as many species that breed in the north migrate to spend the winter at southern latitudes. Many forest birds depend on trees as nesting sites, foraging substrates and shelter, and forest ecosystems with high structural and compositional diversity and complexity support particularly rich bird communities (Mikusiński et al. 2018). Species often associated with Norway spruce include coal tit (*Periparus ater*) and goldcrest (*Regulus regulus*), whereas species associated with Scots pine include the western capercaillie (*Tetrao urogallus*), parrot crossbill (*Loxia pytyopsittacus*) and common redstart (*Phoenicurus phoenicurus*). An admixture of deciduous trees in conifer-dominated forest increases bird diversity compared to pure conifer stands (Mikusiński et al. 2018). Aspen and rowan are key tree species; aspen being a preferred nesting tree for many cavity nesters, while rowan is the most important berry-producing tree. In boreal forests, woodpeckers play a key role as producers of cavities which are later used by a range of other bird species, mammals (e.g., bats) and insects (Remm and Lohmus 2011, Walsh et al. 2019). Seven of the nine European species of woodpeckers breed in Norway. Some bird species reach their highest densities in the mountain birch forest, such as red-throated bluethroat (*Luscinia svecica*) and willow grouse (*Lagopus lagopus*).

European forest birds include insectivores (80%), seed/nut eaters (37%), frugivores (32%), and carnivores (22%) (Mikusiński et al. 2018). Most of the common boreal forest species are facultative forest species which can breed in other types of habitats than proper forest. Of Europe’s 160 boreal bird species, 36 are considered forest specialists (Mikusiński et al. 2018). All the five resident European boreal forest specialists breed in Norway; Northern hawk owl (*Surnia ulula*), Siberian jay (*Perisoreus infaustus*), Siberian tit (*Poecile cinctus*), Pine grosbeak (*Pinicola enucleator*) and two-barred crossbill (*Loxia leucoptera*).

Due to habitat loss, fragmentation and internal changes in forest attributes, many forest bird species have suffered population declines, e.g., willow tit (*Poecile montanus*) (Stokke et al. 2021a) and three-toed woodpecker (*Picoides tridactylus*) (Stokke et al. 2021b). The negative effects have been particularly severe for species dependent on attributes such as dead wood, old trees, and structurally complex forests (Mikusiński et al. 2018).

2.3.5.7.2 Bats

All of the 11 bat species found in Norway are insectivorous, and all rely on forests for foraging, commuting, migrating, breeding, roosting, hibernating, social sites, or some combination of these (Dietz and Kiefer 2016). Forest bats are mobile and, like forest birds, typically need a large three-dimensional space to thrive (Law et al. 2016). Forest bats require roosting sites, typically in tree holes or cracks (Law et al. 2016). Most bat species change roosts frequently, and many roost sites are needed for the survival of a bat population (Law et al. 2016). Forest bats also need high-quality foraging habitats, drinking sites, and features that provide connectivity among landscape elements (Law et al. 2016). As predators that rely on insects and spiders, bats are good indicators of ecosystem change (Jones et al. 2009).

2.3.5.7.3 Rodents and lagomorphs

Rodents are mostly herbivorous and play a key role in forest food webs and population dynamics as consumers of understory plants and as prey to many species of predators (Boonstra et al. 2016). The cyclic "boom and bust" dynamics of small rodents in European boreal and alpine ecosystems lead to regular disturbances that have cascading effects on foodweb- and ecosystem dynamics. During cyclic peaks, browsing voles *(Myodes rufocanus, M. glareolus and M. rutilus*) reduce the abundance of dwarf shrubs (Ericson 1977), while bryovorous lemmings (*Lemmus lemmus* and *Myopus schisticolor*) reduce the cover of mosses (Anderson 1993, Rydgren et al. 2007). These pulsed disturbances of understory vegetation likely enhance nutrient recycling, productivity, and diversity (Ericson 1977). Specialized boreal rodent predators, such as some owl species (*Strix nebulosa*, *Aegolius funerus* and *Surnia ulula*) depend on regular high-amplitude, cyclic vole peaks to reproduce successfully (Björklund et al. 2020). Mountain hare (Norw: *hare*) *Lepus timidus* is an important herbivorous species in boreal forests (Pedersen and Pedersen, 2012). The Eurasian beaver *(Castor fiber* Linnaeus, 1758) is also an important ecological engineer that through dam building may kill trees and influence forests in river valley ecosystems (Zwolicki 2005).

2.3.5.7.4 Large herbivores

The large herbivores of Norwegian forest ecosystems are all ungulates such as moose (*Alces alces*), red deer (*Cervus elaphus)*, and European roe deer (*Capreolus capreolus*), of which moose and red deer play the largest ecological roles with large numbers and wide distributions, including partly seasonal migration. Roe deer is locally also very abundant. The non-native wild boar (*Sus scrofa*), which is an omnivore although plants make up most of its diet, has become increasingly frequent in Norway since the mid-2000's and is currently spreading from populations in Sweden and escape from captivity (farming) (VKM 2018).

Large herbivores affect the composition of the forest understory by removing woody biomass and by dispersing seeds, and regulate succession by feeding on shoots, bark of mainly young trees, but also seedlings and juveniles affecting recruitment and successional patterns (Lilleeng et al. 2016). Dense populations may often hamper the rejuvenation of pine, rowan, aspen, and willow (Hegland et al. 2021), but as many other biotic disturbances they may also increase understorey plant diversity and create winners (forbs, grasses and bryophytes) and losers (woody species; Hegland et al. 2013; Hegland and Rydgren 2016). They are also important prey or carrion resources for many vertebrate predators and scavengers, and for decomposing invertebrates (Ståhlberg et al. 2020).

2.3.5.7.5 Mammalian predators

Large mammalian top predators in Norwegian forests include brown bear (*Ursus arctos*), wolf (*Canis lupus* Linnaeus, 1758), wolverine (*Gulo gulo*), and lynx (*Lynx lynx*). In addition, the red fox (*Vulpes vulpes*) is the most common mid-sized predator, while small mustelids (*Martes martes* and *Mustela erminea, M. nivalis, M. putorius*) form a functionally important guild of small predators (Boonstra et al. 2016). All mammalian predators in boreal forests have large natural geographical distributions, though the wolverine is considered a northern distributed species while red fox and lynx are considered southern species (Elmhagen et al. 2015).

Large predators in Norway are managed according to population targets determined by the Norwegian Parliament, which keep population sizes low and limit the species' geographic ranges (Stortinget; https://lovdata.no/dokument/SF/forskrift/2005-03-18-242)

2.3.5.8 Insects

2.3.5.8.1 Pollinating insects

Many pollinators, including those found in open and agricultural habitats, have parts of their life cycles in forests whether it be for nesting, foraging, or overwintering. The most prominent and functionally important group of pollinators in boreal regions are bees and hoverflies, with moths, flies and others also playing important roles (Kevan et al. 1993, Devoto et al. 2011, Rodriguez and Kouki 2015). Of the bumblebee species, about ten can be regarded as common and frequently occurring in forests (Ødegaard et al. 2019).

2.3.5.8.2 Saproxylic insects

Saproxylic insects form a species-rich and functionally important group of species that share a dependence on dead wood with saprotrophic fungi. In natural forests, they make up a large proportion of the insect fauna (Stokland et al. 2012). Together with saprotrophic fungi, saproxylic insects contribute to the wood decomposition process and also play important roles as vectors for wood-decomposer fungi. Like saprotrophic fungi, many saproxylic insects are highly sensitive to forest management; many species depend on specific decay stages or tree species and are less frequently present in intensively managed forests (Jokela et al.

2019, Jacobsen et al. 2020). Many boreal saproxylic insect and fungi species show a clear preference for a single tree species (Burner et al. 2021, Nordén et al. 2013). The degree of dependence of saproxylic insects on high connectivity between suitable forest habitats is debated (Ranius et al. 2019), but there is evidence for increasing habitat aggregation being associated with a greater number of saproxylic species of conservation concern per dead wood unit (Schiegg 2016, Nordén et al. 2013, Burner et al. 2021).

2.3.5.9 Fungi, saprotrophs, and mycorrhiza

Fungi are the major decomposers (saprotrophs) of dead organic matter in forest ecosystems, and hence play key roles in releasing carbon back to the atmosphere (Stokland et al. 2012). Saprotrophic fungi have evolved a variety of enzymes and non-enzymatic systems for decomposition of plant cell-wall polymers such as cellulose, hemicellulose, and lignin. These complex molecules make up most of the biomass in forest ecosystems and, hence, the rate at which they are decomposed by saprotrophic fungi is of utmost importance for carbon dynamics in forest systems, as well as for the global carbon cycle (Clemmensen et al. 2015). Many saprotrophic fungi depend on the presence of dead wood. Since the abundance of dead wood, especially large and old dead wood units, is considerably lower in managed compared to natural forests (Jonsson and Siitonen 2012a,b, Jokela et al. 2019), many saprotrophic fungi are considered threatened (Artsdatabanken 2021).

Most plants, in forests and elsewhere, live in symbiosis with mycorrhizal fungi. Three major mycorrhizal types are associated with plants. Most of the trees in Norwegian forests form an ectomycorrhizal symbiosis: spruce, pine, downy birch, oaks, alders, alpine willow, and quaking aspen. Ericoid plants, like bilberry and lingonberry, form ericoid mycorrhizae, while most other plants form arbuscular mycorrhizae. The three mycorrhizal symbioses differ in their biological attributes and ecosystem functions, but they all absorb nutrients from the soil (most importantly, nitrogen and phosphorus) and exchange these for carbon compounds derived from their host plants (Smith and Read 2008). Mycorrhizal symbiosis is especially important in nutrient poor ecosystems, where a high proportion of the nitrogen comes to plants via the mycorrhizal partner. Mycorrhizal fungi, in particular some ericoid and ectomycorrhizal fungi, can also obtain organically bound nutrients from dead plant litter, and thereby contribute to the decomposition of soil organic matter and release of carbon (Lindahl and Tunlid 2015). Dead fungal mycelia contribute to build up forest soils 'from beneath' (Clemmensen et al. 2013), and different types of mycelia have varying retention time in the soil, which is of importance for carbon turnover rates and carbon sequestration (Fernandez et al. 2016). Especially the dark melanized fungal mycelia seem to have a longer retention time in the soil (Fernandez et al. 2016), which may contribute to the build-up of high and resilient carbon stocks in forest soils (Fernandez and Koide 2014, Clemmensen et al. 2015, Martino et al. 2018, Van-Geel et al. 2020).

As fungi rely primarily on passive airborne dispersal to reach new resources (such as dead wood), density of suitable habitats and distances between them (connectivity) is of importance. Rare and specialized wood-decomposer fungi are dispersal limited at the scale of tens to hundreds of meters (Edman et al. 2004, Norros et al. 2012, Moor et al. 2021). Red-listed wood-decomposer fungi are seldom found in forests with less than 20-30 m^3 ha^{-1} of dead wood (Junninen and Komonen 2011), which typically are set-asides in the contemporary boreal forest landscapes (Storaunet and Rolstad 2015, Jonsson et al. 2016). The likelihood of occurrence of red-listed wood-decomposer fungi increases strongly with forest age after the trees have reached maturity (Nordén et al. 2018, Moor et al. 2021). Most red-listed species prefer closed-canopy conditions (Nordén et al. 2013), likely due to the moist microclimate and the buffering impact of the canopy on temperature and moisture extremes. Long-distance dispersal events seem rare (Peay et al. 2012, Golan and Pringle 2017, Abrego et al. 2020), especially for species with thin-walled or hyaline spores (the majority of boreal wood-decomposer fungi) that lose viability when exposed to ultraviolet light during dispersal (Norros et al. 2015). This is in contrast to species with thick-walled or dark spores, such as many pathogens, that may more readily disperse over large distances (Brown and Hovmøller 2002). When long-distance dispersal events do take place, they are potentially influential both for maintenance of genetic variation in the population (Bohrer et al. 2005) and spread of diseases.

2.3.6 Native and alien pests and pathogens

2.3.6.1 Native and alien insects that kill or defoliate trees

Outbreaks of insects and fungal pathogens continually shape forest landscapes, creating environmental heterogeneity and impacting ecosystem services. Only a few forest insects and forest pathogens are potential drivers of ecosystem dynamics, but these contribute significantly to biotic disturbances and can have major consequences for intensely managed, semi-natural or natural boreal forests.

Globally, the most important insects in boreal forests in a climate change context are eruptive wood borers and defoliators. In Norway, the most important eruptive insects are the spruce-killing bark beetle *Ips typographus* (Økland et al. 2011, Marini et al. 2017) and the geometrid moths *Epirrita autumnata* and *Operopthera brumata* that jointly defoliate birches (Jepsen et al. 2013). A second bark beetle species, *Ips acuminatus*, is not currently important in this context in Norway but has become an important source of pine tree mortality elsewhere in Europe in recent years (Liska et al. 2021).

Tree-killing bark beetles are recognized as keystone species due to their strong and multifarious effects on ecosystem dynamics (Martinson et al. 2013, Samonil et al. 2020). Bark beetles are also the most economically important forest insects in boreal forests worldwide (Biedermann et al. 2019). The European spruce bark beetle normally colonizes recently killed, dying, or stressed trees. In late spring, overwintering adults emerge and seek out fresh host material. Males find suitable hosts and release pheromones that attract both females and other males, and consequently trees are often densely colonized. Females tunnel just under the bark, laying eggs as they progress, while males block the tunnel entrance. During summer, larvae feed in the inner bark, then pupate in the fall and overwinter as young adults.

Outbreaks of tree-killing conifer bark beetles directly affect forest structure and the animal and fungal communities associated with dead wood. They can also have major indirect impacts on the geomorphology of temperate and boreal forests, since mass mortality in low-diversity conifer forests can affect soil formation and soil structure, hillslope erosion and hydrology (Simonii et al. 2020). Several large outbreaks of *Ips typographus* were recorded in the 1900s; the most recent outbreak in Norway (1971-1981) killed millions of spruce trees (Bakke 1989).

While bark beetle eruptions are unpredictable in timing and extent, the autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) exhibit population cycles with peaks (outbreaks) approximately every 10 years (Jepsen et al. 2016, Vindstad et al. 2018). The intensity of the outbreaks varies in time and space and can impact mountain birch and shrubs over large areas. Defoliated trees and shrubs are weakened and sometimes killed. Defoliation results in a sudden release of nutrients to the soil via frass from moth larvae feeding on leaves, and produces an abrupt increase in the amount of light reaching the ground; these changes have major impacts on both flora (the understory community) and fauna (rodents, ptarmigan, and ungulates) (Jepsen et al. 2013, Henden et al. 2020). An extensive outbreak of geometrid moths in northern Fennoscandia during 2002-2008 was estimated to have impacted an area of 10 000 km^2 based on remote sensing (Jepsen et al. 2009).

The pine weevil (*Hylobius abietis*) kills on average at least 9% of young spruce planted on clear-cuts in Norway (Hanssen and Fløistad 2018) and is an important limitation of biomass production in commercial forest ecosystems if dead plants are not replaced. Pine weevils breed in the roots of stumps on clear-cuts, and emerging insects feed on the stem of newly planted seedlings. However, the extent to which the pine weevil limits production in natural ecosystems is little studied.

The native European pine sawfly, *Neodiprion sertifer* (Geoffroy), is a primitive wasp the larvae of which feed in small groups on pine needles. The natural history and ecology are reviewed by Virtanen et al. (1996) and Kollberg et al. (2015). The sawfly is a major defoliator of pine in Northern Europe, and mass occurrences are seen locally almost every year in Fennoscandia. When they occur in large outbreaks, they can defoliate large numbers of pines regionally. Their feeding activity does not usually kill trees, but outbreaks affect primary production, carbon budgets, and nutrient cycling. Eggs are laid in clusters on pine needles in the fall; larvae hatch in the spring and feed gregariously on needles. The main natural enemies of larvae are various invertebrate predators and parasitoids, but a viral disease also can be important in regulating populations (Bird and Whalen 1953). Pupation is on the ground, where small mammals are the main predators, and it has been suggested that small mammals regulate sawfly populations at low densities (Kuoki et al. 1998). The sawflies overwinter as eggs inside needles, where they are vulnerable to low temperatures: the critical value for egg mortality is -36 ^{o}C.

Several beetles are potentially important alien invasive species for Norwegian forests. The genus *Agrilus* in the jewel beetle family Buprestidae includes some species native to other parts of the world that can easily be transported to new regions in wood materials or wood chips (Flø et al. 2015). Larvae feed in the inner bark of live host trees, and their long, meandering tunnels cut through the host's conducting tissues. If larval density is high enough their feeding can severely weaken or kill their host trees. Of particular concern is *Agrilus planipennis* Fairmaire, the emerald ash borer, which is decimating ash populations in much of North America (Sobek-Swant et al. 2012, DeSantis et al. 2013, Flø et al. 2015). This species was introduced to Moscow sometime before 2008, and has spread to 18 Russian provinces as well as to Ukraine (Volkovitsh et al. 2021). It attacks both native European ash (*Fraxinus excelsior)* and planted trees of the North American species green ash (*F. pennsylvanica*). The infestation in Moscow has led to the mass decline of several thousand European ash trees.

The Asian long-horned beetle *Anoplophora glabripennis* (Motschulsky) (Cerambycidae) is native to eastern China and Korea, where it is of no economic consequence. Outside of its native range, it is listed among the 100 worst invasive species in the world (Lowe et al. 2004). Similar to *Agrilus* species, the Asian long-horned beetle can damage and kill trees in many of the broadleaf tree genera found in Norway (Hu et al. 2009). First detected in 2001, this species is now found in at least nine European countries; it was found in Finland (near Helsinki) in 2015, but successfully eradicated (EPPO reporting 2021). Though it is currently only a pest of urban and plantation trees: the concern is that it could begin to attack hosts in natural forests (Javal et al. 2017).

Vector-borne diseases associated with forest environments in Norway include tick-borne diseases like babesiosis (the first human case of *Babesia divergens* in Norway being described in 2007 - Mørch et al. 2015), lyme disease (Borrelia sp. infection), anaplasmosis (Analasma sp. infection), Tularemia (see below), tick-borne encephalitis (TBE virus infection). Of the 13 tick species so far observed in Norway, the sheep tick (*Ixodes ricinus*), is by far the most common. They need a set of hosts (often moose, roe deer, red deer, foxes or domestic animals), as well as smaller hosts (mice, lizards, birds), suitable vegetation and ground conditions, moisture and temperature. Thus they are often associated with forests and pasturelands with some developed vegetation. Especially deciduous forest litter seems to provide good habitat for between-host tick phases (Vanwambeke et al. 2016).

2.3.6.2 Native and alien pathogens that can kill trees

Many fungal pathogens colonize forest plants. Some may kill their host plants (necrotrophic fungi), whereas others live within living plant tissue (biotrophs) some of which are classified as pathogens and others having little negative impact on the host plant, althouh they may reduce the plant host's photosynthetic activity and hence, the level of fixation of carbon from the atmosphere.

The most infamous fungal pathogens in boreal forests are the root pathogens in the genus *Heterobasidion* (Venäläinen et al. 2020). Two species are present in Fennoscandia: *Heterobasidion annosum* (Norw. *fururotkjuke*) which primarily attacks pines, and *H. parviporum* (Norw. *granrotkjuke*) which primarily attacks spruces, and which infects a high proportion (about 25%) of *Picea abies* trees in Norway (Solheim 2013). These species colonize living trees of their respective hosts via wounds or freshly cut stumps, from which mycelia grow and spread vegetatively via tangled interconnected root systems and can infect uninjured neighboring trees (Gonthier 2019). *Heterobasidion* species cause extensive decay in the center of tree trunks (in the heartwood); the decay weakens trees, reduces tree growth, and lowers the value of wood products (Felton et al. 2020). In data compiled from over 45,000 Norway spruce trees felled from 1983 to 2001, an average of 25% of mature individuals were found to be infected by root rot (Thor et al. 2005). *Heterobasidion* root-rot is considered of minor importance in more natural forest ecosystems (Nordén et al. 2018); the fungus is especially destructive in managed forest monocultures, and high levels of disease have been reported in some mixed or regenerating forests (Gonthier 2019).

A mortality factor of possibly increasing importance for the three native *Ulmus* species in northern Europe is the vascular wilt disease caused by the fungal pathogens *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, collectively referred to as Dutch elm disease. Dutch elm disease has killed billions of elm trees worldwide including over 90% of elms in Europe (Martin et al. 2010, Menkis et al. 2015) and hundreds of millions in North America (Brasier 2001) and European Russia (Jürisoo et al. 2021a), altering both natural, agricultural, and urban landscapes. Dutch elm disease has killed elms in northern Europe for over a century (Jürisoo et al. 2021a). Here, the fungi are spread mainly by four species of *Scolytus* bark beetles (Jürisoo et al. 2021a). In Norway, the disease is vectored primarily by the native elm bark beetle *Scolytus laevis*.

European ash is threatened throughout its range by an invasive ascomycete fungus, *Hymenoscyphus fraxineus,* the causal agent of ash dieback (Gross et al. 2014, Ghelardini et al. 2016). European ashes show little resistance to this pathogen, which has spread from

Asia (Ghelardini et al. 2016). The fungus causes cankers and kills shoots, gradually leading to tree death. The disease is already extensive in Norway, with >80% of young trees and >40% of intermediate-aged trees in southeast Norway being affected by 2016, with a similar trend in the more recently infected ashes of western Norway (Timmermann et al. 2017).

Oomycota, or water molds, include several highly virulent invasive alien tree pathogens in the genus *Phytophthora* that are spreading globally and could significantly impact broadleaf forests in Northern Europe in the near future (Stenlid and Oliva 2016, Strømeng et al. 2016, Pettersson et al. 2020). Most species cause root, root collar or stem necrosis on susceptible hosts, leading to wilting, defoliation, and plant death.

A two-year survey of soil samples associated with plants imported from European countries detected 19 species of *Phytophthora* (Talgø et al. 2019, Pettersson et al. 2020). Many were already known to infect landscaping plants or plants in nature; only *P. alni* and *P. cambivora* are known to have damaged a significant number of trees in Norwegian forests (Strømeng et al. 2016).

Phytophthora alni (also referred to as *P.* x *alni*), the causal organism of alder decline, arose as a hybrid between a hybrid species of unknown origin and an alien species, and hence is considered an invasive alien species in Europe (Marçais 2021). It has been spreading since the 1990s and is currently found throughout Europe (Aguayo et al. 2014). Mortality of grey alders (*Alnus incana* (L.) Moench) due to this species has been widely reported from eastern Norway, particularly along the banks of the Glomma River (Strømeng et al. 2016). In the study from Glomma, both the alder specialist *P. alni* and the more generalized species *P. cambivora* were isolated from infected *Alnus* spp*.* Though most of the observations were of infected or killed trees of grey alder, they caution that black alder (*A. glutinosa*) is also vulnerable to both *Phytophthora* species in Norway. The host generalist *P. cambivora* was also found infecting European beech.

Phytophthora cinnamomi is currently not an important pathogen in Northern Europe, though it has been the driver of massive diebacks of *Quercus*, *Castanea, Eucalyptus* and other genera worldwide (Stenlid and Oliva 2016, Strømeng et al. 2016, Serrano et al. 2021). This species has been found in greenhouses, at garden plant sellers, and in a bilberry field, but apparently has not yet been recorded from natural forests (Pettersson et al. 2020). This species is of particular concern as it has been recorded from over 900 host plants and is on the IUCN list of 100 of the world's worst invasive species.

2.4 Recent assessments of climate impacts on the ecological conditions of Norwegian boreal forests

This section provides a brief overview of the most central previous assessments of the consequences of climate change on Norwegian forests.

2.4.1 Framstad et al. (2006): Effekter av klimaendringer på økosystem og biologisk mangfold

In 2005, the Norwegian Directorate for Nature Management initiated a project aimed at summarizing existing knowledge about the ecological consequences of climate change on Norwegian nature. The purpose of the project was to facilitate the inclusion of climate change effects in future Norwegian nature management. Project findings were reported in Framstad et al. (2006), which compiled existing knowledge regarding the effects of climate change on species, ecosystems, and the main land-cover types in Norway. The report also provided an updated overview of climate projections for Norway, including regional differences in temperature, precipitation, and wind. The report was based to a large extent on material provided voluntarily by Norwegian research groups and as such was not a comprehensive review of relevant climate change research. Regarding the impact of climate change on Norwegian forests, Framstad et al.'s (2006) overall conclusion was that although climate change will impact forest ecosystems in a number of ways by affecting a range of ecological processes as well as the distribution and abundance of plants and animals, the current evidence suggested that climate change was unlikely to fundamentally alter most Norwegian forest ecosystems. For further details, see Framstad et al. (2006).

2.4.2 Forsgren et al. (2015): Klimaendringenes påvirkning på naturmangfoldet i Norge and Aarrestad et al. (2015): Naturtyper i klimatilpasningsarbeid. Effekter av klimaendringer og klimatilpasningsarbeid på naturmangfold og økosystemtjenester

In 2015, the Norwegian Institute for Nature Research (NINA) and the Norwegian Institute for Water Research (NIVA) provided updated assessments of the ecological consequences of climate change on Norwegian nature on behalf of the Norwegian Environment Agency. Findings were reported in Forsgren et al. (2015) and Aarrestad et al. (2015) which compiled existing knowledge on the effects of climate change on species, ecosystems, and land-cover types as well as an updated overview of climate projections for Norway. The reports were not comprehensive literature reviews of relevant climate change research, but rather syntheses aimed at covering the breadth of the topic with examples from Norwegian nature. Regarding the impact of climate change on Norwegian forests, Forsgren et al. (2015) and Aarrestad et al. (2015) reported that:

- Increased mean temperature and extended growing season are expected to contribute to an increase in total forested area due to both increased forest growth as well as up-slope and northward movement of the treeline.
- Increased temperature could lead to increased drought-related stress, increased frequency and intensity of insect and fungus attacks, as well as increased frost damage if the onset of bud burst advances so as to begin before last winter frost.
- The interplay between increased climate-induced forest mortality and drought could lead to an increased risk of forest fires.
- Climate change could alter the species composition of vegetation types, but new regimes of interspecific competition are unlikely to alter forests to such a degree that they go extinct or change into other land-cover types.
- Climate-induced increase in total forested area could have a positive effect on the distribution of forest-dwelling birds.
- Climate change could lead to increased regional differences in overwintering conditions for forest-dwelling mammals.
- Climate change will impact most ecosystem services provided by forests, either positively (no examples in the report, but a prolonged growing season is one example) or negatively (such as reduced regulation of runoff from catchments).
- Several forest types may be adversely impacted by climate change:
    - Alluvial forests may be severely impacted by increased precipitation. Increased precipitation will lead to increased waterflow and soil erosion in alluvial and riparian forests. Dependent on amount, increased precipitation can have positive or negative effects on the total area of alluvial forests.
    - Spruce forests and lichen-rich conifer forests could be severely impacted by increased temperature. Increased summer temperature in combination with increased precipitation could lead to reduced lichen ground cover in lichen-rich coniferous forests in central eastern Norway due to increased competition from vascular plants and mosses. Lichen-rich coniferous forest thus could change into other forest types that are more dominated by mosses, herbaceous plants, and grasses in the ground layer. However, more days of precipitation could benefit epiphytic lichens.
    - Deciduous forests dominated by elm and ash and northern boreal forests dominated by birch could be impacted by an increase in insect outbreaks and attacks by fungal pathogens. Such forests are not generally threatened by climate change as they are currently increasing their range and as such are regarded as climate winners.

For further details, see Forsgren et al. (2015) and Aarrestad et al. (2015).

2.4.3 Framstad et al. (2021): Vurdering av økologisk tilstand for skog i Norge i 2020

In 2020, the Norwegian Environmental Agency initiated a national assessment of the ecological condition of the Norwegian forest ecosystems. The assessment was undertaken by NINA, and is reported in full in Framstad et al. (2021) as well as in an abbreviated English version (Framstad et al. 2022). This was the first quantitative assessment of ecological condition of Norwegian forest ecosystems based on the Norwegian Ecological Condition Framework (Nybø et al. 2017), as operationalized in the Index-based ecological condition assessment framework (Jakobsson et al. 2021; see section 3.1.1). The assessment was based on a comparison of the current condition of boreal forests in Norway against a reference condition defined as an 'intact ecosystem' with minimal human impact (see 3.1.1). The comparison was made with respect to seven 'characteristics' that cover the structure, functions and productivity of ecosystems (Nybø et al. 2017). For each of these seven characteristics, data on one or more indicators that reflect the current condition of Norwegian forests were collated from national monitoring and other public data. These were assessed against data reflecting the reference condition, and a limit value for good ecological condition, both of which were defined based on empirical data from reference areas, theoretical expectations, or expert knowledge.

To enable comparison and combination of several indicators into one numerical estimate for each of the seven characteristics as well as an overall value for the ecosystem, the indicators are scaled to a common scale between 0 (very degraded ecosystem) and 1 (reference condition 'intact nature'), with the limit value for 'good ecological condition' set at 0.60, using non-linear rescaling of the indicator when necessary.

The assessment identified 13 indicators for which national empirical data were available, and for which reference conditions and limit values could be set. These reflected six of the seven characteristics for good ecological conditions. The indicator availability was limited by data availability from monitoring as well as knowledge of expected indicator values under the reference condition "intact ecosystem" (see their Table A and our section 4.2). The reliability of the conclusions was assessed using a broader set of supplementary indicators.

The conclusion of the assessment was that the ecological condition of Norwegian forests falls well below the limit for good ecological condition: the overall condition value is estimated at 0.42 (with 95% confidence interval 0.41-0.43) (Figure 8a), which is clearly lower than 0.6, the limit value for good ecological condition. The condition was estimated to be largely consistent across all of mainland Norway although the county Vestlandet in western Norway deviated somewhat negatively (0.37).

Six indicators contributed most strongly to the low overall condition value (scaled values in parentheses): large carnivores (0.05), coarse woody debris (0.04), dead wood total (0.13), rowan-aspen-goat willow (0,15), area without technical infrastructure (0.18) and biologically old forest (0.24). The nature index for forests (0.41, a biodiversity indicator) and bilberry cover (0.47) were also well below the limit value for good ecological condition. Other indicators have scaled values near or above this limit value (two-sided indicators with values for lower/upper limit value): NDVI (0.88/0.77), Ellenberg N (0.55/0.69), Ellenberg F (0,76/0.68), large cervids (0.71), and absence of alien species (1.00). There were no time series available for three of the indicators and only short time series for the other ten. Except for area without technical infrastructure, most indicators with time series show a slight increase over time. The short time series for supplementary variables vary between slight increases and slight decreases. Two of the supplementary variables, indices for top predators and decomposers, have such low levels that it indicates a substantial deviation from the reference condition.

The aggregated condition values for the ecosystem characteristics are below the limit value for good condition for the characteristics distribution of biomass between trophic levels (0.38), functionally important species and biophysical structures (0.34), landscape ecological patterns (0.21) and biological diversity (0.41). The condition values for primary production (0.70) and abiotic factors (0.64) are above the limit value. There were no indicators available for the characteristic functional composition within trophic levels.

Framstad et al. (2021, 2022) attributed each indicator to one or more global change drivers, and found that low scores for the majority of indicators and ecosystem characteristics can be linked to the profound anthropogenic transformation of the Norwegian forest, and especially factors related to industrial forestry, infrastructure, and hunting of large carnivores (Figure 8b, see also section 2.1.4). Seven of the indicators were associated with climate change, with a mean condition value of 0.67. Framstad et al. (2021, 2022) discussed how although climate impacts are as of yet modest, future climate change can potentially be of great importance for the ecological condition of forests due to up-slope movement of the treeline, increased tree growth, facilitation of immigration by alien species, and increased disturbance by extreme weather events and harmful organisms. Changes in temperature and growing season were hypothesized to be most important. As of 2021, Framstad et al. thus concluded that few observed changes in Norwegian forest ecosystems could yet be directly linked to climate change as the available indicators showed limited response to climate change. For further information, see Framstad et al. (2021).

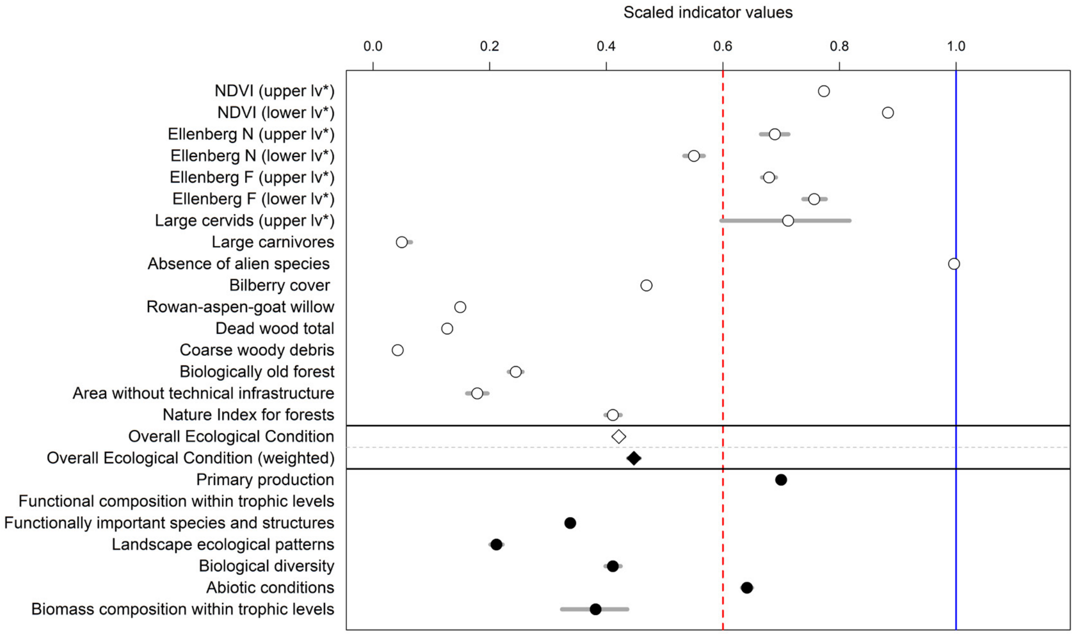


Figure 8a

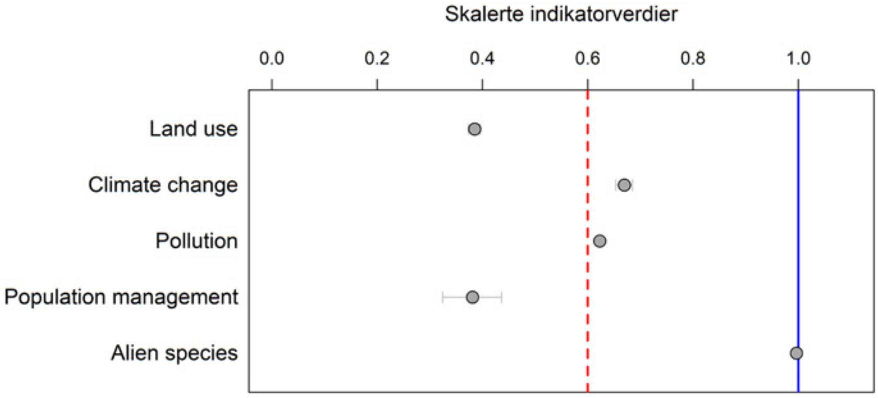


Figure 8b

Figure 8. Indicators and drivers of ecological condition of boreal forests of Norway, based on the IBECA method. Figure from Framstad et al. (2022). Panel (**a**) shows scaled ecological indicator values for 13 indicators of the seven ecosystem characteristics (white circles), the unweighted (white diamond, mean across all indicators) and weighted (black diamond, mean across the seven characteristics) summary value, and values for each of the seven characteristics for ecological condition (black circles). Panel (**b**) shows aggregated scaled values for forest indicators associated with main categories of anthropogenic drivers. The symbols show median values for indicators or average condition values, and grey and black bars show the 95% confidence intervals (some are

hidden by the symbols). The blue vertical line marks the reference value, and the red dotted line marks the limit value for good ecological condition.

2.5 IPCC Sixth Assessment report (2021-2022)

For an overview of how this report relates to the most recent round of reports from the IPCC, see section 7.

3 Materials and Methods

Overview: Here we describe the data and analyses performed to address the specific requests made in the ToR (Terms of Reference) given by the Norwegian Environment Agency. In section 3.1 we describe how we interpret and operationalize the ToR. In section 3.2, we describe how the relevant data and projections on climate changes and associated climate-related factors (as requested in the ToR) were selected and synthesized. In section 3.3, we first present our search of the literature for evidence of impacts of climate change and climate change related factors (as described in the ToR, see 3.1) on a large number of biotic and abiotic responses encapsulating the seven characteristics of ecological condition (see 3.1.1) as well as other aspects requested in the ToR (see 3.1.4-3.1.7). We then present our methods for synthesizing the knowledge gained from literature to specifically answer the ToR regarding the seven characteristics of ecological condition, as well as for biodiversity target 1 (3.3.2). Finally, we used the Norwegian red list data to assess climate change as a threat to biodiversity, addressing biodiversity target 2 (3.3.3).

3.1 Interpretation and operationalization of the ToR

The ToR and background provided for this assignment state the need for an updated assessment of climate effects on Norwegian forests, based on current national and international research and linked to the seven ecosystem characteristics for ecological condition, as defined in Nybø et al. (2017). Key Norwegian forest nature types should be included. The assessment should review how climate factors and projected climate changes (e.g., changes in temperature, precipitation, wind, extreme weather) and other factors that may be related to climate change (e.g., pests and diseases, and harmful alien species) are directly and indirectly expected to affect ecological conditions in Norwegian forest ecosystems. Information on different effects on key tree species, stand ages, habitats and regions should be clarified, if possible, with reference to endangered and near endangered habitat types or habitat types with central ecosystem functions. Biological and ecological threshold values should be identified if possible. VKM is requested to assess resilience, robustness, and vulnerability factors of importance for forest management and adaptation, including achieving national biodiversity target 1.1 'that the ecosystems should be in good condition' and target 1.2 'that no species and habitats should be eradicated and the development of endangered and near endangered species should be improved' (target 1.2), under projected climate change. Finally, the ToR requests a summary and prioritization of knowledge gaps.

Here we outline how we relate to key concepts in the ToR (as emphasized above). The climate modeling, literature searches, other data collection, and methods for synthesizing data and knowledge are described in section 3.2.

3.1.1 The Norwegian Ecological Condition Framework (NECF)

The ToR explicitly states that the report should assess how climate change affects the ecological condition of forests (i.e., National biodiversity target 1.1), using the Norwegian technical system for the assessment of good ecological condition (Nybø et al. 2017). This is an empirically-based ecological condition assessment framework, based around seven general ecosystem characteristics that together encapsulate key aspects of the ecosystem's diversity, structure, and functioning (for more detail, please see Nybø et al. 2017, Jakobsson et al. 2021):

- *Characteristic 1: Primary production [C1].* Primary production constitutes the total annual production of live plant biomass per unit area. The primary productivity varies within and between ecosystems depending on site- and system-specific constraints and processes such as climate, soils, disturbances, and biotic interactions, and it is important in that it controls the carbon and energy resources available for all other trophic levels.
- *Characteristic 2: Distribution of biomass across trophic levels [C2].* This characteristic describes how total ecosystem biomass is distributed among trophic levels including primary producers, decomposers, and different groups of consumers (herbivores, carnivores, etc.) in the food web. The trophic structure of ecosystems is governed by biotic and abiotic regulatory properties and trophic interactions: for example, relative rates of primary production and decomposition, and to what extent food webs are bottom-up or top-down controlled.
- *Characteristic 3: Functional composition within trophic levels [C3].* This characteristic describes the functional composition and variability within each trophic level of the ecosystem. Functional variability reflects variation in key traits, such as organismal size, life span, energy capture and consumption rates of species within the same trophic level. This variability is governed by abiotic and biotic conditions, and has

bearing on overall ecosystem functioning and dynamics, as well as on the response and robustness of the ecosystems to environmental change.

- *Characteristic 4: Functionally important species and biophysical structures [C4]*. This ecosystem characteristic focuses on species that are critical in maintaining functions and/or biophysical structures that are essential to the functioning and integrity of the ecosystem. This characteristic can encapsulate dominant species at different trophic levels, as well as less abundant species that maintain essential functions as keystone species or ecosystem engineers.
- *Characteristic 5: Landscape ecological patterns [C5].* This characteristic refers to the spatial distribution and dynamics of biota on landscapes. Landscape ecological patterns are affected by spatial structure and spatio-temporal biological processes including disturbance regimes, and they are key to the long-term survival of biota and spatial distribution of energy and resources.
- *Characteristic 6: Biological diversity [C6]*. This characteristic focuses on the diversity of species and genotypes in space and time. Biological diversity is linked to maintenance of ecosystem functioning, and resilience and robustness against external impacts.
- *Characteristic 7: Abiotic factors [7].* This ecosystem characteristic includes the chemical and physical state variables within an ecosystem that interact with biological processes and structures. Important abiotic ecosystem characteristics include cycling of carbon, water and nutrients, along with biophysical structures and states.

Based on these seven characteristics, the Norwegian Technical System for the Assessment of Good Ecological Condition characterizes "good ecological condition" as ecosystems that do not significantly deviate from a reference condition for each ecosystem, defined as "intact ecosystems" (sensu Nybø et al. 2019, see also Stoddard et al. 2006). "Intact ecosystems" in this context are defined as representing the natural or semi-natural biodiversity and ecosystem functioning of the ecosystem in question (e.g., a boreal forest type).

To be consistent with the national red list and alien species frameworks, and to avoid setting baselines that reflect a distant and unknown or unknowable past condition, "intact ecosystems" are defined such that

- species introduced before 1800 CE are regarded as native,
- climate conditions 1961-1990 form the fixed normal period (see 3.2.2), and
- modern intensive or large-scale human pressures are absent.

Note that this framework does not consider human impacts *per se* as precluding the ecosystem from being in good ecological condition, as long as the human impact type and intensity is at a magnitude below or comparable to that of natural processes or other organisms (Nybø et al. 2019). Management regimes can thus be present as one among many environmental drivers and processes within an otherwise naturally functioning ecosystem and are often seen as a historically integral part of the system. The system is related to ecosystems and habitats, but is not a classification system for landscapes. Instead, the system thus encompasses, and can be used to assess, semi-natural habitats, such as extensively managed grasslands, heathlands, and forests (Halvorsen et al. 2020).

Since the publication of the Norwegian Technical System for the Assessment of Good Ecological Condition framework, considerable effort has been invested in developing and communicating methodologies for quantifying and assessing ecological state and condition, based on available data from nature monitoring and other sources (Jakobsson et al. 2020, Jakobsson et al. 2021, Töpper et al. 2018, Framstad et al. 2021, Framstad et al. 2022, Jepsen et al. 2020, 2022, Pedersen et al. 2021, Jakobsson and Pedersen 2020). These empirical assessment approaches are important and valuable, but are also necessarily limited by the availability of data. Indeed, in their requests for these reports, the Norwegian Environment Agency explicitly constrained the methodological development to indicators and variables that are already part of 'existing or planned monitoring schemes', and that 'are or can soon be operationalized'. While a large body of relevant data and knowledge exists, as exemplified by the reports mentioned above and more generally by the Norwegian Nature Index (Jakobsson and Pedersen 2020, Pedersen et al. 2021), there is thus an inherent risk that important aspects of the impacts of climate change on ecological state and condition will not be captured by existing variables. Indeed, Nybø et al. (2017) pointed out that the lack of long-term, science-driven ecosystem-based monitoring in Norway represents a deficiency for making comprehensive ecosystem state assessments.

This report thus complements the previous empirically based and data-driven approaches, as the ToR explicitly requests an overview of the knowledge status about how the forests in Norway will develop in a changing climate. Unlike the efforts listed above, the ToR does not limit our assessment to only consider data or variables available from the 'existing or planned monitoring', as described above. This allows a broader and more open-ended assessment encapsulating all the existing evidence for climate change impacts on boreal forests, and thus may identify important impacts or responses beyond those covered by existing or upcoming monitoring schemes.

The ToR specifies that the assessment should focus on characteristics 3, 4, 5, and 6 if there is a need to delimit the assignment. However, primary production (no. 1) and trophic structure (no. 2) are intimately connected to other central terms, such as biodiversity, ecosystem services and robustness or vulnerability to the extent that we choose to include all seven characteristics in our assessment. Furthermore, abiotic factors (no. 7) are fundamental as they connect the abiotic climate to the biotic ecosystem. We therefore aim for a comprehensive assessment, covering all seven characteristics. We base the selection of functionally important groups and species in forests (characteristic 4) on our collective professional judgment, building on Nybø et al. (2017), and Framstad et al. (2021, 2022).

The assessment of climate change impacts on ecological condition in forests is based on literature searches to uncover the scientific knowledge on impacts of climate change on response variables reflecting the seven characteristics, as described in section 3.3. In conducting these literature searches, we took a broad and inclusive approach to try and capture as many as possible of the potentially relevant responses and climate relationships for each characteristic. We supplement the data with our own analyses where a minor effort could bridge a gap or serve as a quantitative illustration of a point. The resulting knowledge is presented in sections 4.2-4.5, and synthesized with respect to the ToR in section 5.1.

3.1.2 Relevant "Nature in Norway" (NiN) classes

The Nature in Norway (NiN) system is a set of concepts and tools for handling classification of natural variation on all scales. NiN is an implementation of the EcoSyst framework (Halvorsen et al. 2020). EcoSyst provides a framework for systematizing natural variation in a consistent manner across different levels of organization. In NiN, nature types with shared environmental characteristics are given an identical name and code.

The ToR requests an overview of knowledge status about climate change impacts on forests, specifically mentioning the nature types 'Forest' (T4 Fastmarksskogsmark) and riparian alluvial forest (T30 Flomskogsmark) from the NiN classification (Halvorsen et al. 2020). In addition to these two types, which cover the majority of the terrestrial forest area in Norway, the current version of NiN (NiN 2.0) also describes a strongly modified terrestrial type (T38 Forest plantation) and two wetland forest types (V8 Tidal and alluvial forest and V2 Mire and swamp forest). Forest in the NiN system is defined by the long-term presence of trees that, at maturity, make up a stand with tree crowns occupying more than 10% of the area. Trees are defined as woody plants more than 5 m tall or that may grow to heights of at least 5 m, or, under poor growth conditions, more than 2 m.

The forest (T4) major type in NiN comprises the full range of variation in forests below the alpine and arctic forest limits. Riparian forest (T30) includes riparian and periodically flooded, non-wetland forest on banks of rivers and lakes, impacted by water-mediated disturbance. Within T4 and T30, there is substantial ecological variation that is related to complex local environmental gradients (*q.v.*) that form the basis for defining minor types within each major type (Halvorsen et al. 2020). Boreal forests are known for their frequently moist understories often rich in peat mosses (*Sphagnum* species), meaning that moist T4 can have a significant element of wetland indicators, and the matrix of lakes, ponds, rivers, streams, bogs and mires form an integrated part of the biome.

NiN forest definitions also include clearcuts if they are replanted immediately or naturally regenerated. However, forest plantation (T38) includes land with tree monocultures intensively managed for production of wood, usually as either pure spruce or pine plantations. Plantations typically consist of dense, even-aged stands with understory vegetation cover that is substantially reduced. T38 plantations were not included in the ToR. However, the Norwegian Biodiversity Information Center notes a knowledge gap in separating T38 and T4, such as when an area is partially planted, or when aging plantations are gradually transitioning into heavily human-affected increasingly semi-natural forest (see Artsdatabanken.no, T38 Treplantasje). Considering the time range of the assessment (until year 2100), today's plantations will either have passed through a cycle of regeneration or in practice have aged out of this category by the end of the period if left relatively unmanaged. Most conclusions in this report will anyhow also be valid for plantations of spruce, pine and other naturally occurring species that form part of the forest matrix (see also Tomter and Dalen 2018, FAO 2018).

Intensive forest plantation management can include soil preparation, application of fertilizer and herbicides, and tree planting, and can comprise plantations of exotic tree species (such as Sitka spruce) or native species planted outside their natural range (such as Norway spruce planted in western Norway). As T38 was not included in the ToR we do not discuss particular aspects of such plantations. Other strongly altered areas that meet the forest definition in terms of tree crown density are characterized as 'woodland' and not included in forest types. In practice, this means orchards, parks, arboretums, and plantations of non-native species. Similarly, the report does not cover areas with an exceptionally short rotation, such as Christmas tree plantations: they mostly fall into other non-forest categories like T43 and are not part of this report.

Thus, we follow the National Forest Inventory, as well as Framstad et al. (2021), in including the wetland types, V2 and V8 in the cover of forest together with T4 and T30, and include climate impacts on T38 where they are not overridden by intensive management. This definition and delimitation of forest, including the treatment of clearcut areas, is also congruent with Norwegian National Forest Inventory (Tomter and Dalen 2018) and the UN Food and Agriculture Organization (FAO 2020).

The forest types listed in the ToR also include mapping units defined based on a combination of NiN types and other characteristics, such as dominant tree species (the definitions are available on the Environment Agency's web pages (Miljødirektoratet 2022).

The considerations regarding forest types described here form the basis for delimiting our literature searches (3.3), where we include species, forest types and other forest characteristics of relevance for forest types, and hence the data feeding into chapters 4 and 5.1. Further, these considerations also inform the discussions of impacts on specific forest types in chapter 5.3.

3.1.3 Climate factors and climate projections

The ToR requests assessment of impacts of a range of climate change related factors, listing factors such as temperature, precipitation, wind, and extreme weather, but implying assessment of other climate-related effects if deemed important. The ToR further specifies that the assessment should be based on climate projections from the Norwegian Center for Climate Services (NCCS) under different IPCC climate scenarios. The NCCS is a collaboration between the Norwegian Meteorological Institute, the Norwegian Water Resources and Energy Directorate, Uni Research (now part of NORCE) and the Bjerknes Centre for Climate Research (klimaservicesenter.no).

NCCS provides the latest official downscaling of global climate scenario projections for Norway based on results in the IPCC's fifth assessment report (IPCC 2014), and where possible updated to capture new information from the sixth assessment report (IPCC 2021). The climate projections used in the assessment are therefore to a large extent those presented in "Climate in Norway 2100" (Hanssen-Bauer et al. 2017) and other work published by NCCS. This work is based on the emission scenarios from the IPCC through downscaling (see 3.2) processes and climate run from 2007 until 2100, which is the end of the time horizon considered in this report.

The methods and specific climate projections chosen are described in detail in section 3.2 and the resulting climate change related variables are presented in section 4.1, and used as a basis for the answers to the ToR in Chapter 5.

3.1.4 Treatment of pests, diseases, and harmful alien species

The ToR requests that the assessment considers 'other factors that may be related to climate change' and specifically mentions pests and diseases and the establishment and spread of harmful alien species (see section 2.3.6 for a description of the importance and role of such species in boreal forests). We collated information on the climate responses of known native and alien pests and diseases in boreal forests. Note that alien plant species were not individually included in this assessment, as the number of potentially spreading plants from gardens (VKM 2021), roughage imports (VKM 2022), travel and trade is too large and no specific candidates of particular relevance stood out beyond those discussed as part of community and succession dynamics. The selected alien species were included in the literature searches described in section 3.3, are reported in section 4.2, and synthesized with respect to the ToR in section 5.2.

3.1.5 Specific effects for tree species, stand ages, habitats, and regions

The ToR requests that, when possible, the assessment should provide information on differences in the effects for different tree species, stand ages, and geographical regions, and that to the extent possible, an overall discussion should also be made on the significance of the expected effects for habitat types that are (near) endangered or that have central functions in forests (listed in their attachment 1).

Information on different tree species and stand ages was captured by our literature searches, which were designed to broadly capture all known impacts on the major tree species in boreal forests, including growth responses, demographic rates, and age- or size- or stand-specific responses (see section 3.3). This information is recorded in sections 4.2-4.5 and summarized in sections 5.1 and 5.3. We do not specifically search for differential impacts across geographical regions, but we do capture information on study location and specifically search for data on range dynamics, and this information is used in our summary and conclusions in section 5.1. We do not specifically search for climate related impacts on all threatened and near threatened habitat types, but any implications captured are synthesized with respect to the ToR in section 5.3 and the table of mapping system classifications attached to the ToR reproduced with result keywords in Appendix I.

3.1.6 Thresholds, resilience, robustness, and vulnerability

The ToR requests a summary of biological and ecological thresholds, and of factors that contribute to resilience, robustness or resistance, and vulnerability of forest ecosystems to climate change. Resilience, robustness /resistance, and vulnerability are related and sometimes used interchangeably, especially in popularized ecological literature. More precisely, resistance and robustness are often used to characterize the capacity of a system to withstand stresses and maintain its initial state. Resilience is often used to mean the size of a disturbance from which an ecosystem can recover (i.e., not shifting permanently to another state), and the rate at which it recovers (i.e., return time). Thresholds refer to non-linear responses to some effect on the system. We use this terminology to highlight that the vulnerability of an ecosystem to climate change is influenced both by its ability to recover from disturbance and by its ability to withstand pressures (Seidl et al. 2016).

Note that we did not specifically address the role of evolutionary or selective responses (including provenance studies) as these aspects were peripheral to the ToR and hence outside the scope of the current report.

Information on thresholds, resilience, robustness, and the associated vulnerability was captured by including terms reflecting these aspects in our literature searches (section 3.3). This information is included where relevant in sections 4.2-4.5, and summarized with respect to the ToR in 5.4.

3.1.7 *Forest management and adaptation*

The ToR mentions management and adaptation, but does not ask for an evaluation of how the climate effects will impact management strategies including forestry, as such assessments are a next step based on knowledge summaries. Our task is therefore to review *climate change* effects on forest ecosystems, not the effects of forestry. However, as nearly all Norwegian forests are or have been affected by human activity either historically, in recent times, or at present, it is necessary to both describe how this impact has affected, and interacted with, the forest ecosystems, as well as how some changes induced by humans interact with climate change. Resilience, robustness, and vulnerability (section 3.1.6) and differential effects of climate on tree species, stand ages, habitats, and regions (section 3.1.5) are affected by forest management, including forestry practices. Hence, we do take a broad approach and include information on forestry and the interaction with climate when relevant. Our approach is aligned with section 10 of the Norwegian Nature diversity act stating that "*any pressure on an ecosystem shall be assessed on the basis of the cumulative environmental effects on the ecosystem now or in the future*" (https://www.regjeringen.no/en/dokumenter/nature-diversity-act/id570549/).

Information on the role of forest management was captured by synthesizing the interactive effects of climate and forest management (section 4.7) knowledge and summarized with respect to the ToR in 5.5.

3.1.8 *National biodiversity targets*

The ToR requests an evaluation of how vulnerability of Norwegian forests to climate change will affect our ability to achieve national biodiversity targets 1.1 '*that the ecosystems should be in good condition*' and 1.2 '*that no species and habitats should be eradicated and the development of endangered and near endangered species should be improved*' under projected climate change. We approach the first biodiversity target via an overall assessment of the evidence that climate change (including the abiotic and biotic climate change related factors identified in the ToR) will impact ecological condition of boreal forests (i.e., a summary across the seven characteristics of ecological condition based on the assessment in section 5.1). We approach the second biodiversity target via summarizing information on the role of climate change in affecting red-listed species in forests in Norway, based on the database of the Norwegian Biodiversity Information Centre (NBIC) red list (Artsdatabanken 2021). We searched the NBIC 2021 red-list species database for species that are (i) red-listed (assessed as critically endangered, endangered, or vulnerable, or near threatened), (ii) categorized as associated with forest habitats, and (iii) for which climate change was identified as one of the 'primary threats'. This assessment is summarized in section 4.7, and the overall assessment vs. the biodiversity targets is summarized in section 5.6.

3.1.9 Knowledge gaps

Knowledge gaps were identified throughout the assessment (Chapter 4) and summarised as part of the knowledge synthesis (Chapter 5). Knowledge gaps are prioritised and discussed in section 6. The main approach for identifying knowledge gaps was by critically addressing models and propositions about the condition of Norwegian forests in the future, and what we would lack for building a conceptual systems model incorporating the processes we discuss.

3.2 Climate data and models for climate analysis and modeling

3.2.1 Scenario selection

Climate change in Norway is tightly connected to global climate change. We must thus make an explicit evaluation of what potential global developments we consider of relevance for this report. The consequences this has for climate and weather conditions in Norway will be discussed in Chapter 4.

As mentioned in Chapter 2, IPCC has operated with several scenario schemes through the years. Climate predictions for most scenarios correspond to current trends, and the outcomes of all currently used scenarios overlap statistically up to the present. Most scenarios also overlap until 2050, with a 1.5 °C increase in mean global temperature expected to be in effect by then. However, for the latter part of the century (2040 to 2100), the scenario family developed by the IPCC framework covers a wide range of possible developments, and we must choose what range of possible futures to focus on.

The NCCS (see 3.1.3 and below) and the most relevant report on Norwegian climate (i.e., Hanssen-Bauer et al. 2015) provide in-depth data only on three main greenhouse gas (GHG) concentration trajectories termed Representative Concentration Pathways (RCPs) established by the IPCC fifth assessment report (AR5): RCP2.6, RCP4.5, and RCP8.5. However, these three trajectories cover most of the range of what the IPCC considers plausible futures (Table 1).

The Norwegian white paper "Climate change adaptation in Norway" (Meld. St. 33, 2012-2013) states that, in accord with the precautionary principle, "the Norwegian government should develop risk assessments for climate change that are based upon the high climate projections". This rules out the strongest successful mitigation scenario (**RCP1.9).** Some data are available for **RCP2.6**, however, it falls for the precautionary principle as it is based on net GHG emissions plateauing before 2020 and starting to decline soon after. **RCP3.4** is a plausible scenario if GHG emissions decrease substantially beyond 2050 and concentrations fall. It is still disregarded here due to a combination of precautionary principle, lack of data and the fact that its range of uncertainty regarding climate outcomes is statistically indistinguishable from those of RCP4.5 and RCP8.5.

RCP4.5 (and SSP2-4.5) is described as an intermediate scenario where CO_2 emissions peak around 2040 and become negative (i.e., net C sequestration) with about 2 Gt CO_2 per year as emissions decline to roughly half of the 2050-levels by 2100. This scenario also requires that methane emissions stop increasing by 2050 and start declining, and that SO_2 emissions decline to approximately 20% of those of 1980-1990. Thus, RCP4.5 assumes effective emission control policies that seem attainable. As such, it forms the lower bound of climate warming we consider for the range of possible futures in our assessment.

The RCP8.5 (and SSP5-8.5) has been called both "business as usual" and "worst case scenario", albeit neither characteristic applies to its mean consensus estimate. On one hand, some studies suggest that the negative consequences from climate change to the global economy in itself would reduce emissions enough to avoid RCP8.5 (Woodard et al. 2019). On the other hand, the estimated climate impact of any emission scenario includes a wide margin of error. Feedback mechanisms where methane and carbon dioxide are released from soil, permafrost and oceans are not well represented in the emission scenarios and may counteract or exceed human efforts to reduce emissions (Steffen et al. 2018, Ritchie et al. 2021).

Table 1. Global mean temperature rise relative to 1981-1999 from the fifth IPCC report.

Scenario	**2046-2065** **Median [likely range]**	**2081-2100** **Median [likely range]**
RCP2.6	1.1 [0.5 , 1.7]	1.1 [0.4 , 1.8]
RCP4.5	1.5 [1.0 , 2.1]	1.9 [1.2 , 2.7]
RCP6.0	1.4 [0.9 , 1.9]	2.3 [1.5 , 3.2]
RCP8.5	2.1 [1.5 , 2.7]	3.8 [2.7 , 4.9]

Despite some recent progress towards emission reduction, RCP8.5 emissions remain in close agreement with net greenhouse gas accumulations (within 1%), and current and stated policies make RCP8.5 likely a good match for emission trajectories at least until mid-century (Schwalm et al. 2020). Some recent analyses argue that a middle ground scenario between RCP3.4 (not downscaled for Norway) and RCP8.5, seeing 2-3 degrees warming by 2100, is the most likely scenario (Pielke et al. 2022) based on energy sector projections. Others note a mismatch between pledges and investments in the main oil companies (Li et al. 2022). System inertia means substantial changes will occur based on past emissions (Samset et al. 2020) even in the event of meaningfully reduced greenhouse gas emissions (e.g., RCP4.5 or RCP2.6) and in absence of positive feedback loops.

A multidisciplinary approach based on the comparison of observed and expected spatial patterns of European forest response to climate change identified four Global Climate Models (GCMs) that are consistent with the observed trends (Bombi et al. 2017). These models were close to the highest range of the consensus intervals for each given RCP, suggesting that current predictions of the impacts of climate change on forest ecosystems could be underestimated. If accurate, this is worrisome as it suggests that even moderate climate scenarios will have stronger ecological effects on forests than otherwise expected (Bombi et al. 2017). Substantial GHG emission reductions are needed to diverge from the further RCP8.5 path between 2050 and 2100.

Thus, an example of a plausible "worst-case scenario" would be (1) greenhouse gas concentrations following an RCP8.5-like trajectory from a combination of insufficient emission control and known feedback effects, such as greenhouse gas release from permafrost, soil, and ocean, (2) the climate forcing effects of those greenhouse gas concentrations turning out to be in the high part of the confidence interval or (3) the ecological effects of a given level of warming being stronger than expected.

For these reasons, balancing pragmatism, caution and optimism, we focus on the outcome space between the median estimate of RCP4.5 and the median estimate of RCP8.5 (see

Figure 9 below), but remain mindful of the multiple sources of uncertainty connecting every step in the chain from emission trajectories to climate responses and ecological effects.

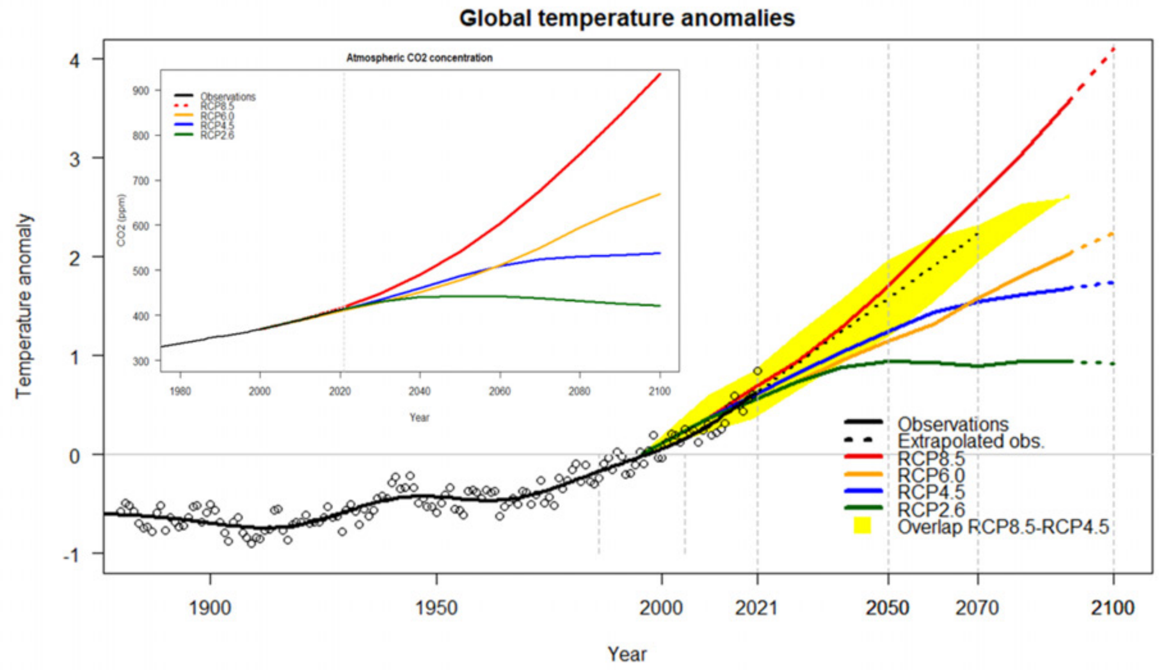


Figure 9. Simplified link between annual global temperature anomalies and emission pathways. Historical global temperature anomalies relative to an arbitrary reference period (1986-2005) shown as open circles (2021 data point being preliminary), together with a smoothing trend extrapolated as a dotted line to show current trend. Colored line shows different RCPs. As climate model ensemble predictions vary for each RCP, the area where 95% of model runs for RCP4.5 and RCP8.5 overlap is shown in yellow. We see that until 2070, a continuation of the current trend is about equally likely to happen for both of those emission scenarios. Only from 2070 towards the end of the scenario do predictions start to become statistically different. Inserted: CO_2 concentration pathways historically and for the different RCPs. Data from IPCC 2013 and NASA 2021.

The sixth Assessment Report (AR6) of 2021 replaces the RCPs with SSPs (Shared Socioeconomic Pathways) for a more integrative and flexible approach combining feedback between social and technological developments and climate forcing. However, as the AR6 is recent, datasets coupled to this new conceptual system and downscaled to Norway do not yet exist, and the NCCS data providing our downscaled climate projections as specified in the ToR are linked to specific RCP–type emission scenarios. Other relevant literature use RCPs for the same reason. We report mostly in terms of RCPs to avoid confusion except where we explicitly refer to IPCC AR6 material. For future comparisons, however, we note that RCP8.5

is a part of SSP5-8.5, and RCP4.5 a part of SSP2-4.5, and we try to integrate the pathway system of AR6 in discussions.

3.2.2 Climate data and projections

NCCS provides the latest official downscaling (see below) of global climate scenario projections for Norway based on results in the IPCC's fifth assessment report (IPCC 2014). The climate projections used in the assessment is therefore to a large extent those presented in "Climate in Norway 2100" (Hanssen-Bauer et al. 2015 and its English version Hanssen-Bauer et al. 2017), as well as following work published by The Norwegian Centre for Climate Services (NCCS). These works are based on the emission scenarios from the IPCC through downscaling processes and run from 2007 until the year 2100, which is taken as the end of the time horizon considered by this report. For a more in-depth description of historical climate variables, their interrelation with topography, and a detailed discussion of future projections for Norway, we refer to the Norwegian version in Hanssen-Bauer et al. (2015).

An important concept when using model ensembles is that the span between the simulations are not the same as statistical confidence intervals, even though these are often confused. Instead, it is common to report agreement intervals from many runs of each model, i.e. the span of projections containing a specific proportion of all simulation runs (often 80%). The median of all simulations are often presented as a simplified projection, but it is important to bear in mind that the span of simulations makes a "cone of plausibility" (often with 20% of model simulations even outside of that cone) surrounding the median projection. Where sufficient data are available, median, high, and low boundaries of these agreement intervals are therefore reported.

Real variation on the scale of years, months, and days, as well as potential climate effects on this variation, is a separate effect from the agreement interval of the projections, but adds to the absolute confidence limits we can set for extreme values we may observe at a specific point in the future.

From a risk assessment perspective, one should be mindful of the difference between regular statistical confidence intervals and the consensus or likely range of results from different model simulations. The range of agreement is not an expression of how much variation we expect to see around the mean value over time, the range over which most of the "future timelines" produced by different models are seen to fall. But we know that some of these models, these "future timelines" will be systematically more correct than others. We just don't know which ones yet. Temporal variations such as the difference between cold years and warm years or between warm weeks and cold weeks, comes on top of this. This is illustrated in Figure 27.

3.2.2.1 Downscaling

Downscaling of climate change models is the procedure of using large-scale models, usually global climate models (GCMs) to make high resolution regional climate models (RCMs) that take local processes and topography into account and produce results at finer scales better suited for local analysis and planning. As there are many somewhat different climate models whose abilities to predict the past are similar, a selection of several model simulations, a so-called model ensemble, is often used to obtain future predictions with less risk of introducing a hidden bias from relying on a single model. This is also a trade-off against regressing the results to the mean by averaging the predictions of the best-performing model together with less well performing ones.

The data from the NCCS are based on an ensemble of ten EURO-CORDEX GCM/RCM simulations, each representing the alternative emission pathways RCP4.5 and RCP8.5 to generate a set of projections for Norway by the NCCS contributors. The resulting datasets are bias-corrected and forced with a spatially distributed, gridded version of the commonly used HBV hydrology model to generate daily time series of different climate components covering the period 1971-2100. These high-resolution projections, despite their limitations, represent a valuable data source for different types of climate impact studies at a national and local scale (NVE 2016). A new updated downscaling for Norway is expected to be finalized by the NCCS in 2023.

3.2.2.2 Standard periods: a new normal

Climate data are often given as anomalies (differences) from a mean value. This mean value is based on so-called standard periods. However, the standard periods may vary. The World Meteorological Organization (WMO) and consequently the IPCC tend to update their standard periods every decade, using the most recent non-overlapping 30-year period as the standard. This means that at the end of 2020 the most common Meteorological standard period shifted from being 1981-2010 to be 1991-2020. However, climatologists who want an unmoving reference point often use a fixed historical standard period. Many (but far from all) use the 1961-1990 period recommended by the WMO, but as the periods starts before most satellite data sets start, the European Copernicus Climate Change Service (C3S), which is a main data source for the Norwegian NCCS, has announced that they will keep the 1991-2020 as the historical normal climate period. The NCEF framework has on their side decided to keep the 1961-1990 standard period fixed for the evaluation of ecological conditions in Norway.

Hanssen-Bauer et al. (2015) and some other sources, however, use a 1971-2000 normal period. When not specifying otherwise, the NCCS follows the WMO and has adopted the new climate normal 1991-2020 from 2021 (which for now also is the same as the fixed period used by the C3S). This new normal differs by +1ºC from the previous (1961-1990) for

Norway. Thus, positive climate anomalies calculated using the new normal will seem one degree lower than previous estimates. Similar effects apply for precipitation and other climate parameters. As most of the available data and literature at the time of writing was made prior to 2021, we report anomalies from the 1961-1990 standard periods unless otherwise noted.

3.2.3 Projected climate zones

In addition to the climate data mentioned above, we also make use of a set of Köppen climate zone projection estimates published as global 1 x 1 km resolution data (Beck et al. 2018; Cui et al. 2021). This dataset consists of projections of the Köppen climate classifications (see section 2.1.1 and Figure 1) from a baseline period of 1980-2016 to their expected states in 2071-2100 under RCP8.5 with 0.0083° spatial resolution (approximately 1 km at the equator). It maximizes accuracy in map classifications by combining temperature and precipitation data from multiple independent sources, including WorldClim V1 and V2, CHELSA V1.2, and CHPclim V1. It then combines climate change projections from 32 Coupled Model Intercomparison Project phase 5 (CMIP5) models to map future (2071-2100) climate classes at the same spatial resolution (Beck et al. 2018). These climate zones provide no direct mechanism and only capture the broad strokes of different vegetation ensembles. However, they are useful for ecological overview and classification because they summarize the observed associations of multiple climate indices that are associated with large-scale vegetation and ecosystem patterns. They thus compliment the NCCS data by summarizing and translating the various future climate indices to show what climate zones they correspond to in today’s system.

3.3 Literature review and knowledge synthesis

3.3.1 Literature search, selection, and summary

A structured literature search was carried out to find an unbiased selection of scientific literature relevant to the topic. Search terms were gathered from relevant publications, existing search strategies, and the working group’s expert knowledge. They were then combined into a string with Boolean operators and refined through testing. The full search strategy is documented in Appendix I.

The search string was used to find publications in two index databases with wide coverage of ecological literature: The Web of Science Core Collection (ISI Clarivate; consisting of the Science Expanded, Social Sciences, Arts and Humanities and Emerging Sources citation indices) and Biological Abstracts (also via the Web of Science platform). The search strategy was focused on the most relevant works by limiting geographically and by publication type.

The aim was to include all relevant publications concerning forests or trees in northern Europe and European Russia and specific tree species or forest types in parts of central and eastern Europe. Only review articles for boreal forests or specific tree species were included from the rest of the world. The resulting literature thus included primary studies and reviews from areas geographically close to Norway, and reviews from other regions of the world.

Due to the breadth of the topic, a substantial amount of literature was found (ca. 18,000 publications), including reviews already summarizing the impacts of various climatological factors. In such situations, carrying out a "review of reviews" can enable a review to cover many aspects of a wide topic while still being manageable. Therefore, the original set of results was retained and used as a supplementary reference library, but only reviews were carried forward to screening (1,432 reviews from the original 18,223 total publications). After title and abstract screening, 523 of these reviews were identified as relevant. These reviews were used as the primary literature foundation of Chapter 4. The reviews were supplemented with additional publications identified based on the panel's expert knowledge of the topic, addressing questions as they arose through targeted searches of the main scientific databases (Scopus, Web of Science, and Google Scholar). Further details on the found reviews and literature is available on request to the authors.

A grey literature search was also carried out to find reports from several institutions: the Norwegian Institute for Nature Research (NINA), Norwegian Institute of Bioeconomy Research (NIBIO) and Center for International Climate and Environmental Research (CICERO) in Norway; the Swedish Forest Agency (Skogsstyrelsen) in Sweden; the Norwegian Meteorological Institute (Met); Gjensidige Insurance; the Finnish Environment Institute (SYKE) and Natural Resources Institute Finland (LUKE) in Finland; and the Canadian Forest Service in Canada. The search strategy for reports can also be found in Appendix I. This included the main previous Norwegian assessment reports (section 2.4), whose findings are generally echoed throughout the circumpolar boreal region from Sweden, Finland, Russia, USA, and Canada as exemplified by Parviainen et al. (2010), Joyce et al. (2014), Lemmen et al. (2014), Eriksson et al. (2015), Vose et al. (2018), Ståhlberg et al. (2019), Leskinen et al. (2020), and Venäläinen et al. (2020).

The literature on climate change impacts on the wide range of biotic and abiotic aspects of the forest ecosystem relevant for ecological condition, is first summarized and described individually per species group for species' phenologies, growth, demographic rates, abundances and distributions (4.2), on the community level (for total and relative abundances and diversity (4.4), and with respect to time-lags and synchrony and transient dynamics (4.5). Finally, we summarize information about interactive effects of forest management (4.6).

3.3.2 Synthesis of climate change impacts on ecological condition and specific factors

To address the request in the ToR to assess the impact of climate change and climate related factors on ecological condition; key tree species and stand ages; alien species, pests, and diseases; and resilience, resistance, and vulnerability to climate change, we synthesize the evidence collated on these aspects as follows: Based on the literature summary in sections 4.2-4.5, we tabulated all observed responses by climate driver, response variable, and species or other biotic or abiotic response variable unit. Each observed response was tabulated by the observed response and drivers and other relevant factors in the original paper, as described in Chapter 4, and then classified by its climate driver, functional group, organismal group, habitat, and response type as follows:

- Climate and climate-related drivers: non-specified/total climate change, increased temperature (near term) increased temperature (long term), increased precipitation (near term), increased precipitation (long term), heat extremes, cold extremes, increasing number of freeze-thaw cycles, drought extremes, increased snow damage risk, decreased frosts, increased rain on snow events, reduced snow cover, altered length of snow season, CO_2 fertilization, increased fire risk, increased fire intensity, windfelling, increased disturbance frequency, increased disturbance size, pests and diseases, alien species, herbivory.
- Functional groups: trees, understory plants, pollinators, herbivores, insectivores, carnivores, omnivores, pathogens and parasites, decomposers, mutualists, ecosystem (the latter also including observations that could not be classified into specific organisms or where multiple species/trophic levels were mentioned).
- Organismal groups: trees and forest stands, ericaceous dwarf shrubs, other understory plants, bryophytes and lichens, ungulates, rodents and lagomorphs, predators, birds and bats, invertebrates, fungi, bacteria, viruses. Combined organismal categories exist for plant communities, vertebrate communities, invertebrate communities, and ecosystems for when responses could not be classified by organismal group.
- Habitat: tree-layer, above-ground, below-ground, intra-organismal, ecosystem
- Response types: abundance, demographic rate, phenology, range shift:leading end, range shift:lagging end, range shift, biodiversity, nutrient cycling, outbreaks, feedbacks, lags.

Each unique 'organism-response combination' was then classified with respect to the seven characteristics of ecological condition, as defined by the Norwegian Technical System for the Assessment of Good Ecological Condition (Nybø et al. 2017, see section 3.1.1), to allow assessment of the impact of climate change and climate change related variables for each of the seven characteristics, and for ecological condition overall. Note that each organism-response combination can contain several 'cases', if multiple drivers were documented in the original sources. Note that responses for alien species were not considered for the seven characteristics, but are instead reported in 5.2.

For each case of an observed organism-response combination, we assessed the strength and direction of the response on a Likert scale (range from -5 to +5) and the confidence in the attribution of the response to a specific driver based on the evidence in the cited literature (as summarized in Chapter 4) as "established" (high quantity and quality of evidence, high level of agreement), "established but incomplete" (low quantity and quality of evidence, high level of agreement), unresolved (high quantity and quality of evidence, low level of agreement), or "inconclusive" (low quantity and quality of evidence, low level of agreement), following IPBES guidelines (IPBES 2018). These data were used to knowledge summaries and figures of relevance for the seven characteristics of ecological condition; key tree species and stand ages; alien species, pests, and diseases; and resilience, resistance, and vulnerability to climate change. For figures, the Likert scale responses are transformed to positive, neutral, and negative responses, and the confidence terms are not shown. These are discussed in the text.

3.3.3 Climate change as a threat to red-listed forest species

As an additional source of information on the impact of climate change on biodiversity target 1.2 (that no species should be eradicated, see 3.1.7), we collated data on red-listed species in Norway categorized as threatened or near-threatened (*Artsdatabanken* 2021). We set the filters on the Artsdatabanken website as follows: Assessment area Norway (excluding Svalbard); categories critically endangered (CR), endangered (EN), vulnerable (VU), and near threatened (NT); taxonomic level species (excluding subspecies and varieties); and main habitat forest. The website's species expert summaries were then examined to determine the habitat requirements and threats, in order to assemble the final table of forest species for which at least one threat is given as climate change. This data is summarized in section 4.6 and the complete table is in Appendix III.

4 Results I: biotic and abiotic responses to climate change

This chapter summarizes the information obtained on climate change in Norway (4.1) and then the impacts of climate change and climate-related drivers on growth, survival, reproductions and ranges of species and species groups (4.2), pests pathogens and parasites (4.3), shifts in communities and biodiversity (4.4.), time lags, asynchrony, cascades, and feedbacks (4.5), managed versus natural forests (4.6), and red-listed species and habitats (4.7).

4.1 Climate change in Norway

In this section, we describe projected climate changes in Norway, and projections under RCP4.5 and RCP8.5. We discuss predicted changes in: temperature medians and extremes (4.1.1); precipitation and the water cycle (4.1.2); climate-related disturbances such as frost, snow and ice (4.1.3; the duration of the growing season (4.1.4); drought (4.1.5); storms and winds (4.1.6); and forest fires (4.1.7). In 4.1.8 we summarize these projections and consequences. Where not otherwise noted, data here are from Hanssen-Bauer 2015.

Updated data and projections for different scenarios and time points can be found and freely explored as maps and graphs at the NCCS web site **https://klimaservicesenter.no**

4.1.1 Temperature: median and extremes

The annual median temperature for mainland Norway increased by around 1°C from 1985 to 2014, with the largest increases being in spring and winter (Hanssen-Bauer et al. 2015). The year 2020 was the warmest on record since 1900, with an average annual anomaly of +2.4°C (met.no, 2021 [Klima fra 1900 til i dag]), and the winter was on average +4.6°C above the 1961-1990 normal (Figure 10).

Regarding seasonal variation, warming is projected to be greatest in the winter season, and smallest during summer (Hanssen-Bauer et al. 2017) (Table 2). The Arctic region seems likely to keep experiencing warming at a rate two to four times the global average (England et al. 2021, Previdi et al. 2020, Rantanen et al. 2021). Changes in mean temperatures are associated with changes in the frequency of extreme values and patterns of variance, not only when it comes to temperature, and to interact with precipitation, moisture, frost, and further characteristics derived from these, as described below.

Climate change affects not just mean values of temperature, rainfall etc., but also extreme values and variation, meaning one sometimes sees strong effects on how often biological thresholds are crossed. This is most easily exemplified for temperature; a moderate shift in median value may dramatically change the number of times daily temperatures cross the freezing point, or how much of the time it stays above it, with profound effects for regional hydrology and ecology.

A related issue is the changes in frequencies of extreme temperatures. Heat waves (with associated drought and heat stress) is a core example of this, as they may cross important physiological thresholds, and the frequency at which they do so may have disproportionate impacts.

Table 2. Mean temperature anomaly (ºC) for Norway for different parts of the year projected for 2071-2100 compared with the 1971-2000 normal period (from Hanssen-Bauer et al. 2015). Months abbreviated to first letter (e.g. Winter = December, January and February).

	RCP4.5			**RCP8.5**		
Season	**Med**	**Low**	**High**	**Med**	**Low**	**High**
Annual	2.7	1.6	3.7	4.5	3.4	6.0
Winter DJF	2.9	1.3	5.0	5.1	3.2	7.1
Spring MAM	2.8	1.2	4.4	4.6	3.1	6.3
Summer JJA	2.5	1.2	3.8	3.9	2.7	5.8
Fall SON	2.8	1.7	4.1	4.7	3.0	6.1

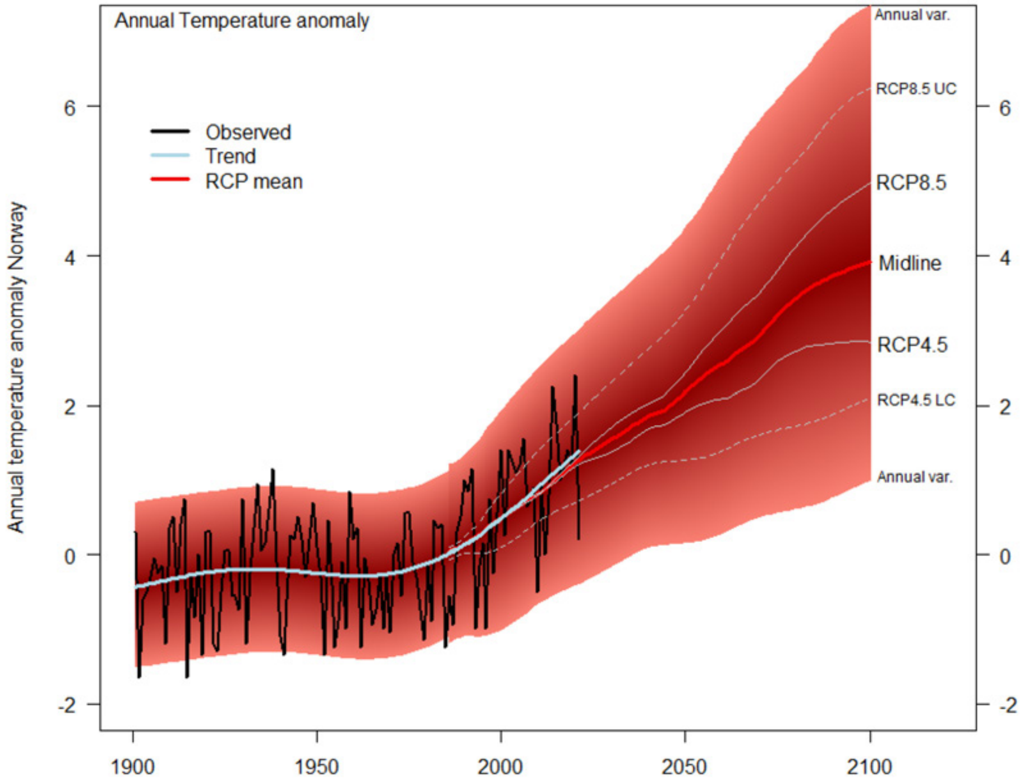


Figure 10. Summary of median annual temperature anomalies (from a 1971-2000 normal period) in mainland Norway 1900-2021 (black line) and projections 2022-2100. A non-linear trend line fitted to observations is in light blue. The RCP4.5 and RCP8.5 predictions are shown in grey, with the average between them in red, and the respective 80% upper and lower projection intervals as dotted lines. The red shading on the other hand is the 80% observation interval for specific years around the trend, continued out to the 80% intervals for the scenarios. Within-year variation is obviously larger still. Data from the NCCS and MET.

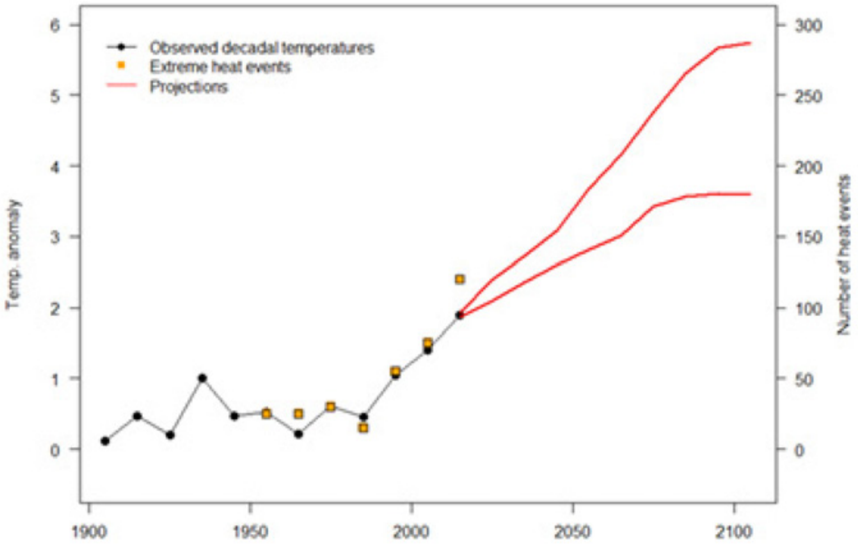


Figure 11. According to data from Sulikowska and Wypych (2021), the number of extreme heat events (defined as days when the daily max temperature exceeds the local 95th percentile of the 1961-1990 period across at least 10% of the surface area).

4.1.2 Intensification of the water cycle

4.1.2.1 Precipitation and evapotranspiration

Mean annual precipitation (1971-2000) for Norway is estimated to be 1600 mm, and has increased by about 18% since the year 1900 (Hanssen-Bauer et al. 2017). The increase has been largest in spring and smallest in summer. The predicted changes in annual precipitation is less dependent on scenarios and the confidence intervals of RCP4.5 and RCP8.5 mostly overlap. According to Hanssen-Bauer precipitation is most likely to increase by about 18% (7% to 23%) until 2100, but the current trend is steeper and between-year variation is large (Figure 13).

A doubling of the number of days per year with heavy precipitation is also predicted, and preliminary analyses suggest that maximum rainfall intensity (the maximum rainfall occurring over a few hours) may increase by more than 30% (Hanssen-Bauer et al. 2017). The changes in different seasons are considerably larger, with expected increased runoff in winter and reduced runoff in the summer season (Hanssen-Bauer et al. 2017).

Annual runoff naturally varies considerably across the country, from more than 5000 mm at the most in western Norway to less than 400 mm in the upper part of Gudbrandsdalen in eastern Norway and in interior parts of Finnmark (Hanssen-Bauer et al. 2017). Of the current annual average precipitation more than 1100 mm goes to runoff, while a little less than 500 mm evaporates. The observed warming has generally led to increased runoff in winter and spring and earlier snowmelt. The median of all projections suggests a relatively small change in total annual runoff for Norway over the next 50 years (Hanssen-Bauer et al. 2017), and the increased precipitation since 1980 until present has not been reflected in a similar increase in runoff, most likely explained by the corresponding increase in temperature having increased evapotranspiration. The observed changes vary over seasons, with the largest increases in winter and spring runoff. The largest increases in runoff are expected to occur in the winter, due to increased precipitation of which more is falling as rain. In contrast, runoff is expected to decrease during summers due to earlier snowmelt and higher evaporation losses during warmer summers. Both emission scenarios, RCP4.5 and RCP8.5 show the same patterns. This is evident over the shorter term, comparing runoff data from 1971-2000 with 1985-2014 for the whole of Norway and different regions within Norway, and in longer-term records (1920-2005) of river flow (Wilson et al. 2010). A likely explanation for this seasonal pattern is that as climates warms, a larger proportion of the precipitation falls as rain rather than snow in the winter and spring seasons. Increased temperatures also lead to earlier snow melt. Spring runoff is expected to decrease at low altitudes, as there will be less to no local snowmelt contributing to spring runoff depending on future climate scenario.

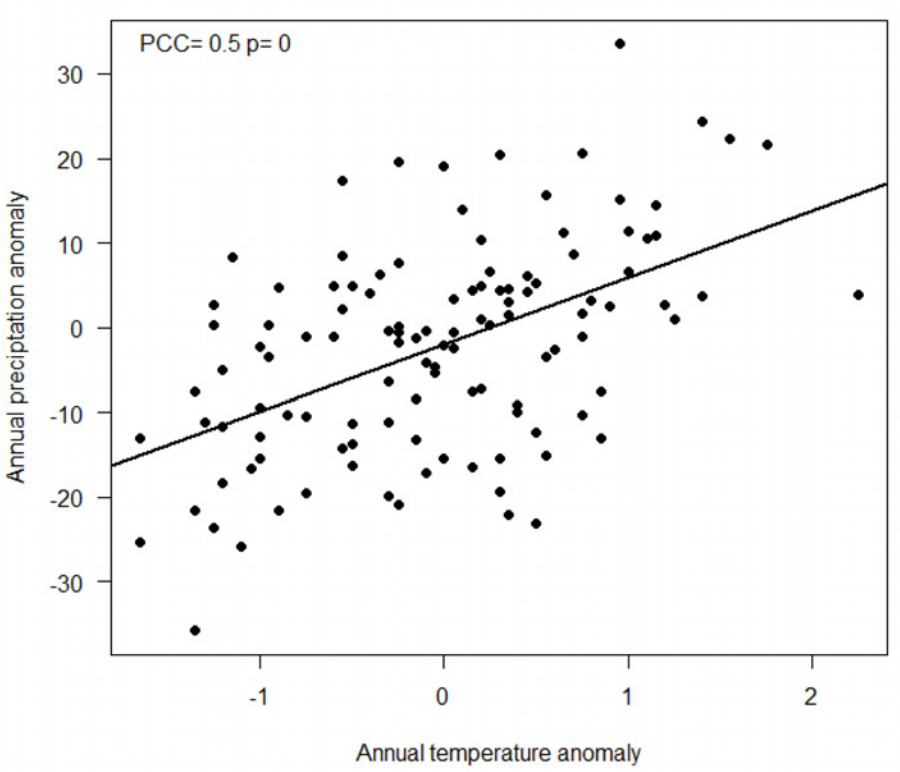


Figure 12. Historical relationship between annual temperature and precipitation anomalies for Norway 1900-2017. Data from the NCCS.

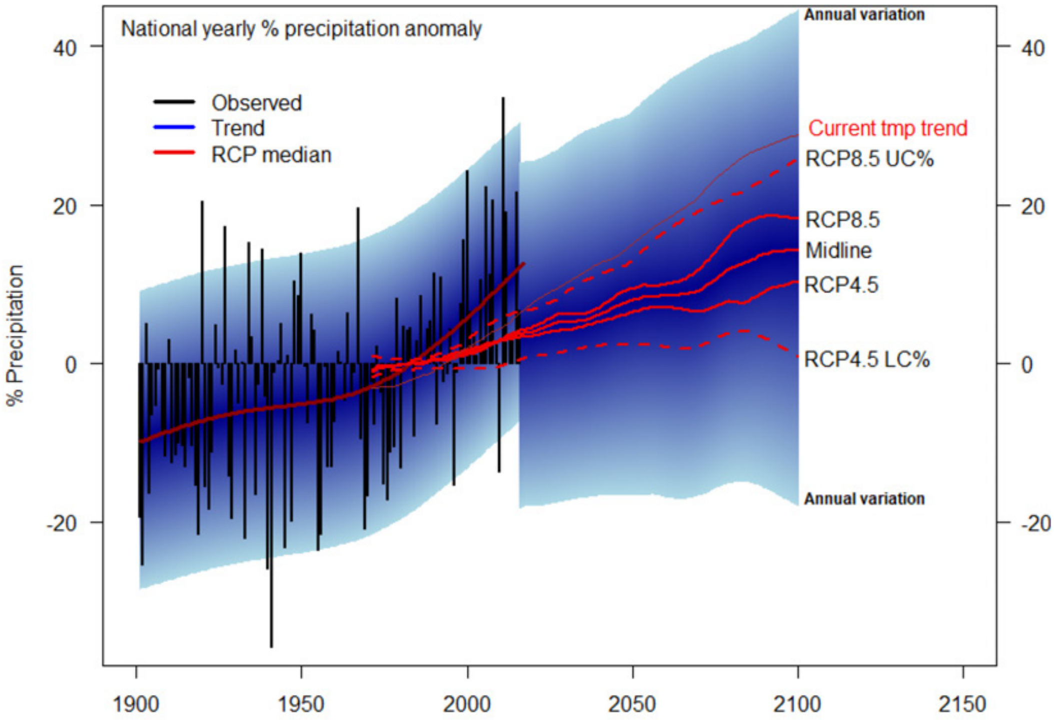


Figure 13 Summary of median annual precipitation anomalies (from a 1971-2000 normal period) in mainland Norway 1900-2021 (black line) and projections 2022-2100. A non-linear trend line fitted to observations is in red. The RCP4.5 and RCP8.5 predictions are shown, with the average between them, and the respective 80% upper and lower projection intervals as dotted lines. The blue shading on the other hand is the 90% observation interval for specific years around the trend, continued out to the 80% intervals for the scenarios. Within-year variation is obviously larger still. Data from the NCCS and MET. We note that currently the trend towards increasing precipitation is stronger than was expected even for RCP8.5 when the projections were made, and projecting on the historical temperature-precipitation trend (Figure 11) suggests a stronger increase.

4.1.2.2 Flooding

Climate change is expected to intensify the global hydrological cycle, i.e. how fast water cycles through the atmosphere, freshwater, ocean and soil. This may lead to an increase in the intensity and frequency of hydrological extremes, including floods. Projections, however, are uncertain and climate change effects on floods may be particularly complex in regions with highly heterogeneous hydrological regimes such as Norway.

Trends in the magnitude and frequency of floods have been analyzed for up to 211 pristine and near-natural catchments for 1962-2012, 1972-2012 and 1982-2012 (Vormoor et al. 2016). Rainfall- and snowmelt-generated events were analyzed separately. Changes in the timing of snowmelt and changes in flood regimes were also analysed. The results show that there are no clear changes in peak discharge over the periods considered, that rainfall-generated floods occur more frequently whereas snowmelt-generated floods occur less frequently. Also, snowmelt occurs earlier and the importance of rainfall for Norwegian flood regimes is increasing, while the importance of snowmelt is decreasing.

Future changes in flood magnitudes (the mean, 200- and 1000-year flood) have been analyzed for 115 catchments using RCM simulations, a catchment-based hydrological model, and an extreme value analysis of the simulated discharge (Lawrence and Hisdal 2016). Changes in the frequency of 200-year flooding events between a reference period, 1971-2000 and a future period, 2071-2100 are illustrated in Figure 14.

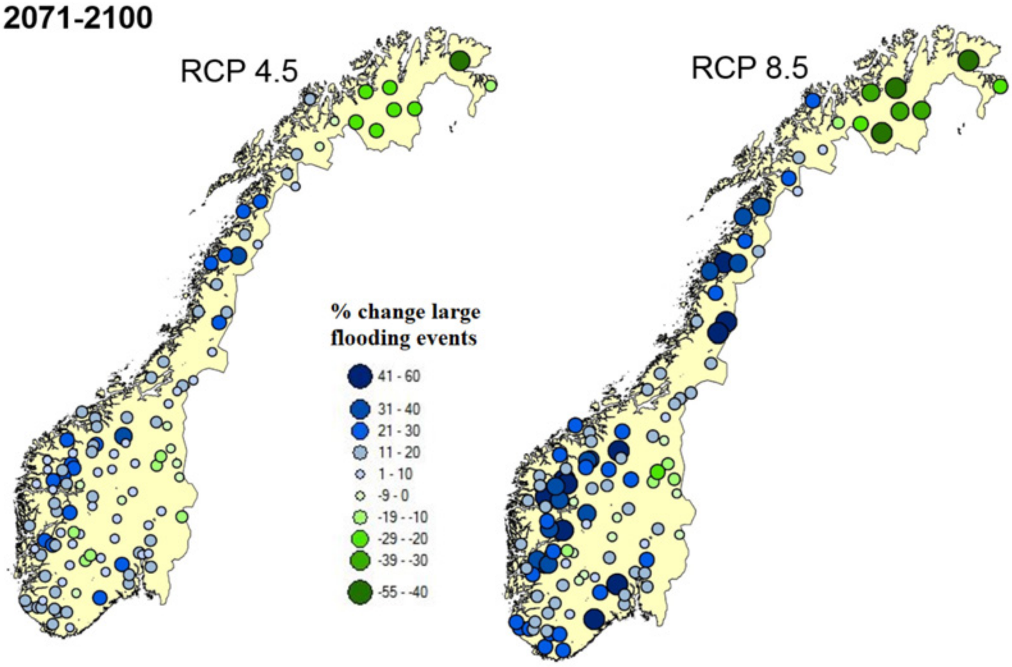


Figure 14. Expected changes in floods, measured in the relative change in frequency of flood events of a magnitude until now expected only every 200 years on average.

We see large regional differences in the projected changes across Norway, with median ensemble projections ranging from -44% to +56% for the daily-averaged flood magnitude. The results show that the observed changes will intensify in the future and that the magnitude of change depends on the emission scenario. One can also expect an increase in the size of rain floods and a decrease in the size of snowmelt floods. In many areas, this is also associated with a change in the distribution of precipitation among seasons.

Rainfall affects erosion through changes in intensity and seasonality of rainfall and flooding, interacting with plant cover to determine nutrient leaching and soil cohesion. An increase in the amount and intensity of rainfall is expected to exacerbate erosion issues along Norwegian waterways, including riparian forests (Blankenberg and Skarbøvik 2020, Hasselquist et al. 2021, Zhou et al. 2021).

4.1.2.3 Sea level rise

Sea level rise is expected to be < 0.6 m along the Norwegian coast in 2100 even at the upper estimates for RCP8.5 (Simpson et al. 2017). While the changes in extreme spring and storm tides, salt exposure and other effects will have strong local effects on infrastructure and coastal habitats, Norwegian topography means this will affect only a narrow band of ground near sea level and thus have only very minor impacts on Norwegian forested areas outside a very narrow coastal band of threatened boreal rainforest and coastal forest. It is thus not discussed further in this report.

4.1.3 Frost, snow, and ice

Snow is an important ecological factor with an ecosystem-wide impact on boreal forests, and changes in snowpack duration, snow depth, and other characteristics can have system-wide impacts. The combined effect of increased temperature and precipitation on the snowpack is already evident in observations. At elevations of 850 to 1350 m a.s.l. in southern Norway, the snow water equivalent (SWE), a measure of the amount of precipitation that falls as snow, has increased since 1931 (Skaugen et al. 2012). The SWE has decreased below this altitude. A similar pattern has been found for central and northern Norway, although it is not as clear as in southern Norway. There is a trend towards a later snow accumulation and an earlier snowmelt (Dyrrdal and Vikhamar-Schuler, 2009; see also Kreyling 2019). over most of the country, a trend that is expected to continue and strengthen in the future. For RCP4.5, the snow season (expected number of days with a snow cover) could become one to five months shorter, and under RCP8.5 it could become one to seven months shorter. At low altitudes where the winter temperature today is only slightly below zero, snowfall will be negligible in most years towards the end of the century under the high emission scenario. The exception is certain high alpine regions where in the medium term snow depth may increase, as the temperature stays below zero and so the increased precipitation still falls as snow.

Snow is a good insulator, and a deep snowpack insulates the ground during the winter months. Under cold and dry conditions, the insulating effect of the snowpack on the ground creates a temperature and humidity gradient that causes ice crystals to sublimate directly from the bottom snow layer as water vapor can diffuse up through porous snow along its partial pressure gradient. This causes a layer of open spaces and porous snow that provides crucial winter refugium and habitat for small mammals, insects, plants, and other organisms. The formation of subnivean space is inhibited by decreasing snowpack depth and ice crusts forming during freeze-thaw events, especially in moist air and with insufficient snow depth to provide insulation. These changes in snow conditions can be exacerbated by increased temperature variance, whereby extreme cold spells can still occur in a warmer climate where snowpack is reduced and icing increased (Stenseth et al. 2002). The number of days where the temperature crosses the freezing point at least once affects ice formation and snowpack characteristics. Along the coast, the number of freeze-thaw cycles is expected to decrease by almost 40 days by the end of the century, while Nordland and Finnmark will see an increase in freeze-thaw cycles.

Permafrost is found on about 23 400 km^2 of the Scandinavian land area. About 56% of that permafrost area is in Norway. The extent of permafrost area has declined by 60% from the period 1981-1990 to 2001-2010. This decline indicates that large areas are thawing, with degradation in the lowland permafrost in northeast Scandinavia, and sporadic permafrost in the coastal mountains in Troms and Finnmark (Gisnås et al. 2017). Thus, while being less evident than in the Siberian and North American parts of the taiga, permafrost thawing with its release of methane and other greenhouse gasses and soil destabilization is also happening in Norway. Duration of frozen ground affects growing season length, the temperature and water regimes of the soil microbe community, and soil anchoring during winter storms (Gregow et al. 2011). While little of the Scandinavian permafrost is in the current boreal zone, these developments are symptomatic of decreasing ground frost in general, and the transformation of current arctic areas into boreal zones.

4.1.4 Duration of the growing season

Climate warming is generally causing a longer growing season (defined as the number of days with mean air temperature > 5°C), especially along the coast (Tveito, 2014). In the period 1981 to 2015, the length of the Norwegian growing season below the tree line increased by about two weeks on average. The larger increases occurred in the areas with the shortest initial season length (NIBIO 2021[Statistikk for vekstsesongen i perioden 1981-2015]).

Along the coast (see Figure 15), the growing season is thus estimated to increase by one to two months by 2031-2060, and by two to three months by the end of the century. The area with a growing season of more than six months will then have increased by approximately 105,000 km^2 by 2031-2060 and by 165,000 km^2 by the end of the century. However, factors like insolation and day length do not change, so the net result with respect to the match between temperature and sunlight will be different from what we observe anywhere today with difficult-to-predict consequences for plant growth (Mølmann et al. 2021).

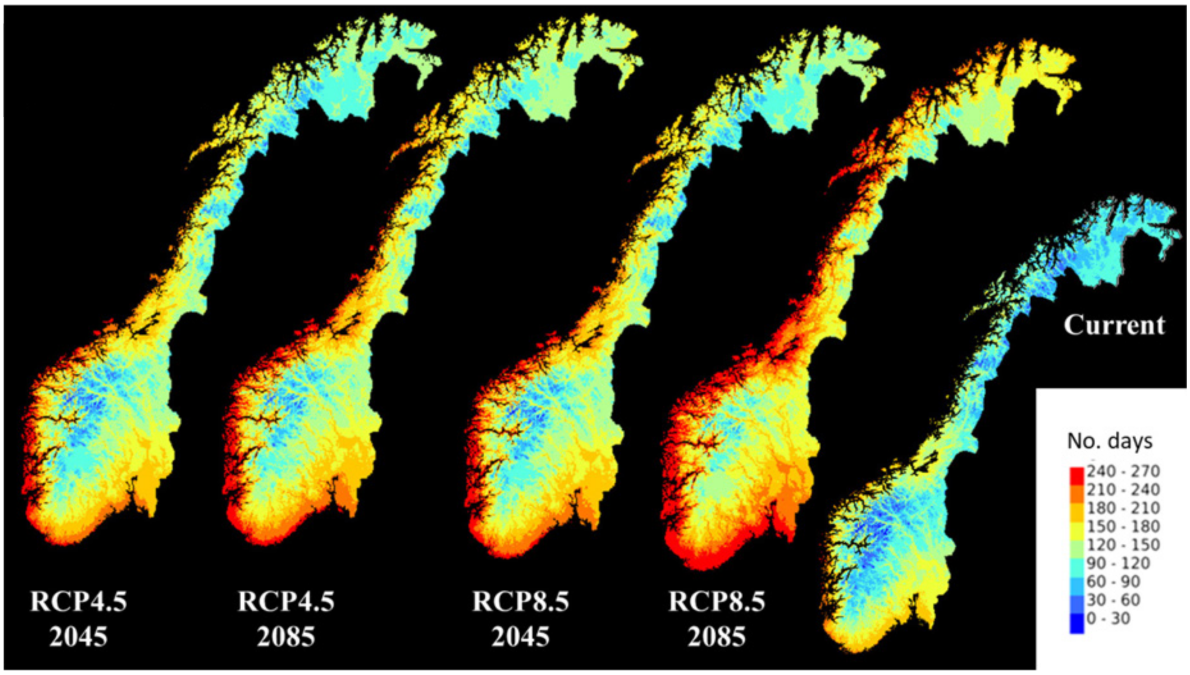


Figure 15. Length of current growing season (no. days >5°C) vs. mid- and late-century, for the two focus scenarios.

4.1.5 Soil water deficit and drought

The spatial and seasonal variability and interactive effects of the temperature and precipitation changes of the boreal zone, as outlined above, have complex impacts on soil moisture conditions. For example, a trend analysis for the period 1930 to 2004 indicate longer periods with low river flow in the summer in southeastern parts of Norway (Wilson et al. 2010). This is explained by increased temperature causing earlier snowmelt at higher altitudes, and higher evaporation losses in the lowlands during late spring and summer. This illustrates how increased precipitation does not automatically cause increased soil moisture or river flow.

In northern Europe, including Scandinavia, drying generally is predicted to occur in spring, corresponding with an earlier melt of snow and soil frost, with the greatest water deficiency in summer with higher temperatures increasing evaporation (see also Ruosteenoja et al. 2018).

Future projections indicate increasing soil moisture deficits towards the end of the century, particularly under RCP8.5. Other studies (Wong et al. 2011) also show that we can expect more severe soil moisture deficits, low groundwater levels and longer low flow periods in the future. Thus, despite the marked increase in winter, spring, and summer precipitation as well as increased frequency of intense precipitation, the risk of hydrological drought, especially during the growing season, will still increase, at least in the south and east, while the north and west may see different trends (Chen et al. 2020), consistent with a trend in streamflow recently noted by Peña-Angulo et al. (2022) showing year-round decrease in Southern Europe streamflow, but in North-West and Central Europe (including Scandinavia) streamflow increasing in winter but decreasing in summer.

4.1.6 Storms and winds

A study of long-term variability of simulated winds over northwest Europe (British Isles, North Sea and Norwegian Sea) concluded that there was no clear trend in the frequency of storms in these seas and coastal areas since 1880 (Feser et al. 2014). An analysis of the frequency of strong winds measured during the period 1957 to 2014 at a selection of Norwegian weather stations concluded that while the number of incidents with mean wind speed over the 90th percentile is increasing, there are negative or no trends for the 90th percentile of wind gusts (Tveito, 2014).

According to Førland et al. (2016), historical wind conditions in Norway are difficult to analyze, both concerning long-term variations and local differences. This is partly because wind observations are strongly influenced by local effects and partly because measuring sites and ways of measuring have changed over time. Consequently, modeled wind speeds calculated from numerical atmospheric models are often used instead of direct wind measurements to describe temporal and spatial wind conditions. In complex terrain, models with very high resolution are needed for a realistic description of local wind directions and speeds.

The wind projections used here are based on ten EURO-CORDEX (www.euro-cordex.net) RCM-simulations for emission scenarios RCP4.5 and RCP8.5. Projections indicate only minute future changes in average values and large wind speeds (Hanssen-Bauer et al. 2017). On an annual basis, the available projections show a very modest decrease in median value for wind speed which is exceeded in 1% of the time both for RCP4.5 and RCP8.5. There is a slight tendency of increasing wind in winter and decreasing wind in summer, and there is projected to be a stronger increase for the highest percentage of wind force. This can be interpreted such that the strongest storm events will be stronger in the future, particularly in winter (Hanssen-Bauer, pers. comm., April 2021). The reduction in wind speed during summer is consistent with results from wind analyses performed in the ECLISE-project (Haakenstad and Haugen, 2014) based on regional climate projections from CMIP3 models (IPCC, 2007; NFR 2021; Nordic Forest Research 2020, Hauglin and Storaunet 2021).

4.1.7 Fire

While temperature and moisture patterns associated with climate change have been conclusively shown to have a major influence on fire regimes for flora and fauna in Siberia and Canada (Baltzer et al. 2021, Palm et al. 2022, Wang et al. 2021, Feurdean et al. 2020), Norway has experienced on average one large-scale fire (>1 km^2) per decade the last 100 years, and the frequency has been relatively stable over this period (Hanssen et al. 2019). This is further supported by the work of Senf and Seidle (2021) who found fire accounted for 7% of disturbances across Europe between 1986 and 2016 with no increase in frequency during this time; the least disturbance due to fires was in Fennoscandia. However, the recent dry summer of 2018 shows that less stable regimes are within the range of potential short-term climate futures. Nordic Forest Research (NFR 2021) stated that the events in 2018 foreshadow how the weather in northern Europe is predicted to become more extreme and more variable.

Warmer temperatures due to climate change can be expected to make the Nordic region more fire prone, being directly linked to increased forest fire risk and risk of accelerated fire spread. Future fires therefore can be expected to last longer and burn larger areas with more intensity. Warmer temperatures also impact groundwater reserves. If warmer temperatures happen earlier in the year, snow melts sooner, leading to lower fuel moisture during the summer, increasing fire risk (Nordic Forest Research 2020, Hauglin and Storaunet 2021). Forest community changes will also affect fire risk on longer time scales: for instance, dense and extensive pine-dominated forests are more prone to fire intensification and crown fires, while a greater admixture of broadleaved trees seems to decrease fire risk (Astrup et al. 2018, Skjølaas et al. 2009). Results from the Canadian boreal suggest this to be due to differences in branch and stem thickness distribution and flammability (Hély et al. 2000; Krawchuk et al. 2006).

Prolonged warm and dry weather conditions enable the accumulated layers of partially decomposed organic matter that characterize northern ecosystems to become a ready fuel source (Feurdean et al. 2020, Abatzoglou et al. 2016, Hauglin and Storaunet 2021). These conditions are key to regional fire phenomena (e.g., holdover fires), to interactions with the global carbon cycle, and to impacts on other aspects of these high latitude environments. Changes in precipitation regimes will also influence fire dynamics. The net effect of increased evaporation, reduced snow cover and increased precipitation is expected to result in an increased summer soil water deficit (see Climate data). This variance in precipitation along with increased temperatures and should lead to an increased frequency of physiological drought, and hence an increased potential for larger forest fires and increased fire frequency in the future (Hanssen et al. 2019, Seidl et al. 2020).

Within Scandinavia, Ou (2017) projected that the drought conditions in northern Sweden would become less severe with consequently a lowered risk of a large annual burnt areas. On the other hand, the drought conditions in southern Sweden could become more severe with an increasing number of drought years followed by large-scale fires, especially in the end of the 21st century (Ou 2017). Up until now, central Sweden has been more prone to large fire events than have areas in the north or south with similar vegetation; weather conditions in central Sweden that are favorable for fire spread are correlated strongly and positively with fire size (Pinto et al. 2020). In Finland, Lehtonen et al. (2016) suggest that the number of large-scale forest fires may double or even triple during the 21st century. This would increase the risk that some of the fires could develop into real conflagrations, which have become almost extinct in Finland due to active and efficient fire suppression.

In a study of 103 unmanaged forest landscapes with a total land area of 28.2×10^6 ha, distributed across five continents, Seidl et al. (2020) found that boreal landscapes were more likely to experience high disturbance activity than their temperate counterparts, with high disturbance activity from fire and consistently linked to years with warmer and drier than average conditions. They conclude that the high climate sensitivity of disturbances across boreal and temperate ecosystems indicates that future climate change could substantially increase disturbance activity.

4.1.7.1 Climate change impacts on fire occurrence in Norway

As only qualitative assessments of the relationship between climate change and forest fire impact could be found for Norway, we conducted a preliminary statistical assessment to see if the claimed relationship between burnt area and climate indices was visible in, and consistent with, modern Norwegian fire and climate observations.

This involved gathering available data on burnt area per year on a national level over the last century from Øien (1998), Tomter and Dalen (2018), and the insurance company Skogbrand (2021). These data were entered as a response variable into a regression model with annual precipitation and temperature anomalies, as well as a moving average of the n preceding years of burnt area, as candidate explanatory variables (*q.v.*). To allow for non-linear responses without assuming a particular parametric response function, a generalized additive model with penalized smoothing splines was used with an overdispersed Poisson response distribution to allow for overdispersion (Wood 2003, 2011 and 2017).

The results of our model showed clearly significant ($p<0.001$) contributions from temperature (more fires) and precipitation (less fires) even when controlling for medium-term trends in control practices. Despite the coarseness and large scales and the inherent degree of stochasticity in fire occurrence, temperature and precipitation together explain about 42% of the variance in annual burnt area data; there was no significant remaining autocorrelation in the residuals (Figure 16).

To assess what this implies for future scenarios, we simulated 1000 versions of the climate indices by combining historical between-year variance with the trends in changing mean values from predictions. Then we predicted one year of the fire model at the time from the end of data in 2020 until 2100, letting the moving average track the simulated burnt area before the next simulated year. The results were consistent with increased potential for burnt area per year, with increasing variance between years, and considerably higher moving average of accumulated burnt area on any scale of a human generation or less ($3 < n < 30$ years) than what we have seen in the preceding century. Examples are shown below for visualization. Notably, the model does not predict an extremely accelerating increase in burnt area but the establishment of a regime with higher average. However, like all such models, it is only valid if species composition remains similar to today and fire suppression efforts are maintained.

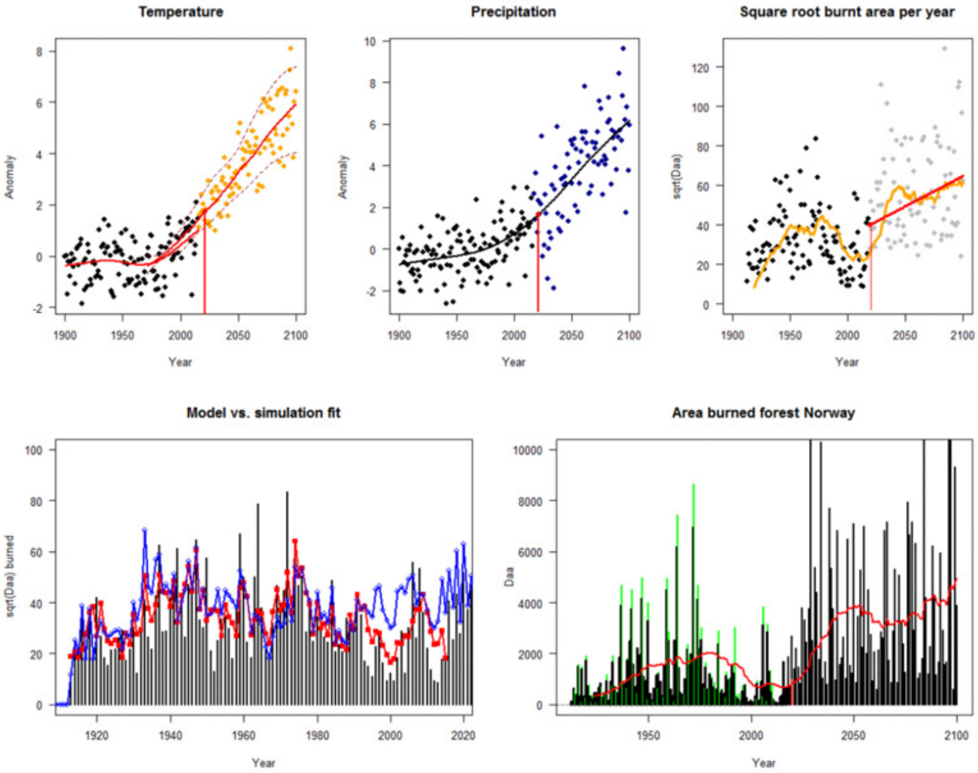


Figure 16. Relationship between temperature, precipitation, and burned forest area in Norway 1900-2020 (modeled data) and 2021-2100 (predicted from model and climate projections). Upper left and middle: Annual temperature and precipitation anomalies (black dots) and single simulated future time series (coloured dots) around the RCP8.5 expected mean trajectories. Upper right: Square root of burnt area per year, with black dots being data and grey dots the simulated values for the simulation run shown here. Orange line shows a 20-year moving average with a red trend line after 2020. Lower left: Square root of burnt area data for Norway shown as black bars. The fitted model using one-step ahead predictions shown in red. A simulation starting in 1930 and running with only climate data as input (no fire data) shown in blue is still consistent with the model predictions (r=0.67, p<0.001) and even with observations (r=0.44, p<0.001), thus lending some confidence to the simulation approach. Lower right: Same burnt area data as lower left just not squared shown as black bars, with green showing the (minor) differences between data sources mentioned above. Black bars to the right of 2020 represent the simulation run. Red line shows 20-year moving average, representing accumulated burnt area over the preceding two decades for the data period (prior to 2020) and simulation (2020-2100).

4.1.7.2 Lightning

Lightning is one of the main sources of ignition, and the most common natural fire starter in Scandinavian forests (Pinto et al. 2020, Holzwoth et al. 2021). Lightning strike frequency is affected by climate change. For the tropics, models are ambiguous (Finney et al. 2018, but also Finney et al. 2020), but both models and empirical data trends predict an increase in lightning frequency with temperature that grows stronger towards the Arctic (Chen et al. 2021, Holzworth et al. 2021, Vaisala 2022). Notably this trend increases with latitude, with nearly twice as much lightning detected north of 80° N in 2021 than in the previous nine years combined (Vaisala 2022). This was not included in the analysis and projections of Norwegian fire data above, but must be expected to strengthen the overall trend (Figure 17).

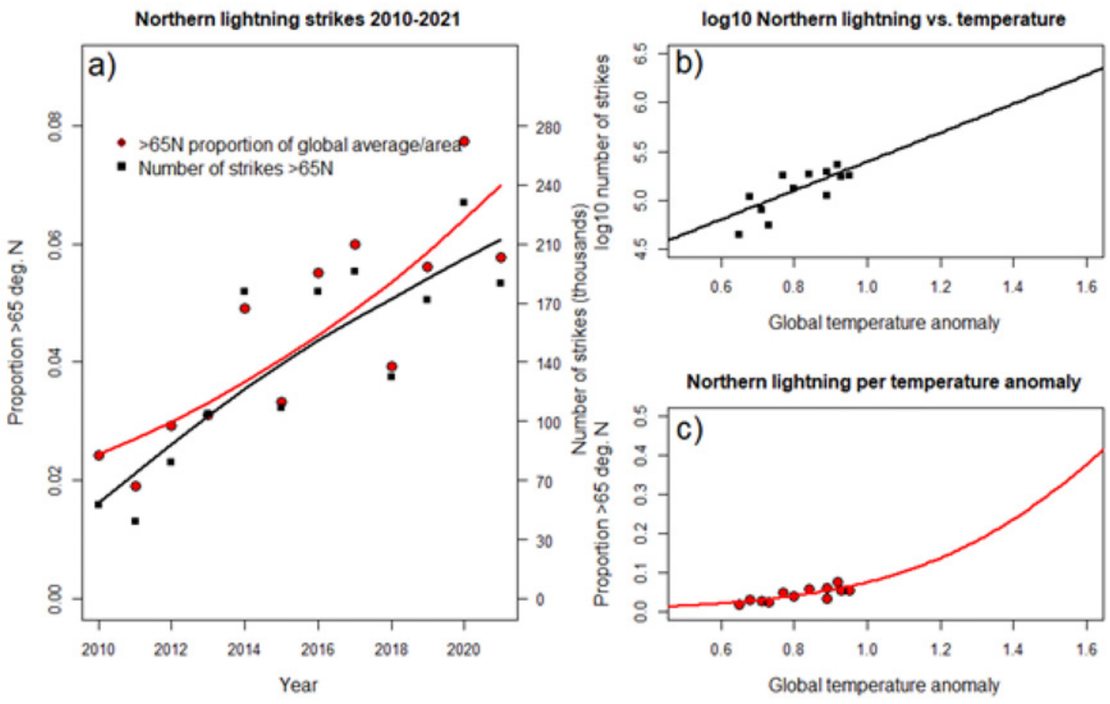


Figure 17. Lightning strikes tend to be less frequent at higher latitudes. Yet, since 2010 there has been a trend towards increasing lightning strikes above 65ºN, both in absolute numbers (corrected for sensor and station density using the Vaisala gld360 network data (Vaisala 2022), black squares) and as proportion of annual global lightning strikes (red dots). **(a)** shows raw data from Holzworth et al. 2021 for 2010-2020, with 2021 data from Vaisala 2022, **(b-c)** shows the data against annual global temperature anomalies instead of years, with trends up to the 1.5°C anomaly expected by 2050. Proportion data **(a, c)** are corrected for the proportion of the planetary surface PS north of this latitude: PS= 0.5*(1-sin(65)). Thus, a temperature anomaly of +1.5°C is at the same time expected to give a number of lightning strikes per surface area above 65ºN latitude that is less than half the global average, yet over three times higher than the number recorded today.

4.1.8 Climate zones

Less research has addressed climate-driven changes in vegetation zones in the northern than in the tropical and Mediterranean landscapes. However, some recent research has used ensembles of climate change model projections and historical climate data to estimate shifts in global climate zones. Huang et al. (2018) compared Köppen climate types from the Medieval Climate Anomaly (950-1250) with the Little Ice Age (1550-1850), present day (1971-2000), the last millennium (850-1850), and the future (2050-2080) to place anthropogenic changes in the context of changes due to different natural climate forcing factors, such as volcano eruptions and solar cycles, occurring during the last millennium. They found that the climate types have remained relatively stable during the last millennium but that compared to preindustrial condition, the accelerated climate type changes 2050-2080 would cause about 32% to 47% of the global land area to shift to warmer or drier climate types under the RCP4.5 to RCP8.5 scenarios. The large shift in climate types by the end of this century suggests possible wide-spread redistribution of surface vegetation and a significant change in species distributions

As an illustration of climate change, Bastin et al. (2019) did a systematic approach and found that, at current rates, climate change at European boreal latitudes corresponds to traveling about 20 km south per year. Specifically, the moderate rate of change associated with RCP4.5 implies that the climate in Oslo in 2050 is likely to correspond to the climate profiles found today in Vienna, Zagreb or Bratislava.

This rate of global climate transition from 20th century baselines to 2100 endpoints is unprecedented (Box et al. 2019) in historical records and implies that unstable transitional dynamics will be dominant and climax vegetation states increasingly rare in the foreseeable future.

Models of current vs. future global climate zones done by Beck et al. (2018) show that if temperatures approach the median value for RCP8.5 scenarios, most of the boreal climate zone, and in particular almost all of the Fennoscandian boreal climate zone, will not remain boreal (Figure 18). The new boreal zone that forms at the expense of arctic alpine and tundra will not have time to be colonized by boreal forest biomes at nearly the rate at which it is lost by being transformed into hemiboreal climate zones. As 2100 is only about one spruce rotation time away from the present, and much less than the maximum lifespan of most forest trees, this means that the boreal biome to a very large extent will find itself outside the climate conditions within we find it today, outside the climate conditions that that shaped it. It seems unavoidable that this mismatch will result in suboptimal conditions for much of the forest community, and changed relative competitive relationships between native and establishing or invasive species.

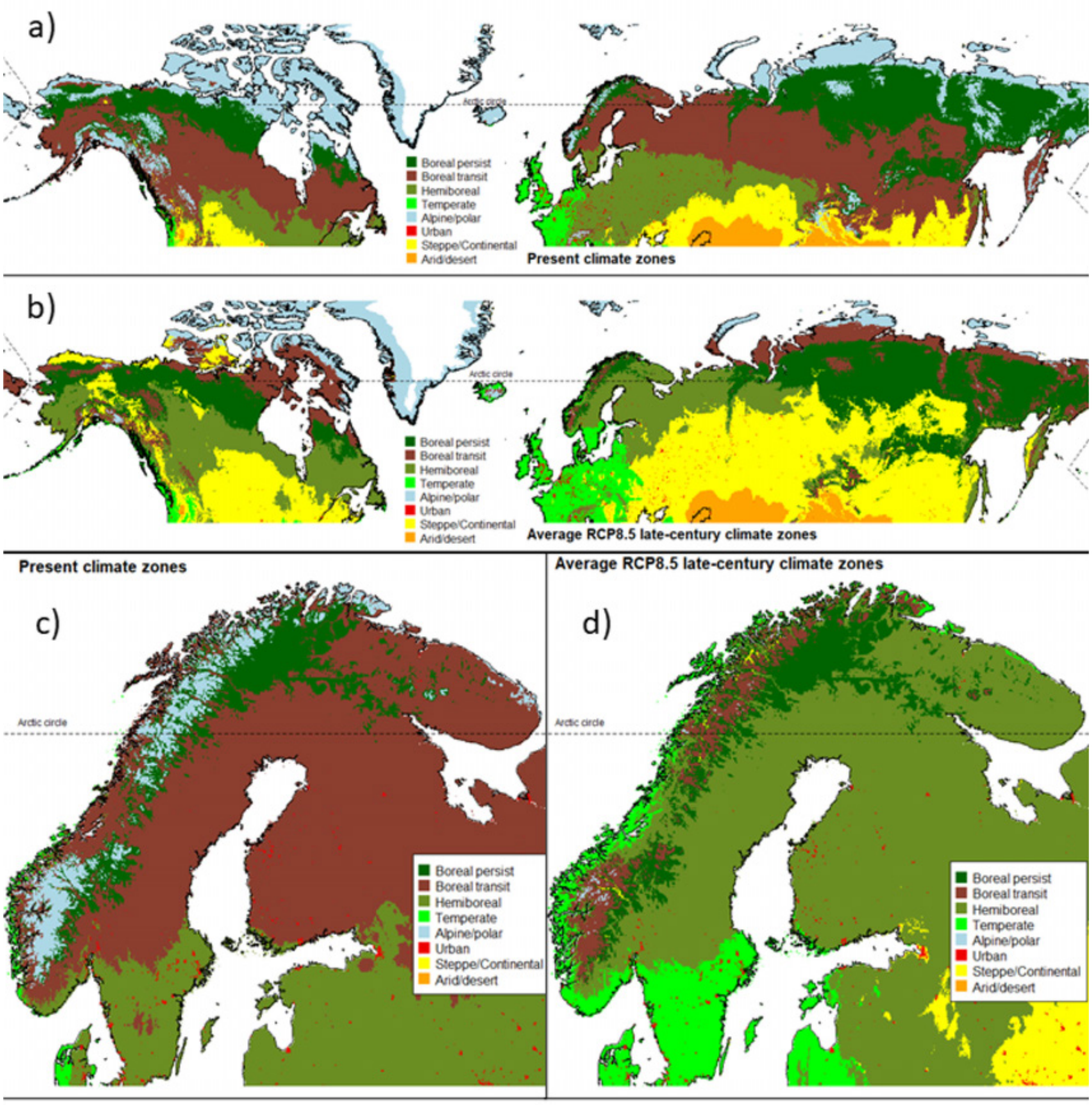


Figure 18. The climate zones associated with major vegetation types today (**a**,**c**) and 2070-2100 (**b**,**d**). The Norwegian forest as we know it today, dominated by spruce, pine and in some places birch, is a product of the boreal zone (dark green and brown). Boreal forests, often called taiga, are currently found in a broad belt across the northern hemisphere (**a**,**b**), including Fennoscandia (**c**,**d**), mostly bordering tundra to the north and hemiboreal, temperate, or steppe zones to the south. Towards the end of the century (**b**,**d**), under a future climate around the mean estimate for the RCP8.5 (see Figure S1), most of the current boreal belt will be outside the climate zone that shaped the biome. Only the areas marked dark green are persistently boreal both in the present and 2071-2100. The part of the boreal zone marked brown in the early period (**a**,**c**) will have transitioned into a hemiboreal climate by the end of the century (**b**,**d**). Likewise, the boreal areas marked brown in the latter period (**b**,**d**) have transitioned from the arctic or alpine climates they are in the present. Notably a change in climate zone does not mean that the vegetation types have had time to change correspondingly. Based on data from Beck et al. (2018) (see 3.2.3).

4.2 Impacts on growth, survival, reproduction, and distributions of species and functional groups

This chapter focuses on the species and functional groups (*q.v.*) and how climate change and climate change-related shifts in disturbance regimes (described in section 4.1) directly impact their growth, survival, reproduction, phenology (*q.v.*), and distributions.

The chapter is structured by the major functional roles of species in boreal forests. We begin with ad forest stands and forest-forming tree species (4.2.1) and then continue to consider other important plant groups including ericaceous dwarf shrubs (4.2.2), other understory vascular plants (4.2.3), and non-vascular plants, such as bryophytes (4.2.3), before highlight the impact of vegetation change for the production of dead wood (4.2.5). We then move to important forest animals: among vertebrates we consider birds (4.2.6), bats (4.2.7), rodents and lagomorphs (4.2.8), large herbivores (4.2.9), large predators (4.2.10), and forest insects (4.2.11). Lastly we then examine soil organisms (4.2.12).

Within each of these subsections, we collate information on how climate change is predicted to impact each demographic rate, summarizing the existing evidence from Norway or the Nordic countries before integrating other global or general knowledge. The information from this chapter forms the basis for assessing impacts at the community and ecosystem level, which are treated in section 4.4, and complex effects operating through changing interactions, trophic cascades, feedbacks, and time-lags that are described in section 4.5. These insights are drawn together in relation to the seven ecosystem characteristics in Chapter 5.1.

The knowledge base varies strongly in terms of the number of studies, their focus, and the level of detail, both within and between, e.g., biota, trophic levels, and functional groups within trophic levels. This is reflected in the text below, as our aim has been to include as much knowledge as possible, rather than balance between species and groups. Specific knowledge gaps are summarized in Chapter 6.

4.2.1 Trees and forest stands

The productivity of boreal forests is limited by short growing seasons, low summer temperatures, and shortage of nitrogen (Kellomäki et al. 1997; Mäkipää et al. 1998). The projected change in temperature will prolong the growing season, and in many cases increase seasonal photosynthesis, enhance the decomposition of soil organic matter, increase the supply of nitrogen, and provide CO_2 fertilization. Climate manipulation experiments indicate that increased temperatures affect tree growth through direct effects on plant physiology, with predominantly positive effects on deciduous species and more variable effects on coniferous species over certain temperature ranges (reviewed by Way and Oren 2010). On the other hand, reductions in growth may result from heat and drought stress, flooding, changing balance between temperature, light, hydrological, and nutrient conditions, and more general mechanisms such as trade-offs between growth and lifespan (Peng et al. 2011; Buermann et al. 2013; Brienen et al. 2020).

4.2.1.1 An estimate of current and future tree distributions

Understanding future changes in the ranges of the major tree species in Norway is highly relevant for addressing several points in the ToR. Mauri et al. (2022) presented a dataset of current and estimated future potential distributions of 67 tree species in Europe at approximately 10 km spatial resolution. Here current weather, soil and land cover data combined with tree dispersal capacity and climate projections gave the most detailed estimate of distribution of major European forest trees to date. This included suitable areas of occupancy for an ensemble of tree species on a set of nine environmental parameters describing key features of climate and soils, projected into the future using 11 regional climate models from EURO-CORDEX, for the emission scenarios RCP 4.5 and RCP 8.5, downscaled to a spatial resolution of five arc-minutes and three time steps (2035, 2065, and 2095). The resulting data-driven projections were made using a group of species distribution models calibrated using EU-Forest, a comprehensive dataset of tree species occurrences for Europe, and driven by seven bioclimatic parameters derived from EURO-CORDEX regional climate model simulations, and two soil parameters. The main parameters were winter and summer temperature and precipitation, precipitation seasonality, mean annual temperature, mean temperature of the coldest month, total annual precipitation, continentality, a humidity index, growing degree days above 5 °C, soil pH, and organic carbon content. They note that considering the relatively low dispersal ability of most European tree species, it is unlikely that natural dispersal will permit forests to compensate for range erosion by colonizing new habitat.

The estimated current distributions, and projected changes from these, were downloaded and computed for all 67 species and shown for the main habitat-building species in this report. Where the species are discussed in individual sections below the data are presented as maps. All other distribution maps are available upon request.

4.2.1.2 Norway spruce (Picea abies)

Growth. Long-term studies of climatic effects on tree growth using tree-ring analyses demonstrate that spruce growth is limited by low June temperatures in most regions and especially at high altitudes, whereas low June precipitation reduces spruce growth in the lowlands in southeastern Norway (Andreassen et al. 2006; Mäkinen et al. 2001). Specifically, at sites with a 30-year mean June temperature below 12-13 °C, spruce responded positively to unusually warm and dry June months, whereas in warmer sites growth was higher in wetter years (Andreassen et al. 2006). Similar regionally variable responses were found for Finland, suggesting that response can be generalized across oceanic and continental boreal climates (Mäkinen et al. 2002). The results align with earlier studies from both countries (Tveite, 1990; Lindholm et al. 2001). Experimental studies of climate change on spruce largely focus on seedling growth and the shoot biomass of spruce increased by 46% during the three first years under a temperature increase of 1.3 °C in an open-air experiment in southeastern Finland (Nissinen et al. 2020). However, 40-year-old spruce in Sweden did not respond to a temperature increase of 3.9 °C in a three-year climate chamber experiment (Sigurdsson et al. 2013).

In southern Scandinavia, experimental removal of precipitation led to reduced growth of spruce, while experimental water application increased growth (Christiansen and Nilsen, 1990; Cienciala et al. 1994). Apart from these few experiments, drought is little studied in the European boreal zone. In a study along an elevation gradient in the Czech Republic, analyses of stem diameter variation showed that severe drought during 2017 and 2018 resulted in an increment reduction of 78% and 61%, respectively, from the levels of the normal year 2016 (Krejza et al. 2021).

Across the boreal forest biome, there is a trend of positive growth responses to warming in colder parts of the range and negative responses in the warmer parts or the range (Obladen et al. 2021, Mensah et al. 2021, Huang et al. 2021). Consistent with this, a global tree-ring study found that spruce seedlings grew more than three times faster in warm areas (3.5 mm ring width/yr, mean annual temp: 12 °C) as compared to cold areas (1.1 mm ring width/yr, mean annual temp: -2 °C) (Brienen et al. 2020). For two spruce species in Alaska, Lloyd (2005) examined the relationships between tree ring width and climate at decadal scales over 232 sites for the years 1902-2002 around the circumpolar boreal region. Lloyd found that negative growth responses to temperature were widespread across species and geographic areas. Negative growth responses to temperature also increased in frequency after 1942, whereas positive responses declined. Spruce species often showed negative growth responses to temperature, especially in the warmer parts of species' ranges. In some cases, the productivity was reduced in dry sites. Together, this evidence suggests that climate warming generally enhances the growth of spruce in cold and humid sites, whereas moisture stress causes negative growth responses to warming in relatively warm and dry boreal climates.

These general patterns are also supported by model-based studies under future climate scenarios. An ecosystem model-based study from Finland projects increased spruce growth in the northern boreal zone, irrespective of RCP scenario, but decreased growth by up to 60% by 2100 in the south under RCP 4.5 or RCP 8.5 (Kellomäki et al. 2018). This is in line with models that project reduced growth in southern Sweden largely due to periods with low water availability (Lagergren et al. 2019; Belyazid et al. 2019), whereas studies of effects of warming alone tend to project consistently positive growth responses throughout Sweden (Claesson et al. 2015; Eriksson 2015) and Norway (RCP 4.5, Antón-Fernández et al. 2016).

In a study of 175 mature spruces from the northwestern edge of its geographical distribution in central Norway, Čermák et al. (2019) found contrasting effects of temperature on growth measured from tree ring width between 1950 and 2015. A positive effect of spring/summer temperature during the current year was balanced by a negative effect from the temperature of the preceding year. In sum, no simple relationship between temperature and growth was apparent for the study period.

Mortality. A recent Norwegian forestry-based synthesis of the causes of forest damage (Hanssen et al. 2019) concluded that most climate-change induced damage and mortality in Norway spruce is likely to be linked to increased storm-felling, increased drought stress, and reduced frost. However, the causal relationships can be complex and interacting (section 4.4). Among the common boreal tree species, spruce is most susceptible to damage caused by wind. High initial stand densities and peaty ground are exacerbating factors (Donis et al. 2018). The extent of wind damage has increased over several decades (Usbeck et al. 2010). This is partly due to a denser and older forest stock and partly due to decreasing root anchoring as frost periods during winter decrease and precipitation during winter increases (Solberg and Dahlen 2007, Hanssen et al. 2019, Venäläinen et al. 2020). Even with largely unchanged wind speed regimes (section 4.1.6), for the above reasons, the amount of windfelling is likely to increase.

Low precipitation and extreme droughts can result in increased tree mortality and damage on drought-sensitive sites in Fennoscandia (Mäkinen et al. 2001; Solberg 2004). A global meta-analysis of drought events at forest locations ranging from semi-arid woodlands to tropical rainforests found that tree death caused by acute drought alone is most common for seedlings or small plants across environments (Bennett et al. 2015). However, the moderately dry summers of 2004 to 2006 resulted in severe hydraulic dysfunction, top dieback, and stem cracking of larger spruce trees on certain sites in southern Norway (Rosner et al. 2018). Solberg et al. (2013) concluded that this was largely a local problem for forests on marine deposits and well-drained soils, though possibly also related to genetic traits. Drought-induced hydraulic dysfunction has been shown to be a mediator of subsequent delayed spruce forest dieback, where mortality often peaks several years after the drought event took place (Anderegg et al. 2019). Wolf (2020) investigated the impacts of the 2018 drought over 300 Swedish forest pairs through a comparative analysis of spatially proximate old-growth and production forest stands, and their associated primary production based on data from satellite photos. The results suggest that old-growth forests were more drought resistant during the summer of 2018. However, why this is the case was unclear. While some studies suggest a buffering effect through higher hydraulic diversity and increased drought resistance through reduced competition in more heterogeneous stands (Gazol et al. 2016; Anderegg et al. 2018), the opposite could be the case, with, for instance, mixed forests more quickly exhausting available soil water than monospecific stands (Grossiord et al. 2013).

Results from the trailing edge of the present spruce distribution, south of the present boreal zone, may indicate what will happen further north under a future climate. Mass dieback of spruce has been observed in the Polish Bialowieza forest in recent years, probably resulting from a combination of drought and warming that impact physiological processes and increased the susceptibility to mass attacks by bark beetles (Boczoń et al. 2018). Norway spruce forests in the Carpathian High Tatra Mountains have been subject to unprecedented tree mortality in recent decades, and while this was largely attributed to attacks by the spruce bark beetle (*Ips typographus,* section 2.3.6, 4.3.1), these attacks followed wind-throw events and periods of increased seasonal temperature (Mezei et al. 2017).

Neuner et al. (2015) used Accelerated Failure Time (AFT) models based on a dataset of almost 30,000 trees from the European Forest Damage Survey (FDS) 1995-2005 to assess the effects of climate, tree species composition, and soils on survival for Norway spruce. They found that heat waves and water deficit events linked to climate change significantly decreased spruce survival probability in Central Europe, with the effect depending on soil conditions and stand structure. The greatest reduction in survival probability, by 27%, was found in 120 year-old spruce stands, whereas survival probability in mixed stands on deep soils was reduced by only 7% (Neuner et al. 2016). Accordingly, Brienen et al. (2020) report decreasing maximum ages from 200 years at 0 °C mean annual temperature to 100 years at 15 °C mean annual temperature for spruce in a global tree-ring study. This is consistent with other studies showing that spruce is very susceptible to summer droughts, especially on well-drained or shallow sites (Lévesque et al. 2013). In Canadian boreal forests, drought stress led to tree mortality rates that increased by an average of 4.7% per year from 1963 to 2008, with higher increases in mortality rate in western than in eastern regions, most likely driven by regional differences in drought (Peng et al. 2011). In Norway, spruce forests are more fire-prone than deciduous forests, but less so than pine forests (Skjølaas 2009). Fire mortality is discussed in 4.1.7, and mortality in spruce due to insect and pathogen outbreaks are covered in section 4.3.

Phenology. Spring bud burst in spruce is mainly triggered by temperature (Hannerz 1999), while growth cessation is regulated by night length and to a lesser extent affected by climate (Koski and Sievänen 1985). Thus, climate warming is expected to advance bud break of trees, which was confirmed in a common garden study of several spruce provenances: bud break started up to nearly three weeks earlier between 1971 and 2005 (Nordli et al. 2008). However, in addition to environmental control, there are also large genetic differences among provenances, with a tendency for high altitude provenances to flush earlier than others (Westin and Haapanen 2013). Hänninen (1991) showed that climate warming is expected to advance bud flush of trees for central Finland, implying a serious threat to tree survival and growth due to increased frost risk. Langvall (2011) demonstrated that climate warming will increase the risk of damage due to early summer frost in southern Sweden, while the risk would be unchanged or even decrease in northern Sweden. As tree generation times are long, phenological behavior could decide which populations survive a future climate. However, spruce also seems to have an epigenetic effect of faster adaptive response, as for example both timing of spring bud burst, bud set and cold acclimation in autumn are delayed by experiencing high temperatures during seed production (Johnsen et al. 2009). This means that seeds produced during a warm year will be better adapted to a warmer climate.

Recruitment. Spruce shows masting behavior, meaning synchronous production of large seed crops at irregular intervals, usually every three to four years in the lowland in southern Norway. The amount of flowering, and to some extent age at first flowering, may be enhanced by high air temperatures and drought during the period of flower induction in mid-summer (e.g., Selås et al. 2002). As proper seed development requires two consecutive warm years (flower induction and then seed maturation the following year), cold summers can restrict seed maturation, which leads to poor regeneration in most years close to northern and alpine timberlines. In northern regions, it often takes 15 to 20 years between each seed year (reviews by Hannerz 1999, 1999). With this background, we would expect both more frequent and abundant flowering with increasing temperatures, especially at higher latitudes and altitudes where recruitment is highly limited by flowering and lack of seed maturation today.

When adapted to the local climatic conditions, spruce is an extremely frost-tolerant species. The seedling phase is most susceptible to stress, especially in open areas. Frost during the period of active shoot growth, especially in spring or during growth cessation and hardiness development in autumn, may affect survival and growth performance of both plants and young trees. Repeated frost damage has the strongest selective effect on young trees in northerly regions (Hannerz 1999). Together with frost damage, the most prominent challenges to successful recruitment are competition with other plants and herbivory (Nilsson et al. 2010, Nordlander et al. 2017), which are factors that may increase under climate change, as more parts of the boreal zone becomes marginal for spruce yet better suited for other (mostly broadleaf) species, and herbivory from insects is likely to increase (see insect sections).

Range. After an initial period of benefiting from a prolonged growing season, spruce is expected to be increasingly stressed in the southeast by warmer summer temperatures and increased occurrence of droughts, which are likely to increase the frequency and magnitude of tree-killing insects and pathogens, be it invasive or native (Krejza et al. 2021; Honkaniemi et al. 2020; Bosela et al. 2021). Thus, it seems likely that spruce in Norway will follow the pattern of spruce further south in Europe and hence be the first tree species subject to large-scale replacement by other species. The rate of such replacement will depend on the rate of climate change and on forestry and management practices, including replanting after cutting and disturbances.

Norway spruce distributions and occurrence were modeled by Mauri et al. in 2022 (see above, section 4.2.1.1). We see (Figure 19) that occurrence of spruce is expected to decline substantially over most of the central European area north to approximately Oslo's latitude for all scenarios, and for futures similar to RCP8.5 the decline is distinct over large parts of Fennoscandia. At the same time, the potential distribution for spruce increases substantially north and towards higher altitudes, but as spruce is not expected to be able to utilize these new areas due to limitations in dispersal capacity and land use on this time scale (Mauri et al. 2022). The net result is a much-diminished range of spruce by 2100 for both RCP4.5 and RCP8.5. Note that while the models include land use and dispersal they do not include biotic interactions with species that may be better suited to changed conditions.

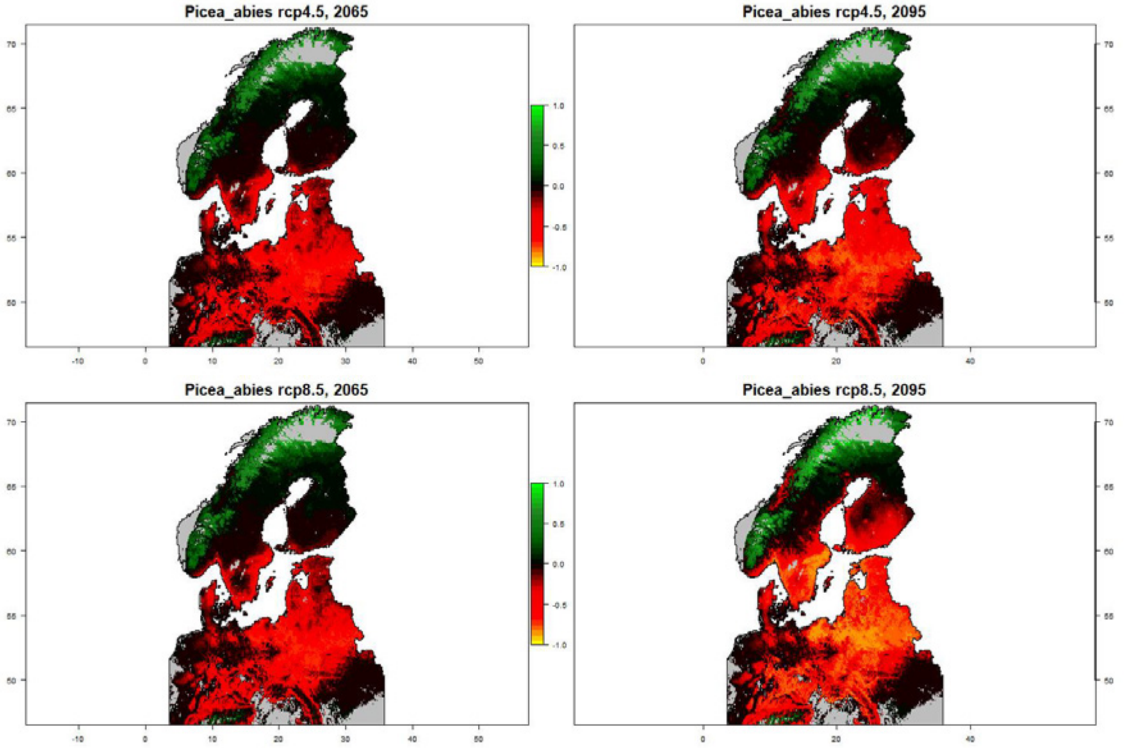


Figure 19a

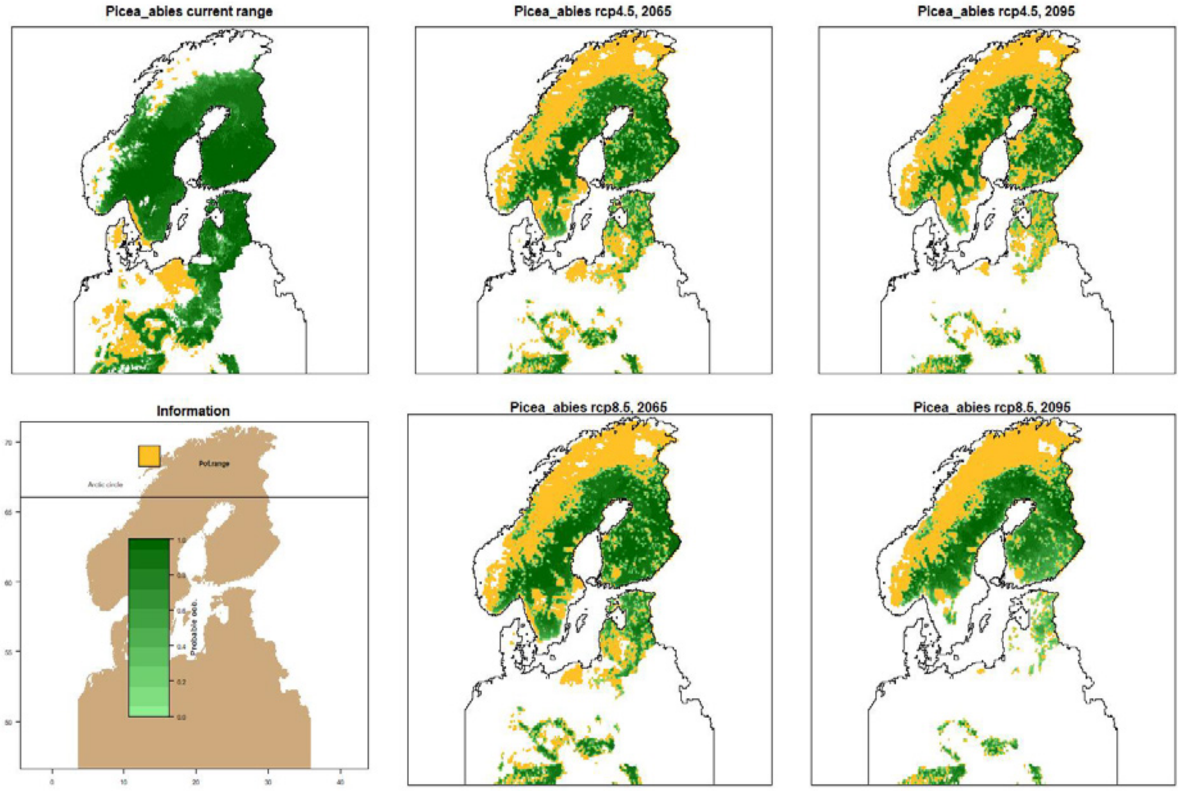


Figure 19b

Figure 19. Current and future distributions of spruce (*Picea abies*) in Europe, estimated for RCP4.5 and RCP8.5 mean scenarios. The analyses are based on the same EURO-CORDEX climate models used by the NCCS, and are coupled with tree distributions, climate-, soil- and land use data to develop a data set of 67 European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers (see 4.2.1.1). Tree dispersal capacity has been explicitly modeled. (**a**) The red color scale indicate change in expected occurrence, i.e. Probability of occurrence at time and scenario T - Occurrence today. (**b**) The green color scale shows probability of the species occurring (from 0 to 1, approximately 10x10km resolution), yellow shows potential distribution. The current range (upper left) shows where spruce is found today, with yellow showing where conditions would have permitted it but it is currently not observed. The lower left panel shows color scales and longitude-latitude. The four right panels show estimates for two future time points for the two climate scenarios. We see that while spruce as a forest-building species is expected to retreat from the south, new climate zones are opening up for potential colonization, but actual colonization at the leading edges happens too slowly to compensate for the loss of range at the trailing edges of the distribution. Hence, spruce range contracts.

4.2.1.3 Scots pine (Pinus sylvestris)

Growth. During recent decades, increased growth of pine in polar regions (Salminen and Jalkanen, 2007; Mathisen and Hofgaard, 2011; Matias and Jump 2012) has provided evidence that the predicted rise in temperature is likely to result in increased growth and reproduction of pine at its northern limit (Reich and Oleksyn, 2008). Young pine shows increased growth under experimentally increased temperature. In an outdoor experiment in southeastern Finland, the shoot biomass of pine increased by 189% in response to a 1.3 °C temperature increase over three years (Nissinen et al. 2020). In a chamber experiment in the same area of Finland, a temperature increase of 2 °C during the growing season over six years clearly increased the height and diameter growth of 20-year-old pine trees (Peltola et al. 2002; Kilpeläinen et al. 2005). A global tree-ring study found that pine seedlings grew more than three times faster in warm (3 mm ring width/yr, mean annual temp: 15 °C) as compared to cold (1 mm ring width/yr, mean annual temp: -3 °C) parts of its distribution (Brienen et al. 2020).

However, in Atlantic sites in northern Norway, years warmer than normal have not led to increased diameter growth of pine (Mathisen and Hofgaard, 2011). Similar results have been found in earlier studies, and it has been suggested that growth-stress due to milder and increasingly wet winters offsets the positive effects of warmer summers in oceanic areas (Linderholm 2002). In line with this, growth simulations for pine for selected sites in Norway, Finland, and Sweden indicate a less positive response to elevated temperature in a milder maritime climate (5-14% in Aamli, Norway), where the current mean temperature rises above 0 °C in February-March, compared with a colder continental climate (13 to 27% in Finland and central Sweden: Bergh et al. 2003). Zweifel et al. (2020) studied legacy effects of mature Scots pine by stopping an 11-year irrigation experiment. Biophysical processes responded within days, but it took up to four years to reach control levels for needle and shoot lengths, crown transparency, and radial stem growth.

Ecosystem model-based studies project positive growth responses of pine to increased temperature, especially in the north, as indicated from studies in Finland (RCP 4.5 or RCP 8.5; Kellomäki et al. 2018), Sweden (Claesson et al. 2015; Eriksson et al. 2015), and Norway (RCP 4.5, Antón-Fernández et al. 2016). The Finnish study projected some negative impacts of drought on pine growth under the more severe scenario (Kellomäki et al. 2018).

Mortality. In a global tree-ring study, Scots pine maximum age decreased from 400 years at 0 °C to 100 years at 15 °C mean annual temperature (Brienen et al. 2020). Despite being drought-resistant, recent mass diebacks of pine has been attributed to heat and drought in the growing season towards the southern end of its range in Romania (Sidor et al. 2019, Matias and Jump 2012). A study of tree mortality under drought conditions reports that pine mortality may be mediated through competitive interactions with other species rather than by direct heat stress (Archambeau et al. 2020). However, a recent German study reported that when pine seedlings are exposed to combined heat stress (experimental heat waves of

42 °C) and drought stress, they experience functional damage and impaired recovery (Rehschuh and Ruehr 2022).

Due to its deep root system, pine tolerates drought stress and exposure to strong winds better than does spruce, but pine has a complex relationship with fire: the thicker bark and higher crown of pine stands reduces the risk of crown fires and makes individual pines more likely to survive fires than individual spruce. However, spruce stands are less likely to catch fire in the first place due to more moist microclimates; a Swedish study suggests that possible ignition days each year are three to four times higher in pine than spruce stands (Felton et al. 2020). In Norway, pine forests are more fire-prone than deciduous forests (Skjølaas 2009), and young pine forests on shallow sloping soils are more prone to fire than those on deep soils (Skjølaas 2009). With summer droughts impacting the soil moisture that protects spruce stands, it seems likely that the net result is an overall higher increase in stand replacement for spruce than for pine (Felton et al. 2020, Hanssen et al. 2019, see also Venäläinen 2020).

Phenology. As for spruce, pine bud burst is mainly triggered by high temperatures, while autumnal bud set may be more sensitive to day length shorter days (Rötzer et al 2004; Salminen and Jalkanen 2015, Way et al. 2015). In a study of a range of provenances from Sweden, Finland, and Russia, more northerly pine origins exhibited earlier onset and cessation of growth and continental origins showed more northern phenological behavior than oceanic ones (Andersson Gull et al. 2018). Since the start of growth is mainly a result of accumulated heat, the authors suggest that pine may suffer from late spring frosts in a warming climate. However, as for spruce, high genetic variability and heritability of phenological traits points towards a large potential for adaptation to new conditions (Ruotsalainen and Persson 2021).

Recruitment. Pine flowers most years in larger parts of Norway but cold summers restrict seed maturation leading to poor regeneration in most years close to northern and alpine timberlines (Kujala 1927). The northern limit of distribution is limited by low temperatures during the growing season (Veijola 1998), and unlike spruce, pine seems to be unable to grow in areas of permafrost that has a shallow active soil layer (Hustich 1966; Boratynski 1991). Thus, a warmer climate will most probably lead to improved seed production, recruitment, and growth at northern and altitudinal distribution limits (Savolainen et al. 2004; Way et al. 2014). However, an additional factor influencing recruitment in some high altitude, snow-rich areas may be the presence of the fungus *Phascidium infestans* P. Karsten, the causal organism of snow blight (Roll-Hansen et al. 1992, S). However, reduced snow cover may reduce this pressure.

Since pine is a pioneer species that regenerates naturally after disturbances, such as after forest fires, it also benefits from disturbances caused by human activities, like harvests (Mátyás et al. 2004). The future distribution of pine will therefore also depend upon interactions between climate and disturbance, herbivory from larger herbivores, and on the level of competition from broadleaved trees and forbs (Mátyás et al. 2004; Krakau et al. 2013; Silvestro et al. 2019).

Scots pine is included in the species models published by Mauri et al. in 2022 (see above, section 4.2.1.1). They project (Figure 20) that occurrence of pine is expected to decline substantially over most of central Europe north to approximately Oslo's latitude for all scenarios, and for futures similar to RCP8.5 the decline is distinct over large parts of Fennoscandia. At the same time, the potential distribution for pine increases substantially north and towards higher altitudes, but as the trees are not expected to be able to utilize these new areas as quickly as they appear due to limitations in dispersal capacity and land use. The net result is a diminished range by 2100 for both RCP4.5 and RCP8.5, similar if somewhat less dramatic than what is observed for spruce (see fig 19 above). Note that while the models include land use and dispersal, but they do not include biotic interactions, i.e. competition with species that may be better suited to changed conditions.

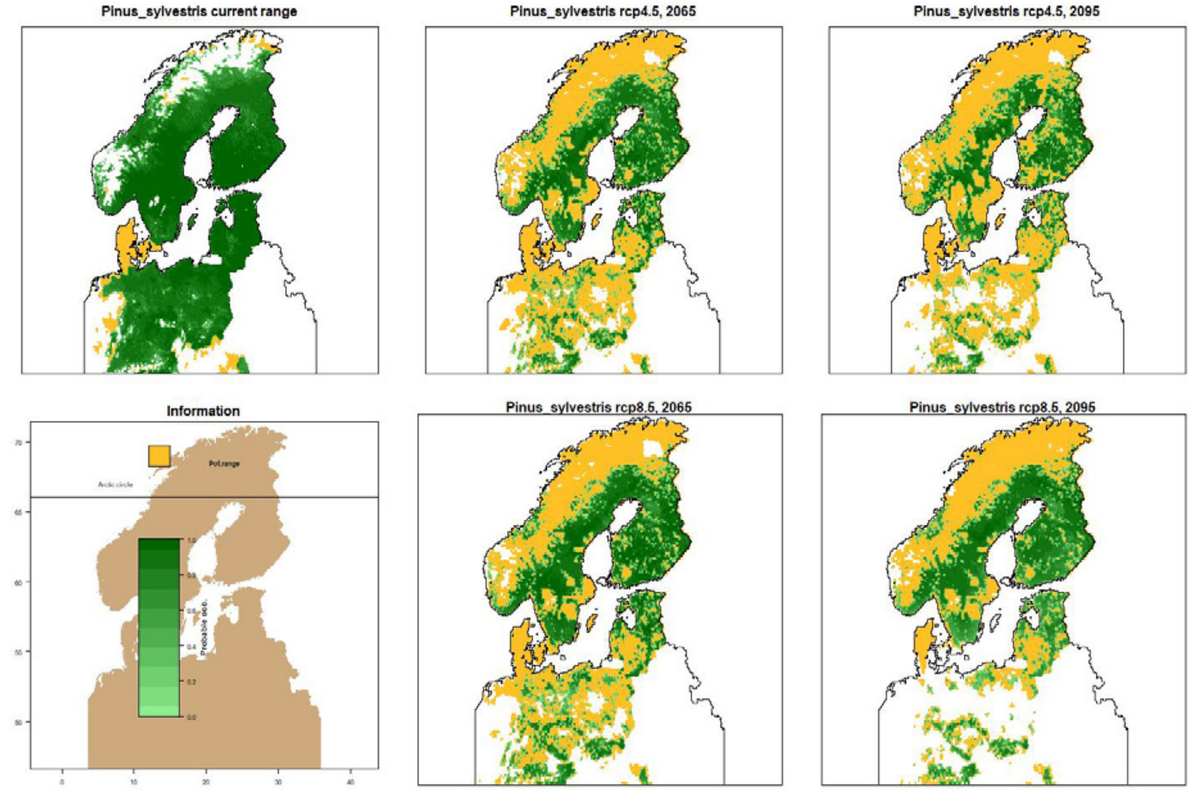


Figure 20. Current and future distributions of pine (*Pinus sylvestris*) in Europe, estimated for RCP4.5 and RCP8.5 mean scenarios. The analyses are based on the same EURO-CORDEX climate models used by the NCCS, and are coupled with tree distributions, climate-, soil- and land use data to develop a data set of 67 European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers (see 4.2.1.1). Tree dispersal capacity has been explicitly modeled. The green color scale shows probability of the species occurring (from 0 to1, approximately 10x10km resolution), yellow shows potential distribution. The current range (upper left) shows where pine is found today, with yellow showing where conditions would have permitted it but it is currently not observed. The lower left panel shows color scales and longitude-latitude. The four right panels show estimates for two future time points for the two climate scenarios. We see that while pine as a forest-building species is expected to retreat from the south, new climate zones are opening up for potential colonization, but actual colonization at the leading edges happens too slowly to compensate for the loss of range at the trailing edges of the distribution.

4.2.1.4 Downy birch (Betula pubescens) and silver birch (B. pendula)

Birch consists of a complex set of species and sub-species with different climate adaptations (Wielgolaski et al. 2001) and therefore also likely different responses to climate change.

Growth. Downy birch *Betula pubescens,* especially the subspecies *B. p. pumila* (mountain birch)*,* has a northern and boreal distribution and forms the alpine and arctic treeline in many regions. Tree-ring studies of downy birch in Iceland showed that growth during 1930 to 2002 was limited by June and July temperatures (Levanic and Eggertson 2008). Downy birch biomass and growing stock are increasing at its northern and altitudinal range limits (Tømmervik et al. 2009; but see 4.2.1.4). However, there are also large sub-regional differences due to variation in local climate and biotic factors that limit recruitment beyond the treeline (Dalen and Hofgaard 2005).

Silver birch *Betula pendula* is a south boreal to temperate species, and experimental studies outdoors indicate that biomass growth of seedlings is limited by summer temperature throughout its range in Fennoscandia (Kellomäki and Wang 2001; Lavola et al. 2013; Nissinen et al. 2020). A common garden experiment on silver birch in Finland found a strong positive temperature effect on seedling growth, with little indication of local adaptations in growth or phenology (Possen et al. 2021). Instead, the authors suggest that phenotypic plasticity and genetic variation allow birch to survive in South-Finland under variable climate conditions. However, the climatic conditions predicted for the end of this century may, at least on poor soils, reduce the survival of silver birch trees in their early growth (Possen et al. 2021).

Ecosystem model-based studies project positive growth responses of *Betula spp.* to increased temperature, especially in the north, as suggested by studies from Finland (RCP 4.5 or RCP 8.5; Kellomäki et al. 2018), Sweden (Claesson et al. 2013; Eriksson et al. 2015), and Norway (RCP 4.5, Antón-Fernández et al. 2016).

Phenology. In a common garden study in Norway, birch advanced its bud burst by almost three weeks between 1971 and 2005 (Nordli et al. 2008). Silver birch in boreal areas of Finland show little south-north variation in spring and autumn phenology (Possen et al. 2021), while downy birch has advanced its bud burst by 0.5 days/year in northern boreal zones in the period 1997 to 2013 (Poikolainen et al. 2016).

Range Shifts. Birch, which forms both latitudinal and altitudinal treelines in many places in Norway, is expected to expand both northwards and upwards as a combined effect of increased temperatures and less human influence (Bryn 2008; Hofgaard et al. 2010). In south-central Norway, the current forest line is about 100 meters lower than the climate potential (de Wit et al. 2014). However, its susceptibility to summer drought may limit the establishment and distribution on shallower and drier sites: birch trees are confined to mountainous areas in southern Europe since they do not tolerate prolonged summer drought (Atkinson 1992, Sanz et al. 2011). Moreover, climate interacts strongly with changes in herbivory in affecting birch range expansion making single climatic effects difficult to disentangle (Tømmervik et al. 2009; Hofgaard et al. 2010; Speed et al. 2010, Vindstad et al. 2018). Spreading outbreaks of defoliating geometrid moths impact mountain birch most severely near the forest line (Hagen et al. 2007). There are also large differences between regions: sub-alpine birch forests in the southern part of Norway have legacies from intense human exploitation (dairy farming), whereas such legacies are only minor in the north (such as in Troms and Finnmark) where the area of mountain birch forests are most extensive. There are even sub-regional differences in birch forest structure in the north due to differing reindeer browsing pressures (Biuw et al. 2014, Bråthen et al. 2017) and geometrid moth outbreak ranges (Jepsen et al. 2009).

The range shifts for *B.pendula* and *B.pubescens* predicted by Mauri et al. (see 4.2.2.1 and range maps for spruce and pine above) are less dramatic than for the conifers. While both birch species are predicted to be considerably reduced in abundance in northern central Europe, their Fennoscandian ranges seem likely to be fairly robust to the considered climate scenarios. They also see the same amount of boreal climate zone opening up northwards and in altitude as the other trees, even though they are as unlikely to be able to colonize more than a small part of it on this time scale (Figure 21).

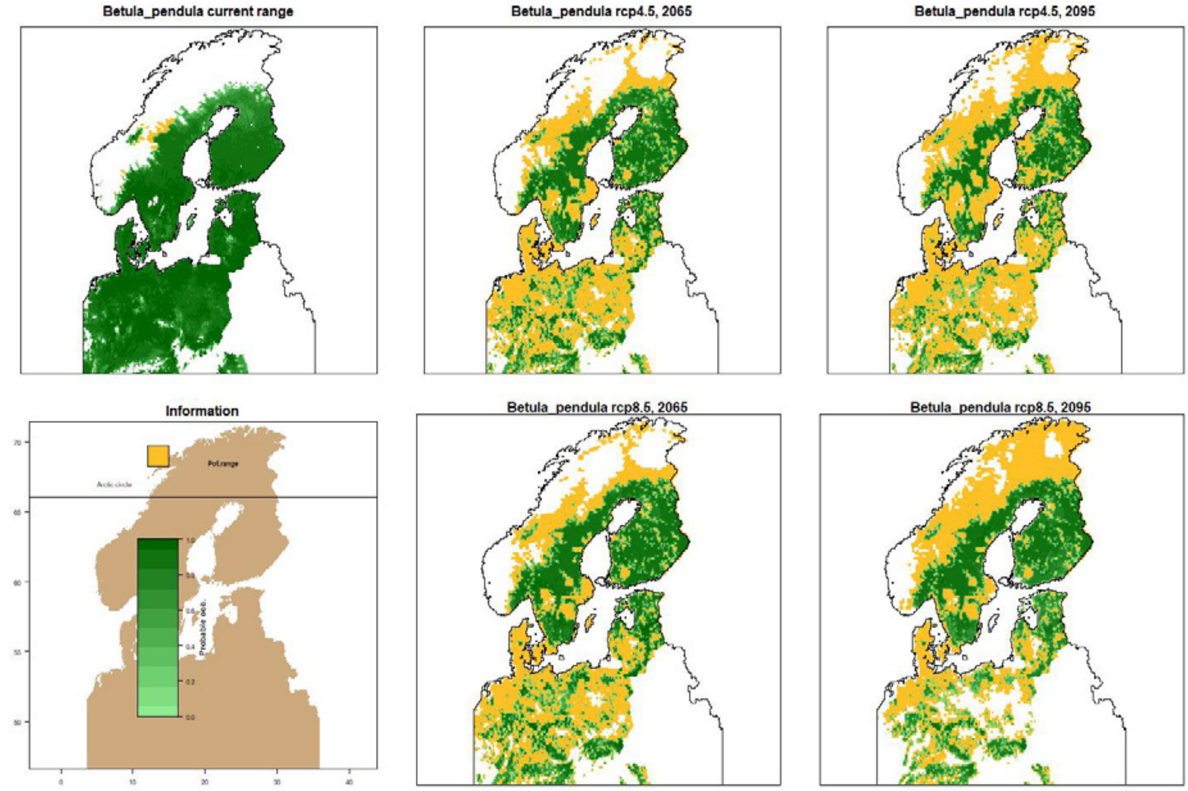


Figure 21. Current and future distributions of the birch species *Betula pendula* in Europe, estimated for RCP4.5 and RCP8.5 mean scenarios. The analyses are based on the same EURO-CORDEX climate models used by the NCCS, and are coupled with tree distributions, climate-, soil- and land use data to develop a data set of 67 European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers (see 4.2.1.1). Tree dispersal capacity has been explicitly modeled. The green color scale shows probability of the species occurring (from 0 to1, approximately 10x10km resolution), yellow shows potential distribution. The current range (upper left) shows where pine is found today, with yellow showing where conditions would have permitted it but it is currently not observed. The lower left panel shows color scales and longitude-latitude. The four right panels show estimates for two future time points for the two climate scenarios. We see that while birch as a forest-building species is expected to be stressed and possibly retreat from some areas, new climate zones are opening up for potential colonization, but actual colonization at the leading edges may happen too slowly and be vulnerable to herbivorous mammals and insects.

4.2.1.5 Rowan, aspen, and willow

Relatively little is known about the effects of climate change on the functionally important group of rowan, aspen, and species of willow, noted for their roles with herbivore and pollinating insect communities. Therefore, their direct responses must be inferred from general ecological knowledge or from studies of related species. Rowan, aspen, and willow tend to be strongly affected by browsing pressure (Bråthen et al. 2017, Biuw et al. 2014).

The distribution of rowan (*Sorbus aucuparia*) has according to the European Atlas of Forest tree species (Mauri et al. 2016) advanced northwards in Fennoscandia as a result of climate warming since the 1950s, and it is predicted to lose suitable habitat in southern and central Europe. Increased damage from moths is also considered a potential climate change driven threat to rowan (Mauri et al. 2016).

European aspen (*Populus tremula*) is found in relatively low density, or small stands, in many different nature types in Europe, indicating a relatively high tolerance to environmental conditions (Rogers et al. 2020). However, some of its relatives are quite strongly affected by drought, and it has been hypothesized that increasing temperatures may affect frost hardening and dormancy, and thus survival in aspen (Rogers et al. 2020). Sudden aspen decline is a syndrome in the North American quaking aspen (*Populus tremuloides*) caused by drought and water stress but the phenomenon has not yet been observed in the European aspen (*Populus tremula*) (Singer et al. 2019). Outdoor warming experiments with aspen in southern Finland induced earlier bud break in spring and extended the growing season by later growth cessation and bud set in autumn (Strømme et al. 2019). Similar patterns were seen when the same genotypes were studied along a natural temperature gradient in southeastern Norway (Strømme et al. 2018).

There are few if any specific reports on goat willow (*Salix caprea*) responses to changing climatic conditions, but as it co-occurs with aspen and rowan it may be expected to experience some or many of the same responses.

Range Shifts: The climate-induced range shifts for rowan and aspen predicted by Mauri et al. (2022 -see 4.2.2.1) are roughly similar to those for birch (above), i.e. not greatly negatively impacted directly in Fennoscandia but also not able to colonize new areas as fast as they appear -with a bit more pronounced negatively impacted distribution in southern Fennoscandia for the warmest scenarios towards the end of the century, and a limited expansion most noticeable in the north of Sweden. Only the white willow (*Salix alba*) is part of the Mauri data sets, but to the extent that it is found in Norway it is predicted to see a limited but clear increase in occurrence (Figure 22).

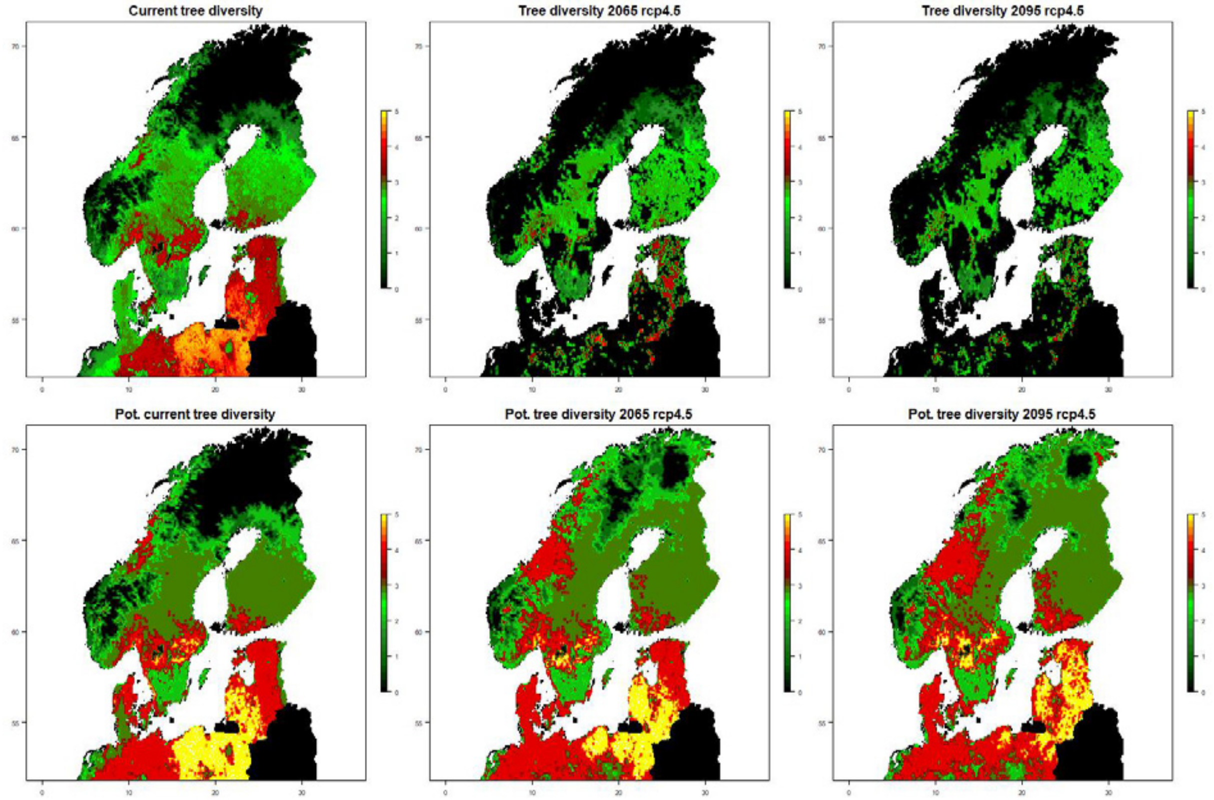

Current tree diversity
Tree diversity 2065 rcp4.5
Tree diversity 2095 rcp4.5
Pot. current tree diversity
Pot. tree diversity 2065 rcp4.5
Pot. tree diversity 2095 rcp4.5
70
65
60
55
0
10
20
30
0
1
2
3
4
5

Figure 22a

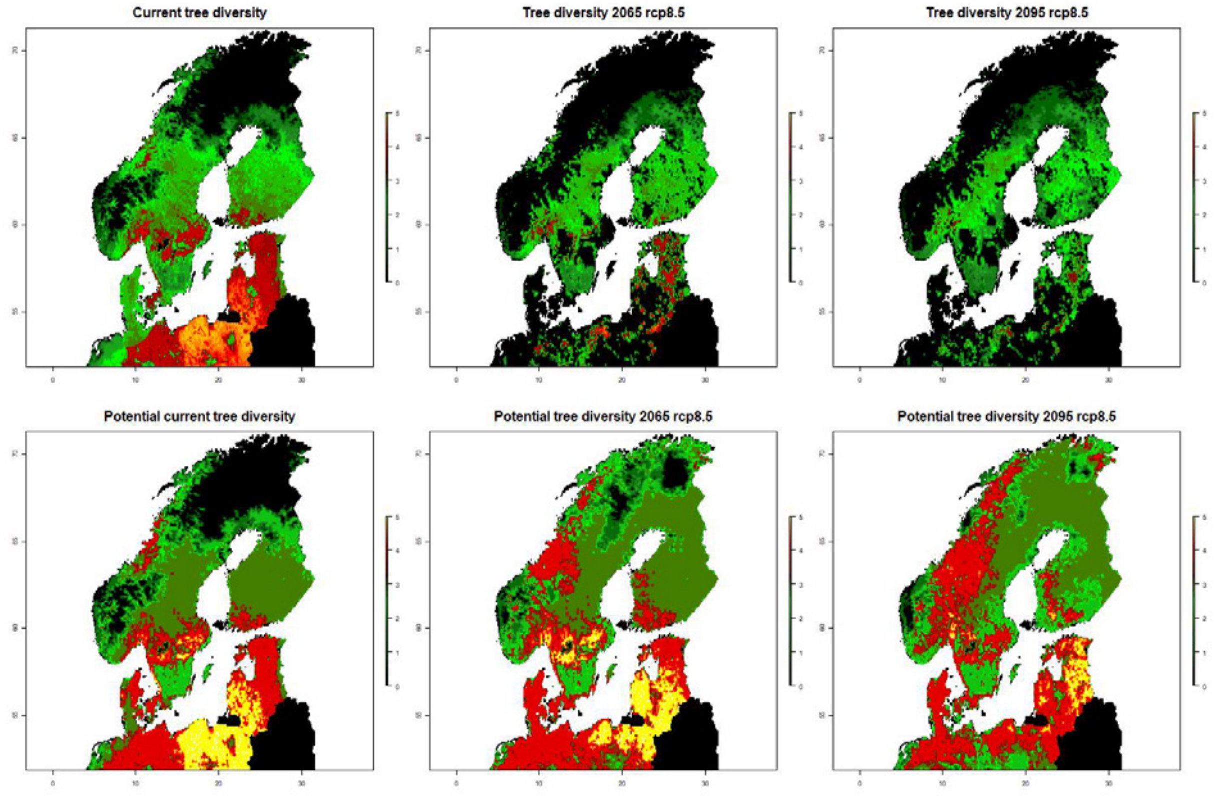


Figure 22b

Figure 22. Current and future summed expected and potential occurrences for distributions of aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), white willow (*Salix alba*), alder (*Alnus incana*), and elm (*Ulmus glabra*) in Europe for RCP4.5 (**a**) and RCP8.5 (**b**) mean scenarios respectively. The analyses are based on the same EURO-CORDEX climate models used by the NCCS, and are coupled with tree distributions, climate-, soil- and land use data to develop a data set of 67 European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers (see 4.2.1.1). Tree dispersal capacity has been explicitly modeled, giving probability of each species occurring (from 0 to1, approximately 10x10km resolution). The upper rows show actual expected distributions today and in the short and longer-term future, when dispersal capabilities and range loss (i.e. both lagging and leading edge dynamics) are taken into account. The lower ranges show the potential distributions, i.e. how many species would be capable of growing in an area if they somehow could instantaneously follow their climate zones. Habitat preparation, active planting and other management strategies might improve the achieved diversities.

4.2.2 Ericaceous dwarf shrubs

Growth. Despite their broad climatic and geographic ranges and dominant ecosystem roles across boreal, alpine, and arctic vegetation zones, dwarf shrubs and their roles in ecosystem functioning can be sensitive to climatic variability. The impact of increased temperatures on the growth and phenology of bilberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*) in arctic, alpine, and boreal areas was assessed experimentally and reviewed by

Taulavuori et al. (2013). This review found that experimental warming of air or soil of at least 5°C above ambient temperature during the growing season caused increased shoot growth of bilberry and lingonberry, as long as sufficient water was available. In sub-arctic crowberry (*Empetrum nigrum*) heaths, an extreme winter-warming event caused up to 87% reduced growth of crowberry during the following summer, and a 26% reduction in vegetation greenness as derived from satellite-derived Normalized Differential Vegetation Index values over an area of 1424 km^2 (Bokhorst et al. 2009).

Mortality. It is becoming increasingly clear that dwarf shrubs may experience increased mortality in the large-scale die-back events known as "Arctic browning"' that are now appearing throughout the Arctic and boreal zones globally, that may counteract the more well-studied "Arctic greening" (Phoenix and Bjerke 2016; Bjerke et al. 2017; Wang and Friedl 2019; Treharne et al. 2019). For most of the dwarf shrubs, these browning events are linked to the sensitivity of dwarf shrubs to complex climate-change impacts, such as changes in snow cover, sudden warm spells, or frost droughts during winter. The events are also linked to increased nutrient loads and changes in biotic interactions, such as large-scale insect outbreaks (Bjerke et al. 2017). However, in this study it appears that it is not climate change directly that has been affecting *Vaccinium* mortality, but extensive outbreaks of leaf-defoliating geometrid moths (Bjerke et al. 2017).

Winter warm spells may be detrimental to frost hardiness and survival of dwarf shrubs, and Taulavuori et al. (2013) reported that frost hardiness was most severely reduced when plants were subjected to 2 to 10°C of warming for a few days in the absence of a snow cover (i.e., experimental snow melt), followed by a return to below-freezing winter temperature. These winter warm spells increased mortality by 50% for bilberry and 80% for lingonberry and may contribute to browning events. Similarly, Bokhorst et al. (2018) found that midwinter warm spells (6°C for 7 days) followed by severe cold exposure (−20°C) resulted in 67-97% and 60-67% mortality in lingonberry and crowberry (*Empetrum nigrum ssp. hermaphroditum*), respectively. Mortality was highest when the cold exposure occurred without snow protection. Both species survived warm spells that were followed by a less severe cold exposure (-10°C). Snow cover may thus play a vital role in determining mortality of *Vaccinium* species. The sensitivity to frost in bilberry and lingonberry is most profound in populations living in cold conditions, which is likely a result of these populations being adapted to permanent snow cover during winter (Taulavuori et al. 2013).

Phenology and recruitment. Long-term bilberry yields are positively correlated with previous summer temperatures (increased floral initiation) and snow cover duration (frost protection), but negatively correlated with high autumn temperature (impaired cold hardiness: Selås et al. 2015). Flowering is one of the main determinants of berry production in addition to sufficient pollination and other factors affecting fruit set. Bilberry flowering can be greatly reduced after warm spells during cold winters (Bokhorst et al. 2008), or after premature de-hardening following mild winters (Ögren 1996). Winter warm spells can delay bud break and have been found to reduce flowering in bilberry by up to 90% (Taulavuori et al. 2013). Earlier snowmelt in spring, with subsequent earlier flowering, may increase detrimental frost effects on bilberry flowers (Selås 2006, Taulavuori et al. 2013).

Fires may affect recruitment processes in dwarf shrubs. Typically, both bilberry and lingonberry recover vegetatively from rhizomes to a pre-fire state after a maximum of four years if the fire does not affect deeper soil layers (Taulavuori et al. 2013). Under an absence of forest fires, Nilsson and Wardle (2005) predict decreased abundance of both bilberry and lingonberry, which benefit crowberry (*Empetrum nigrum*), indicating that these *Vaccinium* species are partly adapted to fire disturbance. Deep-burning fires can damage or kill rhizomes but stimulate colonization from seeds, resulting in a prolonged regrowth trajectory. As *Vaccinium* species are often dominant in boreal understories, fire disturbance and removal of this layer may positively affect recruitment of grasses and trees (Mallik 2003, Taulavuori et al. 2013), and hence influence successional trajectories.

As dwarf shrubs are affected by changes in both climate means and extremes, the net effect of climate change on their phenology, reproductive output, and abundance is hard to predict. Also, there is a need for more long-term research that targets the many biotic interactions of *Vaccinium* shrubs with mutualists and antagonists. Such information enables more precise predictions of these functionally important species responses to climate change. In sum, the findings presented above indicate that variable snow and temperature conditions during winter may be a major climate-change induced stress factor for ericaceous dwarf shrubs. The deciduous bilberry may be sensitive to changing winter- and spring conditions, whereas the evergreen lingonberry is more robust. Crowberry (*Empetrum nigrum*) is more drought tolerant than lingonberry (Shevtsova et al. 1997) and may benefit from a drier climate.

4.2.3 Other understory plants

In Nordic boreal forests, the non-woody species, such as vascular plants, ferns, bryophytes, and algae in the forest understory, is generally only about 5% of the total primary producer biomass (Nilsson and Wardle 2005; Muukkoneni and Mäkipää 2006; Wardle et al. 2012; Søgaard et al. 2019). These plant groups often have high turnover rates and high total ground cover and can therefore play an important role in the recovery of carbon stocks after disturbance (Dirnböck et al. 2020). The understory plants may thus take up amounts of CO_2 from the atmosphere equivalent to the uptake of trees (Wardle et al. 2012). A substantial proportion of the carbon that the understory plants take up is transported below ground to roots, mycorrhizal partners, and into the soil as exudates (Nilsson and Wardle 2005).

Increasing temperatures, increasing precipitation, and a longer growing season are expected to cause an increase in the growth rates in the understory (Abramoff and Finzi 2015). Understory plants cay also play an important role in the establishment and succession of trees in presently unforested areas beyond the current forest line, where they may facilitate movement by modifying microclimate and soil conditions (MacDougall et al. 2021; see 4.4 for more on range shifts) or inhibit tree regeneration via competitive interactions (Tingstad et al. 2015). Generally, natural disturbances that open gaps in the forest canopy have a positive influence on understory plant biomass through improved light conditions, and understory plant biomass tends to recover relatively quickly to a level exceeding the pre-fire conditions (Certini 2005). Dwarf shrubs are vulnerable to a suite of climate-change factors, maybe most importantly to reduced snow cover and so-called frost-drought during winter. Both bilberry and lingonberry seem to be especially vulnerable but little is known about their resilience to interacting climate-change factors. Reduced productivity of palatable dwarf shrubs is expected to have cascading impacts in the food web, because several boreal rodents, grouse and ungulates are dependent on these plants .

Based on data from the Swedish National Forest Inventory, Hedwall et al. (2019) compared changes in occurrence of a large number of ground flora species during a 20-year period (1994-2013) in boreal and temperate Sweden and concluded that a majority of the common ground flora species have changed their overall frequency from historically observed patterns. The changes are caused by combined and often confounded effects of climate warming, nitrogen deposition and changing land-use, where forestry is the most important factor (Hedwall et al. 2013). An increase of species with more southern and western distribution limits suggested ongoing effects of a moister and milder macroclimate in southern Sweden (Hedwall and Brunet 2016).

Literature reviews find that fine-root lifespan is expected to decrease with increasing temperature and drought, especially for forbs, shrubs and grasses (Cudlin et al. 2007; Chen and Brassard 2013). The lifespan of the fine roots affects the capacity of a plant to take up water and nutrients from the soil, thereby influencing plant growth (McCormack and Guo 2014).

4.2.4 Bryophytes and lichens

Bryophytes (mosses, liverworts, and hornworts) are susceptible to changes in environmental conditions as they lack mechanisms to regulate water content, and are therefore expected to be particularly affected by increasing temperatures (He et al. 2016), as well as changing water availability (Greiser et al. 2021). Photosynthesis by bryophytes can occur at low temperatures but rarely operates above 26°C in tundra systems. Consequently, a limited capacity to adapt to warmer temperatures could reduce performance of bryophytes under increasingly warmer conditions (He et al. 2016). However, responses to temperature depend on water availability. A transplant study in southern Sweden found bryophyte and lichen performance increased under warming, when there was high soil moisture availability, particularly during hot and dry growing seasons (Greiser et al. 2021). Increasing temperatures may also result in shorter growth periods during the year, contrasting the trends for vascular plants, and cause a reduced bryophyte biomass. On the other hand, the ongoing climate warming has resulted in prolonged autumnal growing seasons for the bryophytes in the boreal forest understory vegetation, which is highly favorable for certain large- and fast-growing bryophyte species. For example, the common and widely distributed moss species *Hylocomium splendens* and *Rhytidiadelphus loreus* have more than doubled their abundance in Norwegian spruce forests over the last 30 years, as documented by long-term monitoring of vegetation change in a broad range of Norwegian spruce forests (Økland et al. 2004; Framstad 2014, Framstad et al. 2021). The expansion of large and fast-growing bryophytes has occurred at the expense of smaller and more slow-growing species, such as liverworts. An increase of large mosses that overgrow small mosses has been attributed to the absence of cyclic population peaks of moss-eating small rodents (Rydgren et al. 2007, Framstad 2017).

Lichens are among the organisms most sensitive to climatic conditions due to their physiological characteristics, growth on exposed surfaces, and sessile lifestyle. For example, lichens cannot regulate their water content and are dependent on moisture in their environment. Due to their tight coupling to climatic conditions, bioclimatic modelling suggests a significant shift in suitable climate space for many lichen species. Sensitivity to climate change is affected especially by the photobiont (algal or cyanobacterial partner) and reproductive mode (Phinney et al. 2021). For instance, trebouxioid species are sensitive to temperature increases, while trentepohlian prefer warmer climates, and trentepohlian species and cyanolichens prefer wet climates (Phinney et al. 2022, Nelsen et al. 2022). Asexual reproduction via soredia or isidia is positively associated with warmer temperatures. Among the hair lichens, *Usnea* species are expected to expand northwards with climate change, while *Bryoria* species will likely decline because of warmer and wetter climates (Phinney et al. 2021). The climate responses of hair lichens, however, depend on interactions with forest management. In Sweden, logging of forests with long continuity of tree cover and excess nitrogen seems to be the main reasons for current lichen decline, suggesting increased disturbance rates would be difficult for dispersal-limited species like *Alectoria* species (Esseen et al. 2022).

Long-term monitoring of spruce forests has shown that on several sites, more thermophilic epiphytic lichens (e.g., *Hypogymnia physodes*) have increased, whereas cold-tolerant species (such as the red-listed *Melanelia olivacea*) have decreased and exhibited higher damage rates (Framstad 2014). Despite the presumed high freezing- and drought tolerances of lichens, changes in freeze-thaw cycles may negatively affect the fitness of some lichen species (Solhaug et al. 2018). On the other hand, a review of studies of epiphytic lichens and bryophytes found that microclimate was not the main factor determining the distributional patterns of the species studied, but rather, diaspore production, early fixation of diaspores, and poor dispersal ability (Znotina 2003).

Lichens and bryophytes are slower to recover after destructive disturbances than other understory functional groups and are as such expected to be more strongly affected if fire frequency increases in the future (Hart and Chen 2006).

4.2.5 Production of dead wood

A recent comprehensive review by Sandström et al. (2019) suggested that climate change could potentially have positive outcomes for a wide variety of boreal fungi, animals, and microbes that are dependent on significant inputs of dead wood (see also Müller et al. 2014). Expected increased tree growth should produce larger volumes of dead wood in boreal forests of northern Europe. However, warmer temperatures also increase the rate of decomposition, thereby reducing habitat suitability for many dead wood organisms (Mazziotta et al. 2016).

Warmer summer temperatures with more frequent periods of drought, combined with more frequent windstorms, may increase the frequency of natural disturbances that create dead wood, such as fires, insect- and disease outbreaks, and windfells from storms. Intensified fluctuations in winter precipitation and temperature during winter would increase breakage from snow and ice, which may further increase amounts of dead wood. Over time, the variety of dead wood may increase if the frequencies of broadleaved trees increase in what are currently conifer forests. This may increase the number of environmental niches and enhance the diversity of species and species interactions (see section 4.2.11.4).

4.2.6 Birds

Resident and migratory birds are greatly influenced by environmental conditions, for example showing declining densities towards northern latitudes (Forsman and Mönkkönen 2003). Hence, there are concerns regarding large scale shifts of species distributions in the bird-rich boreal forests, leading to novel competitive interactions that may alter community dynamics (Grinde and Niemi 2016). Our knowledge of climate change effects on the distribution of forest birds in Norway is, however, limited.

The bird community in subarctic birch forest in Finnmark experienced only a moderate reduction in abundance and species richness after the forest was severely impacted by geometric moth outbreaks linked to climate change (see 4.2.11.2). This bird community was less impacted (and thus more resistant) than expected based on the massive loss of living tree stems (Vindstad et al. 2015). In Swedish alpine- and boreal bird communities, species have changed their distributions according to climate change predictions: southern species have expanded their range further northwards, while northern species more often experienced range contractions (Elmhagen et al. 2015; Tayleur et al. 2016). In general, alpine and northern bird species in Sweden have declined in abundance, which possibly may be caused by a warmer climate (Elmhagen et al. 2015).

Studies from Finland also report reduced abundance and diversity of typical boreal bird species. Studies from Finland show that many forest birds have declined in abundance during recent decades, also in protected forests (Virkkala and Rajasärkkä 2011). Bird populations in close to a hundred protected areas in Finland were compared over a mean time of 14 years. The results indicate that northern species had declined by 21% and southern species increased by 29% in boreal protected areas during the study period, alongside a clear rise in mean temperatures. In managed Finnish forests, studies have also found declines in the south, where the total number of nesting pairs in managed forest areas declined by 18% in 22 years, which was due to both climate change and forestry (Virkkala 2016). Lehikoinen et al. (2018) found that northern boreal bird species were better able to adjust to rapidly changing climatic conditions in protected areas than in areas subjected to more anthropogenic disturbances.

The high bird species turnover observed in northern Europe could affect the functional diversity of species communities (Lehikoinen et al. 2016, Virkkala and Lehikoinen 2017). True woodpeckers (Picinae) are important ecological engineers that benefit other cavity nesting species, especially in managed forests, and are dependent on a diversity of tree species and on the availability of dead wood and accompanying invertebrate food resources (Remm and Lohmus 2011). Walsh et al. (2019) suggested that woodpeckers are a good indicator species of forest ecosystem dynamics (see also Angelstam and Mikusinski 1994 on this point) and that they are correlated with forest avifauna community diversity. Climate impacts on woodpeckers may both act through changed availability of food resources (mostly saproxylic insects) and suitable nest trees, although we are not aware of European studies that have specifically investigated the impact of climate change. However, one may hypothesize that woodpeckers will benefit from improved habitats under climate change in the short term. Bursts of dead wood after large-scale disturbances, such as insect outbreaks, storms or fires benefit some woodpeckers, but changes in tree composition, particularly after fires, could pose longer term problems for woodpeckers (Walsh et al. 2019). Increases in rainfall could also play a role. In a global study of the distribution of tree cavities in forests, cavity density was strongly correlated with precipitation (Remm and Lõhmus 2011).

Most birds have advanced their arrival time and onset of breeding in northern Europe (Lehikoinen et al. 2019). An analysis of over 820,000 nesting records of 73 bird species across the boreal region (not just forest birds) in Finland found an advanced onset of breeding, but no systematic variation between north and south. One-third of the bird species contracted their breeding period in at least one bioclimatic zone, which was found almost exclusively in resident and short-distance migrating species (Hällfors et al. 2020).

The abundance of grouse species is generally declining across their ranges (Storch 2007, Moss et al. 2010). Decline in capercaillie (*Tetrao urogallus*) and black grouse (*Lyurus tetrix*) in Norway appear to be primarily caused by intensified land use and forestry practices creating younger and denser forests, as well as increased predation rates, which may be enhanced by climate change (Jahren et al. 2016). Regarding potential phenological mismatches impacting forest grouse population, see Section 4.5.3.

4.2.7 Bats

Many bat species are predicted to move north in response to climate change (Rebelo et al. 2010). Habitat specialists are at greater risk of extinction than generalist species (Safi and Kerth 2004). For example, for bat species depending on old mature forests, the climate-induced changes may be too fast to accommodate required shifts in bat distributions (Jones and Rebelo 2013). Bat species associated with colder climates, like in Fennoscandia, are more likely to be negatively affected by climate change, compared to Mediterranean and temperate zone bats (Rebelo et al. 2010). Climate change is affecting the distribution of bat populations, and leads to changes in phenology, i.e., timing of birth, hibernation duration, and temporal mismatch with food availability (Jones and Rebelo 2013). Direct climate effects that affect bat survival and reproduction include scarcity of water, and changes in the microclimatic conditions within roosts, which could affect crucial life cycle stages such as breeding and hibernation (Jones and Rebelo 2013).

4.2.8 Rodents and lagomorphs

Climate has a large impact on small rodents, such as voles and wood lemmings, and on their population cycles (Ims et al. 2008; Korpela et al. 2013), suggesting that rodents will be affected by climate change. A recent review by Andreassen et al. (2021) concluded that it is hard to predict the effect of climate change on the population dynamics of rodents, and that this is one of the main questions for future studies of rodents.

Temperature fluctuations around the freezing point can lead to ice formation from undercooled rain and accumulating ice on above-ground parts of plants and other structures, making food less accessible to many animals (Mölle et al. 2022; Kausrud et al. 2008).

The cycle amplitudes and spring densities of rodents have generally declined in Europe over the past 50 years and changing winter and snow conditions may be important explanatory factors for this decline (Elmhagen et al. 2015). Shorter periods with snow cover are likely to affect winter survival of voles and lemmings negatively before the turn of the 21st century (Andreassen et al. 2021) and, consequently, it has been shown that the dampening of cycle amplitudes was a result of reductions in population growth rates during winter (Cornulier et al. 2013), probably in interaction with specialist predators (Kausrud et al. 2008). However, the cycle amplitude has increased over the two last decades (Elmhagen et al. 2015), underscoring the complexity of the relationship between small mammal population dynamics and environmental factors, and that the dynamics may be subjected to a great deal of change in cyclicity (e.g. transient dynamics; Henden et al. 2009). The gray-sided vole (*Myodes rufocanus*) is one of few species where population cycling may have been lost more permanently in parts of its range in boreal forests (Elmhagen et al. 2015), however, the cause of the loss is not clear (Magnusson et al. 2015). The disruption of population cycles of field voles and tundra voles (*Microtus* species) has a clearer link to the frequency of freeze-thaw cycles during winter (Aars and Ims 2002). Bank voles (*Myodes glareolus*) are among the most abundant rodents of boreal forests, but the species can decrease in density in years after warm summers (Selås et al. 2011). In Finland, the influence of climate dynamics on the population dynamics of voles differs among the bioclimatic sub-zones within the boreal forest (Korpela et al. 2013), with longer plant growth seasons appearing to counteract the adverse winter effects in the southern regions.

The mountain hare populations in Fennoscandia and Scotland have been declining during the last decades, and the species has recently been categorized as Near Threatened on the National Red Lists in Norway, Sweden, and Scotland (Mathews and Harrower 2020, Thurfjell et al. 2020, Eldegard et al. 2021, Pedersen et al. 2021).

The mountain hare appears to be negatively affected by climate warming (Pedersen et al. 2012, 2017, Rehnus et al. 2018).

Pedersen et al. (2017) found that the number of hares was negatively associated with a short duration of snow cover, and that this effect was stronger in areas with a high number of predators. Pedersen et al. (2017) expect a further decline in mountain hare populations in the future, caused by the combined effects of reduced period of snow cover, increasing densities of generalist predators, and the hare's limited ability to adapt to the ever-increasing degree of "mismatch" between fur color (summer / winter fur) and the environment. This color mismatch is induced by climate change, and it makes the hare more vulnerable to predation due to poor camouflage. Recent studies from Scotland confirm that the mountain hare is unable to adapt its seasonal coat change to changes in the duration of the snow cover, and that the degree of mismatch is increasing (Zimova et al. 2020). Zimova et al. (2020) suggest that the costs of mismatch in the form of increased predation pressure, can have greater negative effects on the hare population in areas with more intact predator communities, such as in Norway.

In Norway, competition between the native mountain hare and the alien brown hare (*Lepus europaeus*) is so far largely limited to Østfold, but the brown hare benefits from climate change. The brown hare is categorized as "very high risk" on the Norwegian Alien Species List because it will likely establish and spread in Norway (Pedersen et al. 2018). The brown hare can affect populations of the native mountain hare, both through hybridization (Levänen et al. 2018) and perhaps displacement, as well as transmission of parasites and pathogens (Pedersen et al. 2018).

Being an aquatic rodent, the Eurasian beaver (*Castor fiber*) may be expected to be more affected by changes in precipitation than by changes in temperature. Studies assessing the effects of climate on Eurasian beaver have found that increased winter- and spring temperatures causes decreased body size and reduced reproductive success (Campbell et al. 2013). Survival was highest in years with low precipitation as well as those with low variability in precipitation and temperature (Campbell et al. 2012). As for many other herbivores, some of the climate effects appeared to work via reduced availability or quality of spring forage (Campbell et al. 2013).

4.2.9 Large herbivores

In addition to climate and natural habitat, the distributions of ungulates in Europe and Norway have been shaped by hunting, land use and management over centuries. The geographical distribution of moose in Europe has, for example, extended both northwards (Tape et al. 2016) and southwards (Jensen et al. 2020) over the last decades and in Norway red deer in the early 1900 only survived in five to six small populations in western Norway (Haanes et al. 2010) but is now present in most parts of the country. Moose can be characterized as a typical boreal and temperate forest species, whereas red deer, roe deer, and wild boar are largely temperate species that prefer milder climates, and that have advanced northwards over the last century (Linnell et al. 2020; Elmhagen et al. 2015).

The extent of the impact of climate change on the different ungulate species will likely depend on the combination of changes during growth season affecting food quality, e.g. early and warm spring conditions reduces plant quality in calving season, and conditions during winter, such as the amount and length of snow cover which may affect access to food in the shrub layer (Langvatn et al. 1996; Post et al. 1997; Holmes et al. 2021). The climatic effects are often studied as impacts on body size, an important determinant of reproductive success that affects population dynamics.

Body mass in autumn of Norwegian moose appear both to be negatively affected by warm winters and springs with rapid plant development which could be a consequence of a mismatch between timing of calving and the availability of high-quality forage (Herfindal et al. 2006). Also, moose calf weight and recruitment rates in Sweden were reduced when spring had more hot and dry days and warmer average temperatures (Holmes et al. 2021). Negative effects of climate warming on moose body mass is particularly evident at the southern range limit in the USA, and may potentially cause increased mortality (Hoy et al. 2018). North American moose populations have been predicted to extend their suitable habitat by gaining new habitat in the northern USA but losing suitable habitat in the southern USA under RCP4.5 and RCP8.5, a habitat that may be lost by year 2070 (Deb et al. 2020, see also Frelich et al. 2012). We may tentatively expect the European moose to experience similar effects, due to the similar ecology of the species. In Norway, the effects of a milder and warmer climate may be driving the reductions in abundance and body weight seen in harvest data from southern Norway as well as the increased abundance and size seen in northern Norway over the last decades (Solberg et al. 2017; Framstad et al. 2021; Statistics Norway 2022[*statbank*]). All these results seem valid for the ongoing, as well as for the projected, climate changes.

Norwegian red deer is also negatively affected by warmer winters inducing rapid plant development in spring with lower plant quality later in season (Post et al. 1997; Mysterud et al. 2008). Also, deep snow conditions caused by higher levels of winter precipitation may reduce availability of forage in winter and has been shown to negatively affect body size and winter survival of, in particular, red deer calves (Loison et al. 1999). On the other hand, warmer winters with reduced snow cover may benefit adult red deer as the loss of body mass during winter may be reduced (Mysterud et al. 2008) and consequently studies on habitat suitability for red deer in Norway predict increasing habitat availability for red deer under current warming scenarios with reduced snow cover (Rivrud et al. 2019). In North America the most abundant deer species, white-tailed deer (*Odocoileus virginianus*), appear to gain more new habitat under these climate scenarios than moose (Deb et al. 2020). This is also relevant in eastern Scandinavia, where the European roe deer (*Capreolus capreolus L.)* has been increasing in abundance at its northern range (Danilov et al. 2017), and white-tailed deer that were introduced to Finland about 90 years ago (Kekkonen et al. 2012) are expanding their range northwards (Aikio and Pusenius 2022). Some findings indicate that in temperate, but also boreal, areas of North American deer species may already be replacing moose, probably because moose is more prone to detrimental physiological effects of warming and is also indirectly affected by climate change via higher susceptibility to many parasites (Frelich et al. 2012).

The Eurasian wild boar (*Sus scrofa* L.) is the progenitor of domesticated pigs. It is distributed from western Europe to eastern Asia and insular southeast Asia and is one of the widest ranging mammals in the world. The species was eradicated from Norway about a thousand years ago, and has only recently re-colonized Norway via Sweden. Though regarded as native in Sweden, the wild boar is considered to be an alien invasive species Norway (VKM 2018). The spread into Norway has likely been facilitated by warmer winters and less snow cover, and the boar is expected to increase greatly in abundance and to spread widely in Norway with further warming (Bosch et al. 2020, Gjershaug et al. 2009). See VKM (2018) and Pedersen (2018) for more information on the expansion of wild boar with possible effects on soil disturbance, plant mortality and seedling recruitment in forest.

4.2.10 Large predators and omnivores

Large and meso- predators in Norway (mainly foxes, wolves, brown bear, wolverine and lynx) are regulated primarily through hunting that holds populations to very low levels. These species are on top of the food chain and as such may be less directly influenced by climate, but relatively strongly affected indirectly by climate induced changes in food availability. The relatively broad diets of large predators may make them relatively resilient to changes in food web structure resulting from climate change. However, all the mammalian predators in boreal forests have large geographical distributions, with a bias toward boreal areas. While there are few studies on these predators' responses to climate change, it is generally believed that climate change will favor southern and generalist species, expanding in range and abundance, while having the opposite effect for northern specialists (Elmhagen et al. 2015).

The wolverine (*Gulo gulo*) is considered a northern species that belongs to alpine-arctic tundra and boreal forest. Wolverines may be vulnerable to changing snow properties, as they seem to prefer deep dense snow and avoid melting parts (Glass et al. 2021) and have a cold-adapted physiology (Thiel et al. 2019). The distribution range of the wolverine has been predicted to become more fragmented and overall reduced as the extent of suitable snow cover is diminished under climate warming (McKelvey et al. 2011).

Lynx (*Lynx lynx*) has a pan-European distribution and is considered a southern species by Elmhagen et al. (2015). Swedish lynx mortality studies seem to indicate an overwhelming influence of poaching (mostly in the ungulate hunting seasons), management, and little direct climate impact (Andrén et al.2021). Thus, climate impacts on lynx seem to be determined through interactions with prey and human land use.

The same is the case for gray wolf (*Canis lupus*), whose historical distribution indicates a much larger potential range than the climate zones in which it is currently found, and mortalities determined by poaching and management (Ståhlberg et al. 2017; Liberg et al. 2020).

The brown bear (*Ursus arctos)* body mass and survival are affected by bilberry production, with fat acquisition prior to hibernation being a critical step vulnerable to a lack of berries (Hertel et al. 2018) and may thus be negatively impacted by climate events that negatively impact bilberry. A paleoclimatic study suggests that the distribution and abundance of the Eurasian brown bear has declined with increasing winter temperature over longer time scales (Albrecht et al. 2017).

The red fox (*Vulpes vulpes*) is the most common mesopredator in European boreal forest (Boonstra et al. 2016). It is an extremely adaptable, generalist predator found in all ecosystems in Europe (even intensively managed agrarian and urban ecosystems; Bateman and Fleming 2012) and hence, is expected to do well under climate change (Elmhagen et al. 2015).

4.2.11 Forest insects

4.2.11.1 Herbivorous forest insects

The biomass of herbivorous forest insects is expected to increase with climate change, and particularly with increasing air temperature (Rubtsov and Utkina 2020), owing to a reduction in generation times and increased reproductive success and survival rates. Reductions in biomass could also occur when there is high mortality during periods of extreme heat, worsening resource quality, or an increased abundance of natural enemies (Chung et al. 2013; Jactel et al. 2019). Longer, warmer summers can increase the number of generations completed per year and thus increase the maximum reproduction possible in one season. However, more generations do not necessarily mean a higher population size at any given time. This is because depending on density-dependence and limiting resources, this would more likely intensify population dynamics by allowing faster population growth, increase the extent of potential outbreaks of bark beetles, or even cause boom-bust cycles (Forrest 2016; Pureswaran et al. 2018; Jactel et al 2019).

Several forest insects associated with conifers in Norway, but which do not seem to currently affect forest production to a significant extent, may increase their abundance in a warmer climate. Haynes et al. (2014) studied the frequency of outbreaks by pine defoliating insects that cause large-scale damage in other parts of Europe today. These insects could affect pine production in Norway in the future even though they do little damage today (Hanssen et al. 2019). They include the pine-tree lappet (*Dendrolimus pini*), the bordered white or pine looper (*Bupalus piniaria*), the pine beauty (*Panolis flammea*), the black arches or nun moth (*Lymantria monachia*), the common pine sawfly (*Diprion pini*), and the European pine sawfly (*Neodiprion sertifer*). Haynes et al. (2014) examined a 212-year record of outbreaks of these defoliators in Bavaria, Germany. Precipitation changes only affected *Dendrolimus pini*, which tended to undergo outbreaks after drought. Responses to temperature were stronger but varied among species: warmer than usual weather periods could increase or decrease outbreak activity depending on the species. However, a shared feature was that climate change was often associated with the collapse of population cycles. Hanssen et al. (2019) concluded that there is yet little knowledge about potential tree damage in Norway under climate change from the aforementioned species. However, as the species are associated with (sometimes severe) damages rather than mortality in the southern parts of their current ranges, it is expected that their effect will be to weaken trees, thereby reducing production and shifting competitive relationships with broadleaf trees rather than simply causing mass tree mortalities in pine.

Hällfors et al. (2020) used a dataset spanning two decades to investigate temporal shifts in phenology (adaptation to climate change) and spatial shifts in northern range boundaries (dispersal success) in response to a changing climate for 289 species of butterflies (Lepidoptera) in Finland. As an example of colonization lag, they found that 40% of the species neither advanced their phenology nor expanded northward. Nearly half (45%) adopted one of the two strategies, while 15% both advanced flight phenology and shifted their range boundaries northward.

The generation time of the pine weevil (*Hylobius abietis)*, a species that breeds in roots of dead trees and stumps on clear-cuts, decreases with increasing temperatures (Bejer-Petersen et al. 1962). Elevated summer temperatures are expected to speed up development of eggs and larvae and increase survival rates (Inward et al. 2012, Nordlander et al. 2017). As the pine weevil may kill on average 9% of young planted spruce, climate change is likely to affect forest production. Mortality of seedlings in natural forests due to the weevil has been little studied but is likely to be correlated with the degree of mortality in managed forests.

We can expect that forest insects (and the plants they depend upon) will gradually shift their ranges northwards and to higher elevations in a warming climate. Pureswaran et al. (2018) find that the effects of climate change on forest insects are species-specific, and that the direction of climate effects on population dynamics (positive or negative) depend on the specific ecological interactions and on how different life cycle stages (eggs, larvae, pupae, adults) are affected by climate, thus making generalizations difficult.

4.2.11.2 Eruptive herbivorous insects

Much of what we know about current responses of forest insects to recent climate change comes from analyses of eruptive insects, which are species which occasionally or regularly exhibit population explosions and have large effects on the forest ecosystems. In a comprehensive general treatise on forest insects and climate change, Pureswaran et al. (2018) reviewed the global literature on insect outbreaks published from 2013 to 2017. They focused on insect range expansion, abundance, impacts on forest ecosystems, and effects on forest insect communities. Effects of climate change were clear for many species and feeding guilds, but responses to changes were species-specific. Some species or guilds had expanded their ranges in response to a changing climate, while others had not, and synchrony between hosts and pests was disrupted in some examples, but not in others.

Bark beetles are likely to respond to climate change by undergoing larger and more frequent outbreaks (Raffa et al. 2008, Seidl et al. 2008, Pureswaran et al. 2018, Beidermann et al. 2019, Bentz et al. 2019, Hlásny et al. 2019, Venäläinen et al. 2020). Extrapolating from studies in Finland (Venäläinen et al. 2020, see also Seidl et al. 2008, Seidl and Rammer 2017, Seidl et al. 2017), areas of southeast Norway might become suboptimal for spruce and likely suffer greater wind damage and more severe summer droughts. Over time, the probability increases for large-scale wind damage followed by widespread *Ips typographus* outbreaks, perhaps amplified by a shift to two generations (bivoltinism) per summer rather than one (Lange et al. 2006, Romashkin et al. 2020). Further, large windfellings will mean increased food availability and may contribute to outbreaks in the next growing season (Marini et al. 2017). An increase in summer temperatures and length of summer could also lead to more frequent and larger outbreaks of currently secondary bark beetles like *Ips acuminatus* in pine forests, a trend that seems to have started in Scandinavia in the last decade or so (Siitonen 2014, Torstein Kvamme, personal communication). Milder falls and winters could also lead to lower winter mortality, as well as allowing an extra generation per year, thereby increasing outbreak risk (Pureswaran et al. 2018).

Defoliating moths have expanded their outbreak ranges and the outbreaks have become more intense in northern Norway. This is likely due to recent climate change, partly because mild winters improve winter survival of eggs on birch twigs (Neuvonen et al. 1999) and partly because there is an improved matching in phenology between hatching of eggs and budburst in birch (Jepsen et al. 2008, Jepsen et al. 2011, Jepsen et al. 2013). The autumnal moth (*Epirrita autumnata*) and the winter moth (*Operopthera brumata*) are the most important insect defoliators on birch in Norway. Large outbreaks cause both tree death and growth reductions in birch. Where outbreaks lead to severe defoliation, there are high levels of birch mortality and long-lasting changes to the understory plant community (a vegetation state shift: Vindstad et al. 2019). During the years 2002 to 2008, one third of the forest of northern Fennoscandia (approximately 10 000 km^2), including regions where moth winter survival used to be limited by low temperatures (Jepsen et al. 2009; Hanssen et al. 2019), was defoliated by these geometrid moths (Jepsen et al. 2009).

Populations of the European pine sawfly *Neodiprion sertifer* are predicted to expand their range to higher latitudes and elevations and outbreaks are likely to become more frequent and widespread in response to warming. Virtanen et al. (1996) studied the patterns of regional outbreaks in Finland in the years 1961-1990 in order to make predictions about outbreaks patterns to the year 2050, assuming a 3.5 ^{o}C increase in winter temperatures from 1991-2050. They tested for effects of winter temperatures, soil type, and forest type, which are three factors known to affect pine sawfly outbreaks. Sawflies (as birch defoliating moths) overwinter as eggs in the forest canopy and are not insulated from winter cold by snow cover but survive down to -36 ^{o}C. As climate change is making such extremely low winter temperatures increasingly rare in Fennoscandia, the sawfly populations may not be affected by such regional setbacks (see also Neuvonen et al. 1999).

4.2.11.3 Pollinating insects

Climate change thus far has led to reduced ranges for many groups of pollinators in Europe, including wild and managed bees (Soroye et al. 2020, Zattara and Aizen 2021). Ranges of many southern or low alpine bumblebees species are shifting to higher elevations while ranges of many northern species failed to track warming by moving up- or northwards (Kerr et al. 2015). In northern Sweden, high alpine species have also spread to previously unoccupied high alpine sites, perhaps due to increased mobility at higher temperatures and increased habitat availability because of melting glaciers (Franzén and Öckinger 2011). These shifts have caused increased species richness at higher latitudes in some regions (Franzén and Öckinger 2011; see also Zattara and Aizen 2021).

Many pollinators, including those found in open and agricultural landscapes, have parts of their life cycles in forests (Åström et al. 2014). European bumblebee populations have declined for half a century (Rasmont et al. 2015), and a dramatic decline is occurring across a majority of insect groups, including pollinators, across the northern hemisphere, possibly globally (Vasiliev and Greenwood 2021, Dicks et al. 2021, Wagner et al. 2021, Kehoe et al. 2021, Hallmann et al. 2021). The degree to which climate change is involved is still uncertain, but climate is likely one of the culprits and the overall insect decline is likely a confounding (and exacerbating) factor to climate change.

There are still relatively few studies on range and abundance shifts in Fennoscandia. In sub-alpine areas in Norway there appear to have been an increase in bumblebee richness at higher altitudes and a decrease at lower altitudes (Fourcade et al. 2019, see also Franzén and Öckinger 2011 for data from Sweden). Large-scale meta-studies confirm this shift towards higher altitudes, combined with a general range contraction through losing southern territories without gaining new habitats in the northern areas (Kerr et al. 2015). Furthermore, climate change likely contributes to widespread declines in pollinator abundance and richness in areas close to species warm limits, whereas climate change may have increased bumblebee occupancy in regions that were previously near species cold limits (Franzén and Öckinger 2011, Soroye et al. 2020). Using a modeling approach, Lever et al. (2014) show that pollinator populations may collapse suddenly once drivers of pollinator decline reach a critical point. A high connectivity or nestedness of the mutualistic network increases the capacity of pollinator populations to persist under harsh conditions, but, once a tipping point is reached, pollinator populations collapse simultaneously.

It should be emphasized that lags in responses to climate change by pollinator populations mean that we do not yet understand the full impacts (IPBES 2018). Since we do not yet know all the effects of climate change that have already occurred, our predictions of future impacts are probably conservative. Further, climate change is not necessarily the only, or even the most significant, factor affecting populations of pollinating insects. As with insects in general, pollinators are strongly impacted by loss or fragmentation of suitable habitats, competing invasive alien species, pesticides, and pollution (Steele et al. 2019).

4.2.11.4 Saproxylic insects

Saproxylic insects (insects dependent upon dead or dying wood) will be affected by climate-induced changes in wood quality and quantity, as their abundance and community structure are highly dependent on abiotic conditions (Bussler and Schmidt 2009, Sverdrup-Thygeson and Ims 2002, Vindstad et al. 2020). A change towards more deciduous trees and greater volumes of dead wood is expected, particularly in southern parts of the country (Mair et al. 2017).

A study from continental Europe observed that increasing temperature partly compensated for lower amounts of dead wood in production forest than in natural forest (Müller et al. 2014). In a study of oak-associated beetles in southern Norway, oak-specialist beetles with a northern distribution increased in species richness with temperature (Gough et al. 2015). In these two studies, generalists were relatively unaffected by climate changes; increased summer temperatures favor a few specialist species, but a larger number of specialists are likely to decline due to increased precipitation (Müller et al. 2014, Gough et al. 2015).

4.2.12 Soil organisms

Soil biodiversity plays a key role in determining the ecological and evolutionary responses of terrestrial ecosystems to current and future environmental change (Bardgett and van der Putten 2014). However, forest soil represents a challenging habitat to study. Soil organisms may be partly insulated against some of the drivers of climate change, including drought, warming and extreme events (Bertrand et al. 2016, De Frenne et al. 2019). The high complexity of the soil landscape could also contribute to making soil biota more resilient to change than above-ground organisms. Despite this conjecture, Bertrand et al. (2016) argue that extinctions of soil organisms have been ignored and overlooked, and that we need to pay more attention to the fabric of below-ground habitats. Moreover, soil fauna, while important drivers of biogeochemical function, soil structure and sustainability, and their trophic interactions, are understudied (Coyle et al. 2017).

Climate change is expected to increase the abundances of broadleaved trees in conifer forests in much of Norway. The species richness, abundances, and community structure of major components of the soil fauna (ants, earthworms, mites, springtails, nematodes, tardigrades, and others) will be affected by greater mixing of broadleaf trees with conifers, but the responses of individual species are variable (reviewed by Korboulewsky et al. 2016). Most studies included in Korboulewsky et al. (2016) show that increased richness in the tree layer has a positive effect on biodiversity, and that the responses of the soil community depend on the species of trees that are present. However, the soil community in a diverse deciduous forest in good ecological condition is not identical to the soil community found in a diverse spruce forest in good condition, and the transfer from one state to another is neither instantaneous nor necessarily fast or unproblematic at human time scales.

4.2.12.1 Oligochaete worms

Oligochaete worms (family Enchytraeidae) are especially abundant in cold and wet environments, where they frequently dominate the soil fauna and can make up as much as 97% of the live biomass of soil animals (Briones et al. 2014). A global meta-analysis of the effects of climate change on enchytraeids (44 published studies, most from Europe) found that the highest densities of enchytraeids were in cold and wet climates with mild summers (Briones et al. 2006). The known physiological limits and the meta-analysis both predicted that regions with mean annual temperatures over 12 °C would see a loss of oligochaete biodiversity. It is unlikely that Norway will see such warm temperatures before 2070. However, they are possible or even likely along the south coast in a belt that stretches further north and inland after 2070, and especially in RCP8.5-type futures (as referred to in 4.1). It seems likely that large temporal gaps in closed canopy conditions, resulting from bark beetle outbreaks or clear-cutting that make the soil directly exposed to sunlight, could result in local extinctions or severe population declines of enchytraeids. Oligochaetes in soils under a dense forest canopy would likely be less strongly affected since forests act as a thermal insulator such that the understory experiences lower maximum and higher minimum temperatures than does open ground (de Frenne et al. 2019) that also regulate soil water and air moisture (Ritter and Vesterdal 2006), providing more humid stable conditions in temperate European forests with more closed canopies (Holuša et al. 2021). For other groups of soil fauna, the literature is fragmentary.

4.2.12.2 Soil fungi and other microbiota

In macroecological and biogeographic community studies of soil microbes, climate factors are important drivers of community composition and richness. For example, for soil fungi, climatic factors, followed by soil characteristics (edaphic factors), were the best predictors of soil fungal richness and community composition at the global scale (Tedersoo et al. 2014, Větrovský et al. 2019). Soil fungi and bacteria will respond to temperature increases, but the strength and direction of the responses appear highly context dependent, being affected by local conditions, such as local plant communities, litter quality and quantity, hydrological conditions, and soil nutrients and pH (Jansson and Hofmockel 2020). Bacterial biomass in boreal forest soils does not seem to change much as a response to temperature increase, but the relative abundances of different types of bacteria, with differing functional roles, are known to change, affecting decomposition, the cycling of carbon and nutrients, and the mycorrhizal symbioses (Llado et al. 2017).

The activity of forest fungi is influenced by temperature and water availability; climate change is therefore expected to affect their ecosystem functions, with cascading effects on the carbon and nutrient cycles (Steidinger et al. 2019). In Norway, we can expect highly context dependent responses, since soil moisture content likely will decrease over larger areas due to higher evaporation with increasing temperatures, while it will increase in other areas, especially western Norway.

In a modeling study based on data from forest inventory plots (including NFI plots from Norway), Steidinger et al. (2019) showed that climate variables and particularly climatically controlled variation in the rate of decomposition were the most important drivers for the global distribution of mycorrhizal symbioses. Using projected climate conditions for 2070, their models predicted that the abundance of ectomycorrhizal trees will decline by as much as 10%, mainly in temperate and boreal forests (Steidinger et al. 2019). Their models suggest that arbuscular mycorrhizal vegetation and trees will move northwards and partly replace the ectomycorrhizal trees in a fifty-year timespan. This can also be expected to happen in Norway. However, their model did not consider time lags between climate change and forest community responses (e.g., dispersal limitations) and it is therefore uncertain how quickly the forest trees, and their associated mycorrhizal fungi, will respond.

The global study by Steidinger et al. (2019) mirrors findings by Jo et al. (2019) from North America. In both studies, researchers observed that the abundances of the two dominant mycorrhizal tree groups, arbuscular mycorrhizal trees and ectomycorrhizal trees, were associated strongly with climate. Based on both modeling of future conditions and using historic data from monitored plots, Jo et al. (2019) showed that anthropogenic influences, primarily nitrogen (N) deposition and fire suppression, in concert with climate change, have increased dominance by arbuscular mycorrhizal trees during the past three decades in the eastern United States. Hence, their study supports the scenarios outlined by Steidinger and colleagues.

Based on correlations between ectomycorrhizal fungal diversity and climate factors, another study by Steidinger et al. (2019) predicts a 26% decline in the diversity of ectomycorrhizal trees in North America in pine-dominated forests by 2070.

The few experimental studies where boreal forest vegetation and soil have been heated have largely provided inconclusive results. In one study, the composition of ectomycorrhizal fungal communities was altered, but only a small proportion of the fungi appeared to be strongly sensitive to warming (Mucha et al. 2018). In another study, it was observed that warming leads to a decline in the photosynthetic rate of boreal forest trees, again associated with a shift towards fewer carbon-demanding symbiotic mycorrhizal fungi (Fernandez et al. 2017).

For fungi that decompose wood, growth and decomposition are affected by climate and by wood quality. Wood quality is expected to change with climate change as increasing tree growth rates will produce less dense wood, as detailed by Venugopal et al. (2016, 2017) for four wood-decomposer species associated with pine. The growth rates of individual species and the overall efficiency of the fungal community function have also been shown to depend on community composition (van der Wal et al. 2015, Venugopal et al. 2018, Maynard et al. 2017, Maynard et al. 2018). More generally, in wood-decomposer fungal communities, the first species to disappear because of environmental change are the ecologically specialized species that typically have low rates of growth and reproduction (Ovaskainen et al. 2013, Nordén et al. 2013). Specialist fungi are competitive and stress tolerant in the environment that they are adapted to (for example, tolerant of low levels of nutrients, cool temperatures, and drought: Krah et al. 2019). Specialization is advantageous in long-lasting habitats, but this competitive advantage can be lost should the environment change rapidly, in which case generalists would be expected to have faster growth rates. The influence of temperature, precipitation, and other climate variables on the distribution of boreal wood-decomposer fungi has not been thoroughly studied, but Mair et al. (2017, 2018) predict overall decreasing habitat suitabilities with climate change for six near-threatened, old-forest associated wood-decomposer species. For rare specialist fungal species, characterised by narrow niches (Nordén et al. 2013), dispersal limitation (Norros et al. 2012), and low rates of local colonisations and high rates of local extinctions (Nordén et al. 2020, Moor et al. 2021) it can then be expected that sufficient area and connectivity of the habitat will be required to allow the tracking of the changing climate.

In a study from the Alps, Diez et al. (2020) observed that many fungal species fruited at significantly higher elevations in 2010 than in 1960, especially soil-dwelling fungi. Wood-decomposer fungi, associated with one or a few host tree species, showed a slower response, perhaps limited by the hosts distributions. Moreover, fungal species growing at higher elevations shifted their altitudinal fruiting patterns significantly further upwards than lowland species. The authors speculate that environmental changes at high altitudes may lead to relatively stronger responses, since high-altitude species live closer to their physiological limit (Diez et al. 2020).

An analysis of herbarium records in Norway for specimens collected between 1940 and 2006 revealed that the fruiting of mushrooms has changed considerably, most likely as a response to climate change. The authors predict that the projected rise of global temperatures will have considerable effects on fungal fruiting phenology. The phenological changes we observe for fruiting bodies likely mirror changes in the below-ground fungal mycelia, as later fruiting likely indicates extension of the growing season of the fungal mycelia and vice versa. This may have cascading effects on other organisms, as fruit bodies act both as habitat and diet for many organisms (Kauserud et al. 2008, see also Kauserud et al. 2012).

Fires can directly and indirectly affect the soil microbiome by altering biomass, species composition, and ecosystem processes (Köster et al. 2021). Direct impacts on soil organisms occur either through combustion or the heat generated by the fires (Jansson and Hofmockel 2020). Indirect impacts occur through shifts in the surrounding vegetation that alter soil properties (Tas et al. 2014). In many instances, the indirect fire effects may outweigh or counteract the direct effects of fire (Köster et al. 2021). The recovery of aboveground vegetation after fires may be particularly slow after a high intensity burn with strong impacts on the soil microbial communities (McLauchlan et al. 2020). Soil fungi, bacteria, and the invertebrate fauna often takes more than a decade to recover post-fire biomass, but recovery rates are dependent upon fire severity (Certini 2005; Allison and Trederser 2011, McLauchlan et al. 2020). For soil microorganisms, high intensity fires can sterilize the topsoil; for fires that are less intense, the biomass of soil microorganisms may be reduced as a result of organic pollutants produced by the combustion process (Certini 2005). In contrast, communities of ectomycorrhizal fungi show a high degree of continuity following low-intensity wildfires in Swedish boreal pine forests (Jonsson et al. 1999). Soil organism survival and recolonization are also indirectly affected by the heat from fires through changes to organic substrates, and the removal of sources of organic residues (Bissett and Parkinson, 1980; Monleon and Cromack, 1996). In boreal forests, fungi are more susceptible to fire impacts than bacteria and also have a slower rate of growth post-fire (Köster et al. 2021). While changes in microbial community composition are relatively undocumented in response to fire, ectomycorrhiizal fungi are noted to more substantially decline relative to other fungal groups, due to loss of vegetation (Köster et al. 2021).

4.3 Pests, pathogens, and parasites

Climate change is expected to increase the risk of establishment and spread of invasive species with a high risk of impacting the ecology of native forest ecosystems. With key vertebrate alien pests covered above (hares 4.2.8, wild boar 4.2.9), here we focus on invasive beetles (4.3.1 and 4.3.2), invasive and endemic fungal pathogens (4.3.3), fungal species causing root rot and butt rot (4.3.3), other plant diseases (4.3.4) and wildlife diseases (4.3.5).

Some potential invasive insects would have dramatic effects, for native forests, species such as the two North American tree-killing bark beetle species in the genus *Dendroctonus* described below. Several fungal pathogens are also spreading in Norway and colonizing a variety of forest tree species. The best known plant diseases tend to be those infecting crop plants and horticulture. Among the tree diseases, the fungal pathogens are associated with most of the climate- driven tree mortalities in the boreal forest. Several recent reviews have emphasized that the potential effects of climate change on plant–pathogen interactions could significantly alter the ecological and functional stability of forests (La Porta et al. 2008, Ghelardini et al. 2016, Biedermann et al. 2019), and a warmer environment will allow some previously temperature-limited species to compete more successfully with native species in Norway. The potentially disease-causing microorganisms (pathogens) that can affect wildlife is in practice to a large extent unknown. By far the most known animal diseases are those which also infect humans (zoonotic diseases), or our livestock.

4.3.1 Invasive bark beetles (Curculionidae, Scolytinae)

As with many other groups of insects and diseases, there are a few bark beetle species that are innocuous in their native habitat where they occur naturally but cause significant damage to forests where they are invasive (Sun et al. 2013, Lantschner et al. 2017). One cannot predict which species could prove to be problematic in the future should they be introduced to and spread in the boreal forests of Norway. Studies have focused on two tree-killing bark beetle species from North America which could each pose significant threats if introduced to Norway: *Dendroctonus rufipennis*, the only other eruptive bark beetle that kills spruce, and *Dendroctonus ponderosae*, a pine bark beetle that is the major source of mass mortality to pines in North America. Predicted climate change in Norway favors the spread and establishment of both species, should they be accidentally introduced, and both species could have long-lasting impacts on conifer forests after outbreaks (Bentz et al. 2010, Økland et al. 2011, Schebeck et al. 2017, Bentz et al. 2019).

Dendroctonus rufipennis breeds in all spruce species in its natural range (Aukema et al. (2016). As with *Ips typographus*, *D. rufipennis* normally breeds primarily in dying felled hosts, as they cannot overcome the array of host defenses in healthy live trees. If host plant defenses have been weakened by stress, such as drought, and beetle attacks are concentrated enough, then the population may become eruptive and kill healthy trees. That is*,* if a local population builds up to the point that it exceeds the carrying capacity that the dead and weakened host trees present, then beetles will begin to colonize healthy live trees in large enough numbers to kill them (Kausrud et al. 2012). Recent epidemics of this species in Alaska and Colorado have decimated millions of hectares of spruce forest. *Dendroctonus rufipennis* has a two- or even three-year life cycle in most of its range (is semivoltine), but it is univoltine (having a 1-year life cycle) in regions with favorable warmer temperatures. The species has a facultative diapause, which can be broken by relatively warm temperatures (Hansen et al. 2001), resulting in a 1-year rather than a 2-year diapause. Significantly, univoltine populations have higher growth rates than do semivoltine populations, and hence the presence of univoltine broods increases the risk of an outbreak or can increase the rate of spruce mortality in an outbreak (Hansen and Bentz 2003, Berg et al. 2006). A temperature-based model by Hansen et al. (2001) predicts that univoltine broods will be more common in a warming climate, and other research has found that *D. rufipennis* kills more trees when there are warm and drier-than-average summers and warm winter and fall temperatures (summarized in Bentz and Jönsson 2015).

The time required to go from egg to adult in *D. rufipennis* and *I. typographus* depends on both the interaction between temperature and diapause mechanisms. Longer and warmer summers could speed up development rates. *Ips typographus* could complete two generations in one summer, and *D. rufipennis* could reduce its developmental time from two to one year (Lange et al. 2006). The numbers of *D. rufipennis* beetles starting to breed in the first generation depends on how many juveniles survived the winter; milder winters increase juvenile survival, though mild winters combined with sudden cold snaps can kill large numbers of beetles (Aukema et al. 2016, Schebeck et al. 2017). Given that the bark beetle breeds in a wide range of *Picea* species, and given warming summer temperatures, it is likely that *D. rufipennis* could survive and spread in Norway should it be introduced. The likelihood of becoming a serious eruptive pest of spruce forests would be greatly increased should warmer temperatures allow for univoltine rather than 2-year life cycle. Model simulations suggest that interspecific interactions between *I. typographus* and invasive *D. rufipennis* could produce more frequent and more severe outbreaks than those caused by the native species alone (Økland et al. 2011).

Dendroctonus ponderosae (the mountain pine beetle) kills many millions of trees each year, and this tree mortality is considered to be the most important disturbance factor in North

American pine forests. Recent tree mortality in western Canada and the United States due to this bark beetle was more than 28 million hectares (Bentz et al. 2019). *Dendroctonus ponderosae* can breed in 22 pine species, including four not native to North America (Safranyik et al. 2010). Notably for Norwegian concerns, *D. ponderosae* attacks and kills unmanaged Scots pine in North America (Rosenberger et al. 2019). Much is known about the biology, taxonomy, ecology, population dynamics and physiology of this species, as it has been under intense investigation by forest entomologists, ecologists, and other researchers for well over a century (Bentz and Jonsson 2015, see also the review of this species in Raffa et al. 2015). The species is univoltine at low elevations but a mix of univoltine and semivoltine at higher latitudes and higher elevations. *Dendroctonus ponderosae* is more aggressive than *D. rufipennis* or *Ips typographus*, as it regularly breeds in standing live trees and rarely in windfalls. Bentz et al. (2019) modeled the risks of intercontinental establishment of both *D. ponderosae* and *Ips typographus*, in the context of long-term climate change. Given the detailed knowledge of the temperature-dependent physiology of *D. ponderosae,* they developed simulation models based on RCP8.5 global climate models. They concluded that winter- and summer temperatures in Europe, including in southern Norway, should be much more favourable in the next two decades for *D. ponderosae* (Figure 4).

4.3.2 Invasive jewel beetles (Buprestidae) and long-horned beetles (Cerambycidae)

Agrilus planipennis, the emerald ash borer, is a jewel beetle native to northeast Asia that breeds in healthy ash trees (*Fraxinus* species). The emerald ash borer is now in Europe (Volkovitsh et al. 2021), having been introduced to the Moscow region in 2005 (Izhevskii and Mozolevskaya 2010), and is spreading rapidly (Volkovitsh et al. 2021). The biology and ecology of the emerald ash borer are summarized in Herms and McCullough (2014) and NIBIO has treated the species in the forest health, invasive insects section (Økland and Krokene 2018). In its native range, beetle densities are low and the host species have defensive mechanisms that confer some resistance. Consequently, the beetle species does not seriously threaten Asian ash trees (DeSantis et al. 2013). Being invasive in eastern Canada and the northeastern United States, the beetle has caused considerable damage in the three decades since it was introduced and it is spreading rapidly at approximately 20 km per year. There are projections that the beetle could eventually kill nearly 100% of the three most abundant ash species (Herms and McCullough 2014, see also model results in Sobek-Swant et al. 2012), in particular because warmer winter temperatures would allow high levels of winter survival (DeSantis et al. 2013).

Less research has been done on other species of *Agrilus* that potentially can become invasive species of concern for Europe (Flø et al. 2015). The two-lined chestnut borer (*A. bilineatus*

Weber) can kill the European oak species *Quercus robur* (Norw. *sommereik*) in North America (Haack and Petrice 2019), and has recently been collected several times in Turkey (Hızal and Arslangündoğdu 2018). The bronze birch borer (*A. anxius* Gory) can kill the two most important birch species in Norway, *Betula pendula* and *B. pubescens.* The hosts of a fourth species, the common willow agrilus (*A. politus* (Say)) are species of maples (*Acer*) and willows (*Salix*); whether they can kill European species of these hosts has not been documented.

Flø et al. (2015) concluded that these four deciduous tree specialists could easily invade much of Europe even under today's climate. Areas in Norway with highly suitable climates are limited to the coasts of southern Norway for *A. anxius* and *A. bilineatus*, while no parts of Norway are suitable for the emerald ash borer under the current climate. However, their analyses suggest that all four species could establish populations in Norway under expected climate warming, with potentially large consequences for biodiversity of the relevant Norwegian forests.

Agrilus planipennis and the pathogenic fungus *Hymenoscyphus fraxineus* could have fatal consequences for ash (Musolin et al. 2017). Given the current high levels of infection by *H. fraxineus,* the causal agent of ash dieback, broadleaf and mixed broadleaf-conifer forests in coastal Norway will likely see considerable community effects in the near- and medium-term future (Timmermann et al. 2017). Additional long-term effects due to climate change are unlikely to be noticeable.

The Asian long-horned beetle *Anoplophora glabripennis* kills or damages a wide variety of hardwood trees. It is currently primarily encountered in urban environments, and there has been little research into potential effects of climate change on the population dynamics and range expansion of this species in Europe. The extensive review by Javal et al. (2019) found that European populations are gradually spreading. A detailed analysis of the distribution on *A. glabripennis* in China found that temperature and precipitation were key variables for explaining the presence of the beetle (Huang et al. 2020). The species occurs naturally or as introduced populations in a wide range of environments and over a broad range of latitude, including as far north as the upper Midwest of the USA and northeastern China and northern South Korea (Townsend Peterson and Scachetti-Perriera 2004, Huang et al. 2020, Shim et al. 2020). Given that the species has come to southern Finland, it is likely that there are now (and will be in the future) parts of Norway with a suitable environment.

4.3.3 Invasive and endemic fungal tree pathogens

Dutch elm disease. Dutch elm disease in northern Europe has not been subject to any known studies, other than to say that a warmer climate with milder winters is likely to favor the population increase and spread of the *Scolytus* bark beetle vectors of Dutch elm disease (Jürisoo et al. 2021a). Dutch elm disease fungi are present in much of Norway but they are currently spreading slowly, and account for a minority of elm mortality (Artsdatabanken 2015, see also Solheim et al. 2011). Elm mortality due to Dutch elm disease has been much higher in Sweden (Martin et al. 2010, Menkis et al. 2015). Elm genotypes vary both in resistance to the disease and attractiveness to the vector, and climate change may both weaken the trees and facilitate spread of the vectors, as well as facilitate the northwards spread and abundance of current and new vector species (Jürisoo et al. 2021a,b)

Phytophthora**.** *Phytophthora* grow best at warmer soil temperatures (Pettersson et al. 2020), so there is concern that at least some species could increase in incidence and severity under warmer future conditions in broadleaf forests, depending on regional changes in temperature, precipitation, and the frequency and intensity of extreme weather events.

Although the interaction of temperature and precipitation has complex effects on the life cycle of *P. cinnamomi*, warmer winters increase the survivorship of the species which should increase the risk of greater tree infection at times when spring and summer precipitation is not reduced (Thompson et al. 2014, Serrano et al. 2021).

For *P. alni*, already an important pest of alder in Norway (section 2.3.6.2), projected increased winter temperatures could lead to larger outbreaks in periods when greater winter survival is not balanced by warmer summer temperatures. Analyses of past outbreaks in French forests found that warmer winter temperatures increased winter survivorship and hot summer temperatures reduced tree decline; on average, establishment of the disease has increased steadily, particularly in the southwest of France (Aguayo et al. 2014). They concluded that, depending on the particulars of the region, climate change could either enhance or decrease the severity of alder decline. This conclusion may also apply to Norway.

Fusarium circinatum**, pine pitch canker disease**. The causal agent of pine pitch canker is currently not found in Scandinavia. However, according to Möykkynen et al. (2014), the climate scenario A1B (roughly similar to the RCP4.5 discussed in this report: IPCC 2000) would allow it to establish in Denmark and southern Sweden by the year 2100. By extension, a future closer to RCP8.5 seems likely to hasten this development and allow pine pitch canker to establish more widely and more quickly. The exact distribution depends on dispersal success and the relation between precipitation and temperature, but all climate scenarios suggest a wider range for this pathogen than its current established range in France and Spain (Drenkhan et al. 2020).

Fungal species causing root and butt rot. Butt rot is mainly caused by *Heterobasidion parviporum* on spruce and *H. annosum* which mainly infects pine but also deciduous trees. It is one of the largest fungal threats to tree primary production in Norway, with every fourth cut spruce tree being affected (Solheim 2006, Solheim et al. 2013). Butt rot occurs predominantly in managed forests where logging activities have been carried out during the warm season. At temperatures above zero, fresh stump surfaces and logging injuries enable spore infections by *Heterobasidion* (Kallio 1970; Stenlid and Redfern 1998). The fungus spreads from stumps and diseased trees through root contacts to nearby healthy trees (Stenlid and Redfern 1998). Both the spread and decomposing capacity of *H. parviporum* are expected to increase under a warmer climate (Hietala et al. 2015; Hanssen et al. 2019). Linking experimental data on respiration of fungal isolates at different temperatures with climate data from Finnish forests, Müller et al. (2014) calculated that an increase in the annual air temperature by 5°C would raise the annual activity of *H. parviporum* in spruce roots in southern Finland by over 50%. Optimum temperatures for most decay fungi in the temperate and boreal zones lie between 20°C and 30°C (Humphrey and Siggers 1933; Wagener and Davidson 1954; Boddy 1984). A nearly linear increase in activity during a temperature rise from 5°C to 20°C is common among decay fungi (Cartwright and Findlay 1934; Boddy 1984).

Other fungal pathogens may also increase in abundance with further climate change (Solheim et al. 2013), including *Gremmeniella abietina, Mycosphaerella pini, Lophodermium seditiosum* and *Armillaria* species. These fungi spread via spores or root contacts and together with *Heterobasidion* cause some of the biggest problems for spruce. More storm activity and less frozen ground would lead to more strain on the roots and easier access for the fungi to spread by root contact, and milder climates with a longer growing season would increase the period for spore dispersal. White rot root disease, caused by species of *Armillaria* (honey mushrooms), have been found to increase in frequency with a milder climate. This will lead to a decline of spruce, and especially in areas where bark beetle infestations are ongoing (Solheim 2008).

Bluestain fungi. Trees invest carbon into specialized defense compounds against invaders, and these processes are strongly affected by stress such as drought. *Ips typographus* and other bark beetles are associated with ophiostomatoid fungal symbionts, which can have several positive effects on beetle life history. They degrade toxic spruce defensive compounds, help exhaust tree defenses, produce beetle semiochemicals (chemicals used in intraspecific communication), and can provide nutrition. Various fungal associates have different temperature optima, and they can influence the performance of *I. typographus* differently under changing environmental conditions. The bluestain fungi form an integral beetle-fungus complex where the fungi are completely dependent on the beetles and vary in virulence. Bluestain fungi have been found to be less pathogenic than earlier believed and should be regarded as beetle facilitators and symbionts (Six and Wingfield 2011; Zhao et al. 2019; Tanin et al. 2021). However, effects of drought on tree-killing by bark beetles are still poorly understood and in need of further research (Zhao et al. 2019, Netherer et al. 2021).

4.3.4 Other plant diseases

Fungal pathogens in plants are much more studied than bacteria (including phytoplasmas), oomycetes, nematodes, and viruses (Juroszek et al. 2019). However, some non-fungal diseases of potential importance are known, and impact suspected.

Pine wilt disease caused by the pine wood nematode (PWN, *Bursaphelenchus xylophilus*) which can cause mass mortality of susceptible trees (mostly pines) and is a quarantine pest in the EU (Vicente et al. 2012). Tuomola et al. (2021) found that around 1400 annual growing degree days were needed for PWN to establish inside healthy trees, based on published PWN population dynamics for 139 locations in Germany. Following the results of Tuomola et al. we see that PWD may establish in Norway along the coast by 2050 for both RCP4.5 and RCP8.5, but most forested area is only suitable for PWD in the higher, more RCP8.5-like scenarios throughout the latter half of the century. This unusually clear published relationship with temperature allows us to adapt the findings for this disease distribution quantitatively (see Figure 23).

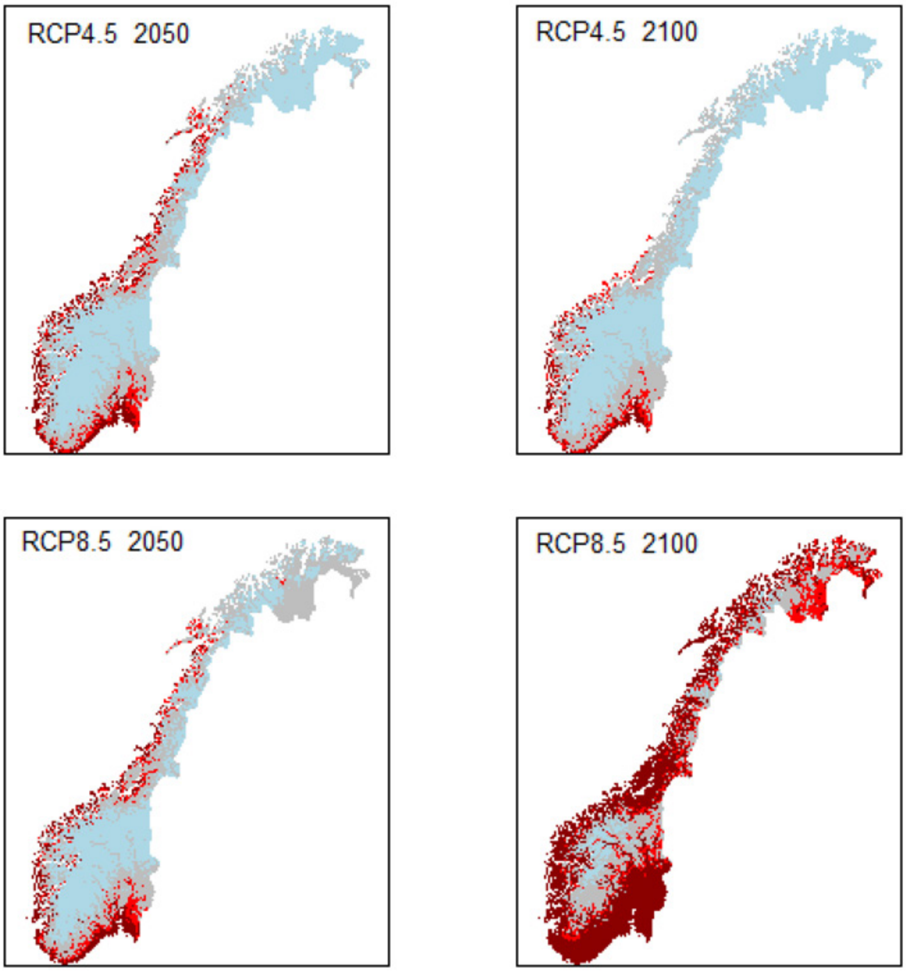


Figure 23. Light red=likely, and dark red=almost certainly suitable temperature conditions for PWD establishment, following the degree day findings and terminology of Toumola et al. 2021. Daily temperature data from the NCCS.

Plant viruses studied on crop plants have been observed to be more effective at replicating at higher temperatures and often vectored by insects, both of which suggest higher infection pressures with climate change (Amari et al. 2021), which seems likely to also apply to boreal forests. Little is known about the role of viruses entering historically naïve plant populations (Schoelz and Stewart 2018).

Bacteria and other parts of the microbiome are also affected by climate conditions in many, often poorly known, ways that may cause disease. For instance, elevated temperature increases the virulence of the bacteria *Pectobacterium atrosepticum,* which may cause soft rot and some seed-infecting microbes that increase disease incidence in plants (Sharma et al. 2022).

4.3.5 Wildlife diseases

The incidence and distribution of many zoonotic and animal diseases are weather sensitive, due to climate effects on the pathogen itself, its host(s) or its vector(s). Thus, their distribution and epidemiology are likely to be changing with climate conditions, not the least in northern areas that have had relatively low disease burdens compared to tropical regions but now experience the largest warming trends (Allen et al. 2017; Bartlow et al. 2019; Yon et al. 2019). For an overview of currently known Norwegian zoonoses with some climate notes, see the annual zoonosis report (Jørgensen et al. 2020). A review of known animal diseases that may occur in the boreal biome and are subject to some form of climate impact is beyond the means and scope of this report, and a there is a general lack of knowledge of the plethora of possible pathogens affecting mammals, birds, insects and other animals, so the selection mentioned here should be regarded as examples, not an overview.

A recent metastudy suggested some generalities applicable to the boreal forest biome (Cohen et al. 2020) to test whether the so-called "thermal mismatch" hypothesis holds true over the gamut of host-pathogen relationships. The authors found that fungal disease risk increased sharply under cold abnormalities in warm climates, whereas bacterial disease prevalence increased sharply under warm abnormalities in cool climates. Warming was predicted to benefit helminths more than other parasites, and viral infections showed less obvious relationships with climate change. However, vector-borne viruses may be an exception as they follow the response of their vectors and hosts (Esser et al.2019).

Pathogen burden of moose (*Alces alces alces*) in Sweden was investigated by Malmsten et al. (2019) through spleen samples from 615 moose collected between 2008 and 2015. Anaplasma spp (82%), Borrelia spp (3%), Babesia (3%), and Bartonella (1%). DNA was found through PCR, showing that moose are exposed to, and can act as hosts of some of these pathogens, and that Swedish moose now are exposed to pathogens more commonly found in regions with warmer climates (Malmsten et al. 2019). Further research is needed to see whether climate change and moose population density interact to create the pattern observed.

Arboviruses (viruses with an arthropod vector) as a general trend have been found to be influenced by temperature and spread north under climate change, as many hosts also spread north and the viruses tend to be more effective, even though specific interactions exist with other factors like drought and host communities (Ciota and Keyel 2019; Esser et al. 2019; Bartlow et al. 2019), and there is no reason to believe boreal or nemoralized forests are exceptions to this trend.

Tick-borne diseases in Norway include babesiosis (the first human case of *Babesia divergens* in Norway being described in 2007 - Mørch et al. 2015), lyme disease (Borrelia sp. infection), anaplasmosis (Analasma sp. infection), Tularemia (see below), tick-borne encephalitis (TBE virus infection). Of the 13 tick species so far observed in Norway, the sheep tick (*Ixodes ricinus*), is by far the most common. They need a set of hosts (often moose, roe deer, red deer, foxes or domestic animals), as well as smaller hosts (mice, lizards, birds), suitable vegetation and ground conditions, moisture and temperature. Thus they are often associated with forests and pasturelands with some developed vegetation. Especially deciduous forest litter seems to provide good habitat for between-host tick phases (Vanwambeke et al. 2016). However, their distribution seems to have been temperature-limited as tick abundance and distribution seem to have increased and moved to higher-altitude and more northern and continental areas over the last decades. In Norway, *I. ricinus* has been found on bank voles up to 1000 MASL both in western and southeastern Norway (De Pelsmaeker et al. 2021). This increase is expected to continue, and may also allow some tick-borne diseases previously not seen in Norway to establish (Hvidsten et al. 2020; Jánová 2019). So while ticks and tick-borne diseases in the forest ecosystem in general are expected to increase, phenological mismatch between hosts and vectors may complicate matters, as has been suggested for some Borrelia species around 2050 (Fernández-Ruiz and Estrada-Peña 2020).

Puumala orthohantavirus, PUUV, is a zoonosis with bank vole (*Myodes glareolus*) as its reservoir host. Sipari et al. (2022) shows that early winters becoming increasingly wet has a knock-on effect on PUUV transmission in its host populations in Northern Sweden, leading to higher incidence even without the host itself increasing in abundance or distribution.

Anthrax (*Bacillus anthracis*) has been associated with climate change in boreal and arctic areas, lately through outbreaks in Siberia in 2016 (Ezhova et al.2021). However, as this seems to have been triggered by the continued thawing of contaminated permafrost followed by hydrological abnormalities, it seems unlikely to be of particular importance in Norway due to less extensive permafrost. One may want to be aware of potential cases spreading in from Sweden, Finland or Russia.

Tularemia (*Francisella tularensis*) has been described as a re-emerging zoonosis in forest animals after an increased incidence globally over the last decade (Yeni et al. 2020). The bacteria has a versatile transmission pathway with multiple vectors (mosquitoes, horseflies, deer flies, and ticks), direct contact and environmental transmission through water or aerosols (Yeni et al. 2020). The disease has been observed to follow rodent and hare abundances in Norway, which are connected to climate (Kausrud et al. 2008), although not necessarily in a linear fashion. A modeling study from Sweden predicts that steeper climate warming do not necessarily lead to steeper increase of outbreaks, and along a latitudinal gradient, and that RCP4.5 type scenarios predict intermittent or general decrease in the south, but moderate to strong increase increased incidence in the mid to northern latitudes of Sweden (which seems likely to apply to boreal regions of Norway as well) (Ma et al. 2020).

European brown hare syndrome (European brown hare syndrome virus, EBHSV) is a virus whose main host (the European brown hare, *Lepus europaeus*, see Pedersen 2018) has been expanding northwards from southern Sweden since the 1800's, likely due to warmer climate. Thus its competitive relationship with native mountain hare (*Lepus timidus*) is affected by different vulnerabilities to EBHSV.

African swine fever (African swine fever virus, ASFV) has so far not been observed in Scandinavia, but has been present as far north in Europe as Lithuania in wild boar since 2014 (Shulz et al. 2021). Wild boar has established in large numbers in Sweden, and seem likely to keep expanding in range and numbers in Norwegian forests and rural landscapes as well, as a result of milder winters with less snow and less frozen ground as well as human management (VKM 2018) – thus constituting a possible bridge for ASF to domestic pigs.

Avian malaria Blood parasites causing malaria like *Plasmodium*, *Haemoproteus* and *Leucocytozoon* genera in birds are widespread all over the world and mainly transmitted by *Culicidae*, *Ceratopagonidae* and *Simuliidae*, vectors respectively, with some avian malarial parasites, including *Plasmodium relictum* listed among the top most invasive species in the world, already transmitted in northern Europe.

Some have been prevalent in mosquitoes up to the arctic circle for over a decade, while others are found only in long-distance migrant birds after annual migration. Evaluation of avian malaria prevalence together with air temperatures over 70 year suggests that 1 °C warming corresponds to a two- to threefold increase in avian malaria prevalence in Europe, found to be alarming by Deksne et al. (2020).

4.4 Shifts in communities and biodiversity

This chapter focuses more on the community and ecosystem level, and how climate change and climate change-related shifts in disturbance regimes (as described in section 4.1) impact community dynamics and diversity patterns. The chapter is structured as follows: forest plant communities (4.4.1), vertebrate communities (4.4.2), insect communities (4.4.3), decomposers, mycorrhiza and wood-related fungal communities (4.4.4) and lastly, biodiversity and habitat specialists (4.4.5).

As organisms respond to climate through range shifts, dispersal through landscape matrices may be influenced by landscape heterogeneity and land-use types (urbanization, farming, forestry etc), and also species-specific dispersal capacities (e.g. reliance on slower-moving mutualists or symbionts). For many or most species, Allee effects (positive density dependence) are an important factor in the rate and distance at which they can colonize new habitats. Consequently, mismatches and lag-effects in species range shifts may arise, and the speed of range expansion at the leading edge and speed of range contractions at the trailing edge are likely to be different, leading some species to expand in range and others to contract. When species are not able to keep up with changing climate but are still present, this can create what is termed "extinction debt" or "climate debt" (*q.v.*). Furthermore, as species are likely to range shift at different speeds, it is likely that mismatches and lag effects will give way to predator- or competitive-release for some species groups. Essentially, predators cannot extend their ranges beyond those of their prey base, but prey can expand, temporarily or permanently, out of range of their predators. Thus, without controlling predators, populations may increase drastically.

4.4.1 Forest plant communities

Increasing temperature typically favors the range expansion of pioneer species, such as birch, pine and poplars, at the expense of late successional species (e.g., spruce and oak). This is because pioneer species typically rely on temperature for spring bud burst, while many late successional species are relatively more controlled by day length (Basler and Körner 2012; Brecka et al. 2018). Many species, including spruce, pine, and Siberian larch, survive and grow above the current Fennoscandian alpine or tundra treelines (Bognounou et al. 2018). There may be an interaction between air temperature and snow cover where seeds from some boreal species can survive better at lower temperatures than those from some alpine species. Thus, paradoxically, a loss of snow cover from warming climate could lead to alpine seed death due to extremes of cold at the soil surface and facilitate boreal forest colonization above the current treeline (Jaganathan et al. 2020). However, there is some suggestion that future capacity to expand into regions above the treeline may not only be bioclimatically limited, but also moderated by biotic factors, such as herbivory. A Fennoscandian study by Bognounou et al. (2018) found seed regeneration of Norway spruce, Scots pine, and Siberian larch at and above the tree line was dependant upon microhabitat availability and mammalian herbivory, including that of reindeer, sheep and rodents. In southern Norway, a study on the forest-tundra ecotone found that despite warming conditions, land use, and in particular herbivory by sheep, was a major factor in limiting upwards tree line movement through restricting seedling and sapling survival (Løkken 2020). In areas of high reindeer abundances during summers in northern Norway, browsing impacts of semi-domestic reindeer interact with insect outbreaks (Biuw et al. 2014, Vindstad et al. 2017). Thus, the treeline ecotone is, while to a large degree ultimately a function of temperature, on shorter time scales a complex and dynamic function of multiple processes including land use by animal husbandry and tree-killing insects (Wielgolaski et al. 2017). This needs to be considered as it adds a time lag to the northwards or upwards movements of spruce, pine, and birch beyond today's treelines.

An effect shared by many tree species modeled by Mauri et al. (2022) is that while they are directly impacted to varying degrees, any negative impacts on the trees happen faster on the vulnerable "trailing edges" (usually more southern, or lower altitudes) than the range expansions at the "leading edge" (more northern, higher altitudes) can compensate (see Figure 24). This effect is intuitive considering the rate of ongoing climate change relative to the long life spans, persistence and often limited dispersal capabilities of habitat-forming tree species, and seems likely to have important but hard-to-predict effects on community structure and biodiversity in periods with quick change. Judging from Mauri et als models, most northern areas get climate zones where more potential distributions overlap -signaling higher diversity - but with the realized distributions being smaller and less overlapping - signaling less diversity and possibly less forest cover until climate stabilizes at some level long enough for forests to catch up. (See Figure 24).

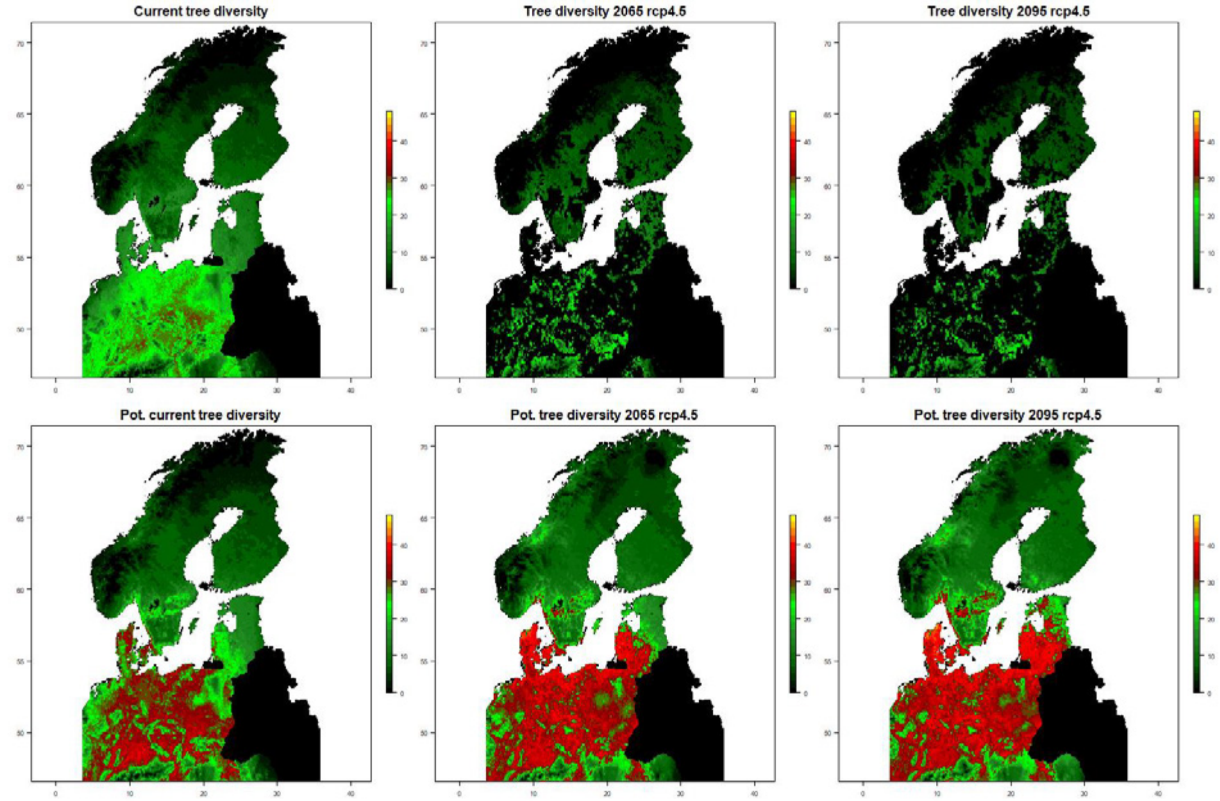


Figure 24a

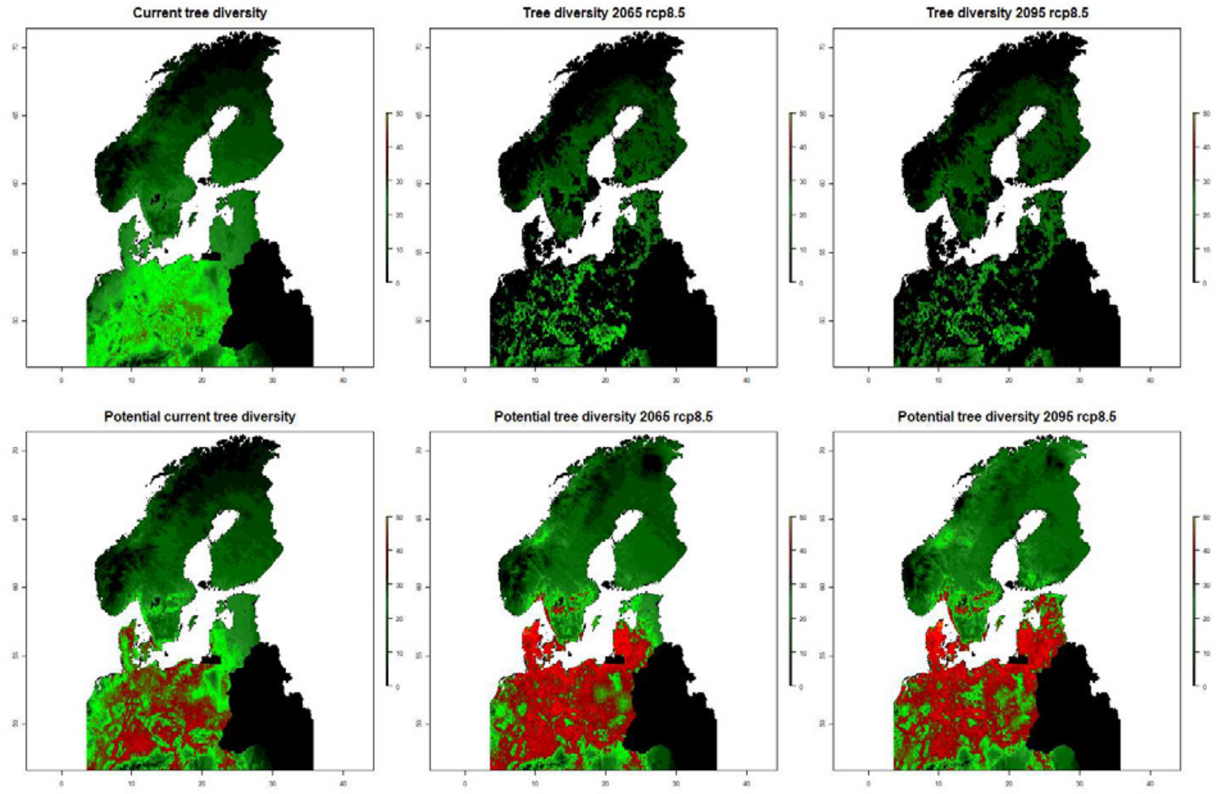


Figure 24b

Figure 24. Current and future summed expected and potential occurrences for distributions of 67 habitat-building, economically and/or ecologically important trees in Europe included in the data set of European forest tree distributions known as "EU-Trees4F" published by Achille Mauri and co-workers (see 4.2.1.1). Their distribution analyses are based on the same EURO-CORDEX climate models used by the NCCS, for RCP4.5 (**a**) and RCP8.5 (**b**) mean scenarios respectively, and are coupled with tree distributions, climate-, soil- and land use data. Tree dispersal capacity has been explicitly modeled, giving probability of each species occurring (from 0 to1, approximately 10x10km resolution). The upper rows for each scenario show actual (expected) distributions today and in the short and longer-term futures, when dispersal capabilities and range losses (i.e. both lagging and leading edge dynamics) are taken into account. The lower ranges show the potential distributions, i.e. how many species would be capable of growing in an area if they somehow could instantaneously follow their climate zones. Habitat preparation, active planting and other management strategies might improve the achieved diversities.

When the effects of climate change on phenology differ between forest plant species, this may also shift their relative relationship and eventually the species composition of a forest (Kramer et al. 2000). For instance, earlier shading by canopy trees influences the light reaching the forest floor in spring (Anderson 1964), which alters growth and recruitment of trees and seedlings in the understorey, in particular for shade-intolerant species that rely on high irradiance levels before canopy closure to flower and fruit (Laube et al. 2014, Whigham

2004, Kudo et al. 2008). Predictions made using a long-term dataset from England showed that while birch saplings in the understory of oaks currently sprout before oaks almost every year, the situation may be reversed by 2040-2069 (Roberts et al. 2015).

Such mismatches in springtime phenological responses between overstory and understory species can impact ecosystem function, and ultimately carbon balances. For example, Heberling et al. (2019) found a significant reduction in wildflower spring carbon budgets in deciduous forests of northeastern United States because of mismatches in leaf-out phenology. However, predicting future changes in spring phenology of communities can be difficult, as illustrated by studies from the Canadian boreal forest highlighting tree species may have complex responses (Flynn and Wolkovich 2018).

Disturbance regime is an important factor in structuring communities and windfelling has been the most important single risk factor for reduced timber productivity in Norway since WWII, being responsible for 53% of all forest damage in Europe (Hanssen et al. 2019). However, increasing frequency of summer drought and heat waves may be replacing wind disturbance as the main cause of Norway conifer mortality starting in southern Norway (Kunert 2020). The impact of any disturbance is determined by occurrence, exposure, and susceptibility. In Switzerland, the size and severity of wind damage has been increasing over several decades and depends on three main factors: damage potential (forest area and biomass), the stability of the forest against wind, and wind conditions (Usbeck et al. 2010). The two first factors have changed and will continue to do so in Norway, as growing stock has increased and is aging, while higher temperatures and increased precipitation during the winter lead to lower degree of anchoring (Solberg and Dalen 2001, Hanssen et al. 2019). However, scenarios concerning wind speed are more uncertain. Even with largely unchanged wind speed regimes in the future (section 4.1.6), the risk of windfelling might increase because of reduced anchoring (especially of spruce) resulting from shorter ground frost period (Venäläinen et al. 2020). It is likely that even smaller increases in gust wind speeds will cause a disproportionate increase in disturbance amounts.

Damage from snow in Norway is expected to decrease due to climate change (Hanssen et al. 2019), as wet and heavy snow can impact forests through the breakage of treetops when the increased number of days passing through zero degrees increase ice formation and wet snow (Hanssen-Bauer 2015; Kausrud et al. 2008), and sometimes even stems and cause tree felling. Snow breakage has increased in Norway during recent years, especially in Agder, Telemark and Vestfold (Hanssen et al. 2019). A lack of frozen ground in winter may also exacerbate the effect of winter storms on windfelling and uprooting, as frozen ground improves soil anchoring (Gregow et al. 2011). In addition to direct reductions in production because of weakened or dead trees, snow-damaged stands may also function as epicenters for bark beetle outbreaks. With increasing winter temperatures, it is expected that the levels of snow damage in forests will decrease in the southern and western parts of Norway as most of the precipitation will be rain, while levels will increase inland and at higher altitudes where the precipitation still will mainly fall as snow (Solberg et al. 2019).

The impact of fire on boreal forest mortality can vary by stand-age, stand-structure, underlying soil conditions, or species composition. In Norway, insurance and fire records indicate that forests that are either young, on shallow soils, or composed of pine or spruce are more prone to fire than those that are older, on deeper soils or composed of deciduous species (Skjølaas 2009). In the future, newly established boreal forests will be dominated by young spruce and pine forests on shallow alpine soils and will hence be more impacted by fire. Changing species composition due to fire regimes may also change the expression of functional traits in a system, and thus ecosystem function. In a long-term study in Alaskan boreal forests, Mack et al. (2021) found that the species composition often changed from black spruce to a mixture of conifers and deciduous broadleaf tree species after fire. The stands that had shifted to deciduous dominance stored fivefold more soil carbon than stands that returned to black spruce dominance. Therefore, the functional traits of deciduous trees compensated for the combustion loss of soil carbon, pointing to a potential mitigation of the feedback effect of boreal forest fire to climate warming. Although short time has passed since the large fires in southern Sweden in 2014, Gustafsson et al. (2016) suggest a similar development in this part of the boreal forest if left to develop without intervention.

Norwegian forests have tended to be more affected by disturbances caused by wind or snow than by fire (Seidl et al. 2014), but this could change if there are more frequent and larger fires in the coming decades, and ecological ramifications will be greater if intervals between wildfires shorten (Whitman et al. 2019).

Large, fast-growing bryophytes also interfere with the growth and establishment success of tree seedlings (Hörnberg et al. 1997), and a future climate driven bryophyte expansion is thus likely to have a general negative impact on natural tree regeneration. However, summer droughts will limit bryophyte growth and increased disturbances from windfalls or forest fires may open better possibilities for establishment by other species.

4.4.2 Vertebrate communities

The functional group composition of animal communities will respond to abrupt events and trail the slower nemoralization of the boreal forest. The abrupt vegetation state shift caused by the extensive, climate change-driven geometrid outbreaks in the birch forest of northern Norway (2002 to 2008), was associated with an immediate decrease of browsing vertebrates, such as reindeer and ptarmigan, whereas grazing voles increased (Jepsen et al. 2013, Henden et al. 2020). Bryovore (moss-eating) lemmings appear to be more sensitive to warmer winters than browsing voles (Ims et al. 2011). Consequently, the last decades' paucity of high amplitude peaks of rodents causing disturbance in the understory vegetation has been suggested to increase the cover of *Hylocomium splendence* in the boreal forest

(Rydgren et al. 2007). A nemoralization of the forest ecosystem is expected to shift the small mammal community towards more omnivores and granivores (such as wood mice, *Apodemus* species) with more stable population dynamics and less browsers (such as gray-sided voles, *Myodes rufocanus*) and bryovores (such as wood lemmings, *Myopus schisticolor*) with cyclic population dynamics (Hansson and Henttonen 1988).

The outbreaks by geometrid moths in northern Fennoscandian mountain birch forests have intensified due to climate warming (Jepsen et al. 2013), with the outbreak in Finnmark (2002-2008) resulting in large-scale defoliation of birch trees and shrubs as well as a region-wide state shift of the understory vegetation from shrubs to grass. This shift cascaded to affect the abundance of both grazers and browsers (Jepsen et al. 2013). While grazing rodents increased (Jepsen et al. 2013), browsing willow ptarmigan declined after these moth outbreaks (Henden et al. 2020).

Climate impacts on keystone species may cause major shifts in vertebrate community dynamics. For instance, least weasel (*Mustela nivalis*) and stoat (*Mustela erminea*) are likely key drivers of the community-wide abundance cycles of small- to medium-sized vertebrates in the boreal forest of Fennoscandia (Boonstra et al. 2016). Both of these small predator species are prone to color morph mismatches in a warmer climate (Atmeh et al. 2018, Mills et al. 2018), which ultimately may disrupt community dynamics (Ylönen et al. 2019).

Increased frequencies and intensities of fires are likely to impact animal communities. Because of the growing use of prescribed fires in forest management in many parts of the world, there has been considerable research on the effects of fire on various groups of animals. This research includes short-term or long-term direct observational studies comparing burned and unburned plots or comparing the same areas pre- and post-burn. There are also reviews and meta-analyses of such literature and simulation modeling (Driscoll et al. 2010). Important variables include (among others) time since burning, how frequently a region has burned, the intensity of burning, wildfires (usually high intensity) versus prescribed burns (usually low intensity) versus natural fires that are deliberately allowed to burn (non-intervention), topography, geographic variation in ecosystems, and life history differences (*q.v.*) among species. Whether fire disturbances are negative, neutral, or positive for animal populations depends on factors, such as body size, mobility, and how organisms use landscape vegetation. Depending on fire intensity, fires can alter plant communities in ways that can be favorable to many types of animals: population increases in insects often follow fires in conifer forests (Muona and Rutanen 1994, Swengel 2001). Moreover, animal responses depend much on the time since the last fire event, and most studies have been to short-term to capture long-term effects (González et al. 2022).

The space underneath the snowpack (subnivean space) is important for winter survival and growth, and its presence or absence can have profound effects on dominance relationships and population dynamics (Kausrud et al. 2008, Boonstra et al. 2016). Due to the loss of the subnivean space resulting from climate change (see 4.1.3), one may observe the paradoxical effect that increasing mean temperatures may make ground-dwelling plants, animals, fungi, and other microorganisms along with specialized organs or life-history stages such as roots, growth meristems, seed banks and other dormant stages in or near the soil surface more exposed to cold during winter (Johnston et al. 2020, Boonstra et al. 2016, Berteaux et al. 2017, Baskin and Baskin 2022). As a result, organisms that normally use the subnivean space have less access to food, habitat, and predator or herbivore protection for parts of the year and under prolonged exposure may freeze to death. However, some freeze-tolerant species may benefit from less insulation (Marshall and Sinclair 2012).

4.4.3 Insect communities

Climate changes are likely to increase range expansion and outbreaks of forest insects, potentially further amplified by synergistic (amplifying) effects, such as hotter droughts or stronger storms though, and perhaps dampened for some insect pests by higher winter mortality where snow cover is decreased. Drought-induced stress and windfellings can facilitate subsequent disturbances, such as insect and disease outbreaks, indirectly amplifying drought and windfelling impacts on forests (Seidl et al. 2017). In turn, insect and disease outbreaks increase host plant susceptibility to drought and windfall. However, lesser-known negative effects are also likely to occur, such as lethal heat waves or thermal shocks, less nutritious host tissues or more abundant parasitoids and predators. The complex interplay between abiotic stressors, host trees, insect herbivores, and their natural enemies makes it difficult to predict overall consequences of climate change on forest condition (Netherer and Schopf 2010, Jactel et al. 2019). Uncertainty pervades predictions about forest insect dynamics, due to complexity, incomplete understanding, unstable relationships, or lack of data (Dukes et al. 2009; Cooke and Carroll 2017). However, because the dynamics of forest insect outbreaks depend strongly on the availability and susceptibility of host trees, such outbreaks will not be driven by climate alone but will be strongly influenced by forest management, with mixed stands of species well adapted to local climate (Klapwijk and Björkmann 2018; Terrier et al. 2013; Chavardes et al. 2021; Ji et al. 2011, Murdock et al. 2013, Ciesla 2015, Scheller et al. 2018; Marini et al. 2022). Changes in forest disturbance regimes can feedback on climate through effects on water and carbon flux in forest ecosystems (Ayres and Lombardero 2000).

Research on dragonflies, butterflies, and ants point to the possibility that color plays a role in how insect species respond to climate change (Zeuss et al. 2014, Bishop et al. 2016, Heidrich et al. 2018), as cold-blooded animals (ectotherms, *q.v.*) often are darker in color in colder climates (Poikela et al. 2021). In a study of oak-associated beetles across a climate gradient in Norway and Sweden, it was expected that increased summer temperature would positively influence all wood-living beetle species whereas precipitation would be less important with a negligible or negative impact (Gough et al. 2015). Surprisingly, few specialist beetles and no generalist beetles responded to a rise of 4 °C in summer. The negative effect of precipitation affected more specialist species than did temperature, whereas the generalists remained unaffected. In summary, this indicates that increased summer temperature is likely to benefit a few specialist beetles within the dead wood community associated with oaks, but a larger number of specialists are likely to decline due to increased precipitation. In addition, generalist species might remain unaffected (Gough et al. 2015).

Habitat heterogeneity involving natural and small-scale disturbances in boreal forests play a role in maintaining pollinator numbers and diversity (Rodriguez and Kouki 2015; Rodriguez and Kouki 2017; Nelson et al. 2021, Raven and Wagner 2021). There is a global trend towards pollinators to be promoted after a wildfire event. However, short fire intervals may be a threat to pollinators, especially lepidopterans (Carbone et al. 2019), and while the mechanisms need further investigation, management promoting diversity seems likely to promote resilience and pollinator persistence (Duflot et al.2022). Mass mortality of trees (and substantial amounts of dead wood) resulting from a climate-induced outbreak of geometrid moths did not cause any major numerical responses in the community of saproxylic beetles in sub-arctic mountain birch forest, suggesting that other limiting factors were acting (Vindstad et al. 2014).

Some seemingly good long-distance dispersers can be slow colonizers due to ecological, behavior, and genetic problems facing very small populations (Allee effects: Johnson et al. 2007), while others in related groups can be very effective colonizers despite Allee effects (Jordal et al. 2001, Fristoe et al. 2021). Menendez et al. (2006), building on Hill et al. (1999), used a detailed century-long temperature and distribution record of Lepidoptera and found only about a third of the range expansions that were expected due to climate warming. They made a case for "colonization lags", as current species assemblages were dominated by host-species generalists that were able to respond quickest to climate change.

Insect diversity and biomass is already declining rapidly in Europe and around the globe, exemplified by an over 75% decrease in flying insect biomass over 27 years reported from a large, long-term study of protected nature areas in Germany (Hallmann et al. 2017). The mechanisms behind this alarming trend are not clear but are suspected to be a mix of land use and habitat fragmentation, pesticides, climate change, and unknown factors (Seibold et al. 2019, Hallmann et al. 2021).

In short, insects are strongly influenced by temperature and, for some groups, by precipitation patterns or by the interaction between precipitation and temperature through phenology and voltinism strategies *(q.v.)*. Temperature and precipitation impact insects directly by altering fecundity or rates of mortality or development; such climate variables impact insects indirectly when they influence the availability of required biotic and abiotic resources, or when they change levels of predator, parasite, or pathogen populations. In addition, the diversity of several insect guilds is influenced by the frequencies and extents of large-scale disturbances, such as those caused by fire, windfelling, drought or outbreaks of insects or pathogens. Higher temperatures may facilitate the dispersal capabilities of some insects. (For an overview of these mechanisms see Halsch et al. 2021 and Pureswaran et al. 2018). These findings suggest that there are important constraints and non-linearities determining how insect assemblages may be able to respond to rapidly changing environmental conditions.

4.4.4 Decomposers, mycorrhiza, and wood-related fungal communities

Climate-induced changes in tree growth rates can indirectly influence the resource quality for a range of wood-associated species, giving a disadvantage for species of conservation concern (Edman et al. 2006, Runnel et al. 2021). This has bearings for both community composition and the functioning of the community. As with plant litter, wood quality has been found to have a more pronounced effect on fungal wood decomposition than climate variables (Venugopal et al. 2016). Venugopal et al. (2016) observed that fast-grown pine wood from managed forests decayed much faster than old, denser, and slow-growing pine wood. Edman et al. (2006) observed the same for spruce dead wood. Hence, a temperature-induced faster growth may lead to a quicker decomposition. In their study, Venugopal et al. (2016) observed that interaction effects between wood quality, temperature, and humidity were highly important. Moreover, they observed that many responses were species-specific to various wood-decomposer fungi, making it hard to generalize how wood-decomposer fungi may respond to climate change. Fast grown spruce trees that die may support a higher species richness of fungi than slowly grown trees, while red-listed species of fungi and beetles prefer slowly grown trees (Runnel et al. 2021). Edman et al. (2006) showed that the specialist red-listed shelf fungus *Fomitopsis rosea* (Alb. & Schwein.) P. Karst. had a competitive advantage in terms of growth rate over the generalist not red-listed *F. pinicola* (Sw.) P. Karst. on slowly grown spruce dead wood, while the two species were more equal on fast grown wood.

Lindberg et al. (2002) reported decreasing abundances of soil faunal groups (enchytraeid, oribatid mite, and Collembola) as a response to summer drought in a spruce forest in Sweden. The abundances increased as a response to irrigation. In addition to the direct effect of drought stress, decrease in fungal biomass was suggested as a mechanism for the decline of these mycophagous animals. More generally, changes in microbial biomass are expected to influence soil faunal biomass (Korboulewsky et al. 2016), for example, many arthropods feed on fungal mycelia. Decreasing extent and duration of snow cover and the increasing number of freeze-thaw cycles are expected to negatively affect the biomass of several groups of arthropods and soil micro-organisms (Sulkava and Huhta 2003, Hågvar 2010, Sørensen et al. 2018) but could lead to population increases in others (Konestabo et al. 2007).

Natural disturbances that create dead wood, such as storms, fire, insect outbreaks and snow damage, may lead to increasing biomass of insects, fungi, and bacteria associated with dead wood (Bouget and Duelli 2004, Parisi et al. 2018), at least in the short term. The impact of climate change on the long-term trends in the volume of deadwood are insufficiently understood and will depend on the balance between the rates of tree death, regeneration, and tree growth, as well as on forest management strategies. As decomposition rates are temperature dependent, they are expected to increase (Rinne-Garmston et al. 2019; Harmon et al. 2020; Jansson and Hofmockel 2020) at least partly counteracting the expected increase in dead wood and associated microbial biomass. Windthrows and insect outbreaks may also create heterogeneous understory conditions, providing many microhabitats or micro-sites for flower-visiting insects, phytophages on saplings and on fallen tree crowns, and ground insects (Bouget and Duelli 2004). Change in abiotic conditions (sun exposure, humidity, and temperature) alter successional trajectories of beetle functional groups in deadwood (Vindstad et al. 2020). Wood decomposers, in particular, can be positively affected by fires, due to increases in both the volume and heterogeneity of coarse woody debris (Jonsson and Siitonen 2012a). Dead wood habitats have declined considerably in Norwegian forests due to the intensification of forestry management (Siitonen 2001, Kaplan et al. 2009, Jonsson and Siitonen 2012b, Jonsson et al. 2016, Framstad et al. 2017).

Indirect evidence supports that the fungal ecosystem component will respond strongly to climate change. For example, climate factors are the primary controllers of fungal distribution patterns (Větrovský et al. 2019, Wollan et al. 2008) and range shifts are expected to occur. Many fungal groups are tightly associated with vegetation types and plants that will experience range shifts (Steidinger et al. 2019). Numerous experimental studies also indicate a close connection between fungal physiology, growth, and climate. However, for fungi that are hidden below ground in boreal forests or within other substrates, we have limited empirical knowledge about climate change effects under natural conditions. This is partly due to the lack of appropriate time-series data, which is very challenging to obtain for these organismal groups. Based on fruit body data, we know that fruiting by fungi responds to climate change, both in phenology (Kauserud et al. 2013) and species' geographic distribution (Diez et al. 2020).

Decomposition of plant litter in forest ecosystems is a key component of the global carbon budget and is regulated by three main factors; climate, litter quality, and soil organisms. Litter decomposition rates tend to decrease with latitude and with lignin content of plant litter, but increase with temperature, precipitation and nutrient concentrations (Zhang et al. 2008). Hence, increased temperatures and precipitation will lead to increased decomposition and higher rates of carbon loss to the atmosphere. In a meta-analysis from cold biomes, it was shown that warming resulted in slightly increased decomposition rates (Aerts 2006). The limited response was mainly due to limited water availability. Hence, global warming will only increase litter decomposition rates if there is sufficient soil moisture (Aerts 2006). However, litter quality accounts for far more of the variation in decomposition rates than climate factors alone (Zhang et al. 2008). This indicates that changes in species composition, such as those arising from coniferous forests transitioning to broad-leaved forests, will have a greater impact on litter decomposition than direct climate responses. A warming-related increase in the biomass of macro-detritivores, such as earthworms, isopods, and millipedes should accelerate the rate of tree litter decomposition in subarctic forests with significant amounts of broadleaf trees, such as birches or alders (van Geffen et al. 2011). Increasing temperatures may mean higher activity levels of boreal decomposer fungi, including higher growth rates and consequently biomass accumulation rates, as well as higher rates of organic matter decomposition. This can have important impacts on ecosystem carbon and nutrient dynamics, promoting quicker turnover and release of plant litter carbon. Expected increasing litter production by trees and understory vegetation may additionally feed into increasing biomass of decomposer fungi (Allison and Tredeser 2011).

4.4.5 Biodiversity and habitat specialists

Climate sets the boundary conditions that govern the distribution of biomes, ecosystems, and their embedded ecological communities (species assemblages) together with hydrology, topography, and geology (Turner and Gardner 2015). Increasingly, habitat loss and loss of spatial and temporal connectivity of habitat or microhabitats (such as in dead wood) drive species declines in all biomes (Wilson et al. 2015), including the boreal forest (Ranius et al. 2019). As the area of suitable forest habitats such as old-growth forest decrease, populations confined to these habitats decline. Likelihood of successful (re)colonization of a habitat patch decreases with increasing spatial isolation and decreasing habitat quality (e.g., stand age, dead wood volume) (Jönsson et al. 2008, Runnel et al. 2015, Nordén et al. 2020, Moor et al. 2021), especially for specialist species for which the density of suitable microhabitats is low in space and time (Norros et al. 2012, Nordén et al. 2013, 2018). Additionally, small local populations are susceptible to local extinctions because of ecological (demographics, environmental fluctuations) or genetic stochastic events (Soulé 1986, Wootton and Pfister 2013). From this it follows that climate change is expected to have adverse influences in particular on the populations of specialist forest species, the habitats of which have for long been in decline because of land use change and forestry.

Increasingly active disturbance regimes resulting from climate change (Seidl et al. 2014; Seidl et al. 2017) might to some degree compensate for other climate change effects that have adverse impact on forest biodiversity (Thom and Seidl, 2016). Results from temperate forests in Austria indicate that increased frequency of disturbances can have positive effects on biodiversity, whereas increased extent of disturbances can have negative effects (Thom et al. 2017). Increased frequency of disturbances was found to lead to more edges and greater heterogeneity in landscape features including open areas and closed canopies, in total adding variation in terms of habitats and ecological conditions. Conversely, increased disturbance size was found to reduce the density of forest edges and increase homogeneity in landscape features. These findings highlight the necessity of going beyond correlative relationships between species richness and temperature or precipitation when addressing the complex impacts of climate change on biodiversity (Thom et al. 2016).

Extinctions and extirpations (regional extinctions) can happen over relatively short timescales while processes of divergence and speciation take much more time, so the impacts of climate change through rapidly changed disturbance patterns or phenological or trophic mismatches across large spatial scales result in a loss of diversity (Radchuck et al. 2019). As discussed under range shifts, for many species, climate change is expected to impose dispersal requirements that surpass species' maximum rates, especially when habitat losses interact with climate change to impair dispersal (Coristine and Kerr 2011). While disturbances favor some species and may eventually lead to fragmentation and selection, currently, the large-scale spatial extent of rapid and extensive climate change impact is leaving less room for refuges and small-scale phenomena and adaptations (Radchuck et al. 2019; De Frenne et al. 2021, but also Morelli et al. 2020).

Species adapted to old-growth forest or otherwise demanding long-term continuity of habitat are clearly particularly vulnerable when climate zones shift rapidly. Even when habitat-forming species keep pace with their climate zones, establishing old habitat takes, tautologically enough, time. Thus, a mismatch is created where habitat of any age can be lost at the trailing edge of the climate zone, while old habitat cannot be quickly created at the leading edge (Figure 25). Somewhat paradoxically, this may make conservation of remaining microrefugia along the southern (trailing) edge all the more important for persistence, and eventually possible speciation and adaptation (Martin et al. 2021; Greiser et al. 2019; Sønstebø et al. 2022). Old-growth habitats are likely to become less available under any increased disturbance frequencies for the simple statistical reason that if the current frequency of disturbance has an average chance p of functionally destroying a habitat, the proportion P of habitat expecting to reach age T intact is $P=e^{-Tp}$, in other words an exponential decay function of the disturbance rate. This means that the higher the disturbance rate, the smaller the part of the habitat will be over a certain age when the overall landscape is at age equilibrium.

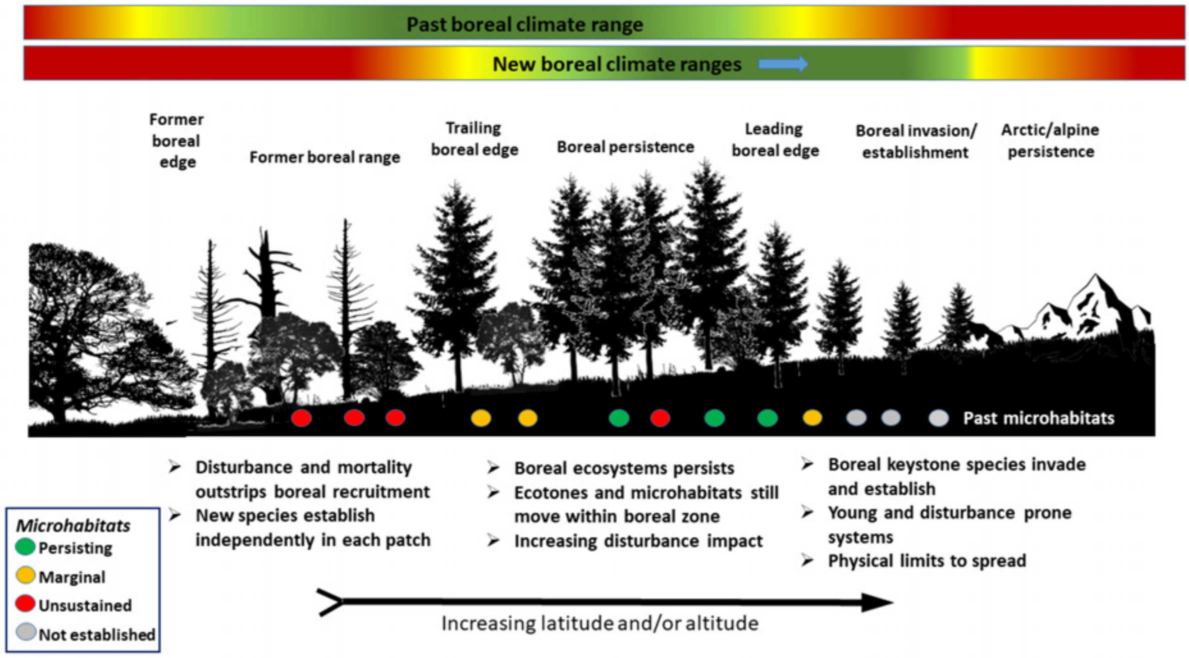


Figure 25 Process sketch highlighting the plight of microhabitats and old-growth dependent species when the habitat-building species undergo major range shifts due to a warmer climate. At one end of the range, assemblages are accruing climate and extinction debts or are at increased risk of major disturbances. At the leading front, new patches of "old" habitat have not been formed yet as components must be established in succession; the retained middle zone will undergo shifts in disturbance regime and other factors.

4.4.6 Ecological stoichiometry: nutrient cycling and CO_2 fertilization

Forests are efficient nutrient recyclers, allowing dense forests to develop on relatively poor soils (Osman 2013). Nutrient cycling is controlled by climatic, edaphic, biotic, and abiotic factors in forest ecosystems. Here we primarily report how changing temperatures and precipitation are expected to affect nutrient cycles of boreal forests directly or indirectly. We also include effects of climate-related disturbances, like fire and windfellings.

Across biomes, the speed of nutrient cycling is closely correlated with primary productivity, which in its turn is closely correlated with global temperatures. Higher latitudes have lower primary productivity and slower nutrient cycling rates because of permafrost (where present), short growing season, lower soil temperatures, and microbial activity which slows rates of litter decomposition and nutrient availability and increases carbon accumulation in the soil (Van Cleve et al. 1991). Hence, nutrient cycling of boreal forests is inherently slow, but is expected to increase with temperature increase.

Kreyling (2019) reviewed the effects of changing winter climate in boreal forest ecosystems, and concluded that increased decomposition and mineralization will enhance primary production. However, the overall effect on nutrient cycling is hard to predict and will vary within the boreal zone since midwinter melting followed by frost or rain-on-snow events might counteract this trend. Nutrient leaching is expected to increase mainly during extreme events, which will limit primary production due to increased climatic variability resulting in more frequent midwinter melting or rain-on-snow events that damage plant organs and can lead to plant dieback (Box et al. 2019, Kreyling 2019, Overland et al. 2020). Plant community composition is altered by these winter climate changes, but the accompanying feedback on decomposition and nutrient leaching is unclear.

The activity of soil organisms is closely correlated with temperature, moisture, and nutrient availability. Here we concentrate on the main nutrients and the ratios between them. Maaroufi and De Long (2020) have reviewed studies on climate change effects on the linkage between forest soil biota and nutrient availability: higher temperatures lead to a decrease in litter phosphorus (P) concentrations, and an increase in litter nitrogen (N) concentrations and N:P and C:P ratios (C = carbon; Yuan and Chen 2009). This could lead to cascading effects for soil biota, as in boreal forest soils, high C:N and C:P ratios (lower nutrient availability) are associated with higher fungal versus bacterial abundance, which have been shown to result in higher temperature sensitivity in respiration rates (Briones, 2014). Further, studies have identified a clear interaction between temperature, litter stoichiometry (relationships among elements in the litter), and decomposer feeding behaviors (Hillebrand et al. 2009).

Drought studies from boreal forests are scarce, but data from temperate and Mediterranean forests suggests that plant litter, root, and soil C:N:P ratios respond to drought in different ways (Maaroufi and De Long 2021). A meta-analysis by Sardans et al. (2017) showed that drought caused a reallocation of P, but not N, from leaves to roots, which may indicate a change in strategy to increase root water uptake (Gargallo-Garriga et al. 2015). If drying and rewetting cycles becomes more frequent (Reichstein et al. 2013), this may increase C and N mineralization rates and release of P due to changes in soil structure, nutrient desorption from soil particles, and disintegration of fungal and bacterial cells (Turner and Haygarth, 2001; Blackwell et al. 2010). Increased drying and rewetting frequency are also expected to decrease microbial biomass, which may decrease nutrient cycling. However, this may also lead to increased nutrient availability to primary producers by the release of P compounds (Fierer and Schimel, 2002; Brödlin et al. 2019).

Increased fire activity may alter soil nutrient composition and ratios between nutrients. Soil nutrients one year post-fire are highly correlated with fire severity (Kong et al. 2018; Kong et al. 2021). Wildfire increased the relative abundances of the elements nitrogen (N), phosphorus (P), sulfur (S), iron (Fe), and aluminum (Al), and reduced the abundances of calcium (Ca), magnesium (Mg), and potassium (K). Fires may result in nutrient losses through volatilization (notably of N and S) and, in some cases, fly-ash losses. Hydrolysis of base oxides in the ash results in increased soil pH, where both the magnitude and the duration of the pH change are influenced by local soil-buffering capacity. While increased pH and sorption after burning may limit the availability of micronutrient metals and phosphorus in the soil, many of the remaining ash nutrients are soluble, plant-available, and highly susceptible to leaching unless plant cover is quickly re-established. This makes the seasonal timing of fires and logging with regards to rain and snow melt important, especially as fire may also directly affect soil hydrophobicity and thus hydrologic behavior (Ballard et al. 2000, Bowd et al. 2019). Unless erosion has caused extreme nutrient leakage in the meantime, most soil nutrient ratios recover to pre-fire levels within a decade or two, but N:P may remain significantly higher (Kong et al. 2018) (see also main section for forest fires).

Hole and Engardt (2008) showed that European emissions of compounds including atmospheric nitrogen would increasingly be deposited over western Norway as a consequence of increasing precipitation and changed circulation patterns. However, reduced nitrogen emissions from Europe have so far reduced atmospheric nitrogen deposition in Norway (Deininger et al. 2020; Kaste et al. 2020). Deposition of oxidized nitrogen will increase more than the deposition of reduced nitrogen. The combined effect of increased deposition and leaching has not been estimated. Increased N load to soil may affect nutrient cycling through effects on the decomposer community. Increased N-availability might favor bacteria over fungi, but could also affect fungal composition so that those groups specialized on recalcitrant compounds are reduced (Mayer et al. 2020). Increased N-availability may lead to imbalance and co-limitation of other nutrients. N deposition has been shown to cause phosphorus (P) limitations of some forest ecosystems (Lorenz et al. 2010; Vitousek et al. 2010; Peñuelas et al. 2012).

The increased atmospheric CO_2 concentration that is a main driver of climate change also may affect plants directly by allowing increased photosynthesis. Chen et al. (2022) quantified this CO_2 fertilization effect (CFE) by combining observations from a globally distributed network of eddy covariance measurements with photosynthetic optimization theories, concluding with an enhancement of photosynthesis and that CFE has played a critical role in the global carbon cycle in recent decades. However, Launiainen et al. (2022) working with eddy-covariance measurements of net ecosystem production, evapotranspiration, light and water use efficiency from a boreal coniferous forest in Southern Finland found similar trends for CFE, but were able to look closer at the mechanism in their system. They found that CFE diminishes when moving from leaf to ecosystem, and that an increasing trend in leaf-area index, in their case stimulated by forest thinning in 2002, was the main driver of the enhanced production of the mid-rotation managed forest. It also compensated for the decrease of mean leaf stomatal conductance with increasing CO_2 and LAI, explaining the apparent proportionality between observed productivity and CO_2 trends. They emphasize the difficulty in attributing trends to their physical and physiological drivers. These results tie in with findings by Searle and Chen (2018) examined changes of tree mortality probability in 539 permanent sample plots 1960-2009 across boreal Alberta. They found an overall loss in tree longevity with global change and that trees with faster lifetime growth rates experienced higher increases in mortality rates than slower growing trees. Analysis incorporating growth conditions found that increasing CO_2 and decreasing water availability were the major drivers of declining longevity and suggested these trends to continue with rising CO_2 .

Xiao et al. (2021) points out conflicting responses of ecosystem respiration to drought as forest net CO_2 exchange depends on the balance of opposite effects of warming and water stress on respiration, and a potential overestimation of global future CFE effects due to increasing water stress and other limitations such as light and nutrients (N, P) as well as the possibility of photosynthetic acclimation. Körner (2022) also points out the limits of soil nutrients on carbon uptake and effect of increased growth on the nutrient cycle, and Terrer et al. (2016) find that ectomycorrhizal assists in overcoming nitrogen limitation under CFE. That the CFE on tree growth may be limited by nutrient imbalances resulting from high N deposition rates, P limitation or increasing water deficit, or by acclimation of trees to the elevated levels has been pointed out by multiple studies (Reyer et al. 2013, González de Andrés 2019, Du et al. 2020).

Sperlich et al. (2020) studied the growth, productivity and mortality of beech (*Fagus sylvatica*) and Silver fir (Abies alba) in the Black Forest (Germany) under RCP2.6, RCP4.5, and RCP8.5 using a detailed biogeochemical forest growth model where both species showed near-term productivity losses in RCP2.6 and in RCP4.5, but productivity gains in RCP8.5. However, all three scenarios had a tipping point (between 2035-2060) when initial gains in net primary productivity eventually turned into losses. Hararuk et al. (2018) used tree-ring data from 5,858 old-growth trees of five species in subalpine forests of western Canada and found decreasing rather than increasing growth responses for the last century. Similar results by Girardin et al. (2016) across the Canadian boreal belt also suggests that increased CO_2 uptake and growth from CFE is unlikely to be experienced by mature or older trees.

Thus, it seems likely that CFE primarily drives increased productivity in young plants, may speed up the nutrient cycle by faster growth in these stages and higher mortality in maturing trees, to the extent limiting nutrients and available water allows when faster evaporation is taken into account. The net effect of these factors grows increasingly uncertain over time and with rising CO_2 levels.

4.5 Time lags, asynchrony, cascades, and feedbacks

4.5.1 Climatic debt and time lags

Biotic responses to climate change are rarely instantaneous, resulting in disequilibrium between the biota and the extant climate, also known as lag effects or climate debt. For example, range shifts in terrestrial species are known to lag behind shifts in temperature isotherms across both latitudinal and elevational climate gradients (Lenoir et al. 2020). These climatic debts include lags in both colonization rates and extinction rates (Bertrand et al. 2016).

A systematic review from Norway reported a trend for the tree line and forest line to move upwards in altitude during the 19th century. However, time lags and impacts of non-climatic drivers, such as land-use change makes disentangling the role of climate from that of other factors difficult (Bryn and Pothoff 2018). More generally, the poleward latitudinal advance of subarctic forest in Fennoscandia and the Polar Ural Mountains (~100 m/year) lag 1 to 2 orders of magnitude behind the range shifts needed to remain in equilibrium with climate (Rees et al. 2020). A modeling study from Austria found time-lags at the scale of 357 to 706 years for the autonomous adaptation of the species composition of a forest landscape to a moderate climate change forcing (*q.v.*) (SRES A1B projections) (Thom et al. 2017). Accordingly, in a circumpolar study, Brecka et al. (2018) conclude that boreal tree species ranges have migrated north and will continue to do so but at a slower rate than climate change.

A circumpolar comparison of forest-tundra ecotones revealed substantial regional variation in the rates and even directions of northward range shifts of boreal trees. This variability was more related to differences in precipitation than to temperature change, thus highlighting that both growing and non-growing seasons are important in determining range shifts (Rees et al. 2020). Similarly, a study found widespread climatic debts in European plants in alpine, Atlantic, and boreal regions. Precipitation plays a role, especially in coastal climates (Duchenne et al. 2021). Frequent and severe disturbances can also accelerate range shifts, decreasing the time needed to attain equilibrium by up to 200 years, whereas increasing disturbance size can have the opposite effect (Thom et al. 2017). As a result, under current rates of climate change, long-lived and sessile organisms, such as trees, are likely to be exposed to novel climates, potentially beyond the species' historic climatic ranges, during the lifetime of a single individual, with potential consequences for various vital rates (section 4.2.1) (Thom et al. 2017).

A study assessing the climatic debt accumulated in French forest herbaceous plant communities show that warmer baseline conditions predispose plant communities to larger climatic debts (Bertrand et al. 2016). With small temperature changes, forest plant communities can still adapt, but as climate warming is expected to accelerate, plant migration and tolerance to climatic stresses may be insufficient to absorb this impact. The authors conclude that future climate change will increase climatic debt and might eventually exceed species tolerance, triggering local extinction events, novel species assemblages, and unknown cascading effects on ecosystem functioning.

Different biological processes and biota may differ in their rate of response to climate change (Lenoir and Svenning 2015), which may lead to differences in climate lags and thus potential mismatches between interacting organisms (Visser and Both, 2005; Elzinga et al. 2007), and across trophic levels, with consequences for ecosystem functioning and stability. In the study by Bertrand et al. (2016) of herbaceous plants in nemoral continental forests, the reason for range shifts lagging behind climate shifts tended to be poor persistence (survival) rather than slow migration. Ecologically specialized species have overall low colonization rates, for example, wood-decomposer fungi seldom manage to colonise habitat patches when habitat quality or connectivity is low (low density of large logs or low stand age) (Moor et al. 2021). High forest age may be important for specialists both because of the long formation time of necessary structures, such as tree hollows or large trunks, or of necessary conditions (e.g., local microclimate) and because the likelihood of successful colonization of specialists increases with time (Nordén et al. 2018). The outbreak range of the generalist geometrid moth *Operophtera brumata* has rapidly tracked the increase in winter temperatures in northern Norway and presently extends ten longitudinal degrees east (400km) of what was the range border a century ago (Jepsen et al. 2008). The community of larval parasitoids in *O. brumata* and *Agriopis aurantiaria* (Hübner, 1799) appears to have tracked their host with a lag of only a few decades (Vindstad et al. 2013). The phenological shift rate in response to climate warming is higher for low trophic level organisms relative to consumers or higher trophic levels (Parmesan et al. 2003; Thackeray et al. 2010, 2016).

In a study from a single locality in Russia over 40 years, Ovaskainen et al. (2013) found that plants, birds, reptiles, amphibians, insects, and fungi shifted their phenologies at different rates in response to climate change, because of the different sorts of climate or environmental cues they used. In particular, plants were responding to short-term climate cues and shifting their phenologies faster than the climate change trends, whereas birds tended to respond slower. However, Ovaskainen et al. (2013) also found between-group synchrony in year-to-year variation among plants, birds, insects and herptiles, though not fungi, possibly suggesting phenological synchrony was less impacted by climate change than expected. Species-specific shifts were similarly noted along an altitudinal gradient in Bavarian forests. Bässler et al. (2013) found that different taxa differed in their upward shift as a response to increasing temperatures, with many insects exceeding the shift expected from climate warming. Consequently, over longer periods, climate change is likely to frequently result in reorganization of plant and animal communities, with highly uncertain consequences for ecosystem processes.

4.5.2 Synchrony and interactions between trophic levels

Changes in phenology—that is, changes in the seasonal timing of life cycle events—are key responses to climate change (Parmesan 2006; Roslin et al. 2021). A broad trend among organisms at higher latitudes is that spring events occur earlier, and autumn events occur later (e.g. Kauserud et al. 2010, 2012; Caparros-Santiago et al. 2021). This implies longer growing seasons and alterations in the timing and regulation of processes such as bud burst, reproductive events, and growth or activity termination. However, there are substantial complexities involving regional variation in importance of climatic factors, such as temperature in the boreal forest (Kramer et al. 2000), relationships with local conditions such as soil moisture (Caparros-Santiago et al. 2021), species responses to temperature and day length (Salk 2020; Delpierre et al. 2016), synchrony between above- and below-ground phenology (Abramoff and Finzi 2015), and delayed impacts (Hanninen and Tanino 2011). Differential species' responses to environmental cues, such as temperature, may result in phenological mismatches that can reduce fitness for individual species, shift community competition, disrupt trophic interactions, and ultimately alter ecosystem functioning (Williams et al. 2021, Renner and Zoner 2018; Parmesan 2006; Schuldt et al. 2018; Roslin et al. 2021, and references therein).

It is predicted that phenological mismatches may be more likely for antagonistic interactions (where one species suffers) in high-latitude Arctic regions, than for mutualistic interactions (both species suffer) in other regions (Renner and Zohner 2018). The phenological shift rate is highest for low trophic level organisms (Parmesan et al. 2003; Thackeray et al. 2010). Hence, primary producers in the boreal forest will start their biological activity increasingly earlier in the spring in relation to consumers as a response to climate warming (Thackeray et al. 2010, 2016; Delgado et al. 2020).

More specific examples of diverging phenological responses may include greater risk of poorly timed leafing out or color moulting, along with altered interactions among species (Zimova et al. 2018, Ylönen et al. 2019, Montgomery et al. 2020, Gougherty et al. 2021). Such responses may vary among populations of the same species. For example, European beech (*Fagus sylvatica*) need long days to initiate bud break in its main distribution area in central Europe, but bud break has advanced by more than 10 days over the last three decades in southeastern Norway (Strømme et al. 2018). This indicates that Norwegian populations are more sensitive to temperature than those in central Europe. Such relationships may affect tree mortality (Cooper et al. 2019) and impact the speed with which nemoral species can move into the boreal zone, and boreal forest species shift into alpine, arctic or tundra (Zettlemoyer et al. 2021).

Seasonal color molting is prevalent in some boreal mammals and birds, including hares, small mustelids, and ptarmigan. This phenological event is predominantly triggered by photoperiod and consequently has been observed to be subjected to mismatches when the snow-free season starts later and ends earlier (Zimova et al. 2018). Camouflage mismatches, such as seasonal color molting, have been proposed to increase predation risk of prey species and may have contributed to long-term population declines in mountain hare (Pedersen et al. 2017) and willow ptarmigan (Melin et al. 2020) in the boreal zone of Fennoscandia.

In the bird-rich boreal forests, there is evidence of climate-induced temporal mismatches in food availability for migratory birds, that is, in insect peak abundance and chick development. A well-known example is that of the pied flycatcher (*Ficedula hypoleuca* (Pallas)), which is an abundant forest bird of northern ecosystems. The pied flycatcher has advanced its laying date, most probably due to climate warming, but this phenological shift is not the same as that of the advancement of caterpillar biomass as a food source. This results in a temporal mismatch between breeding season and prey availability (Both and Visser, 2001; Visser and Both 2005). For migratory species, mismatches and other climate change related effects can be exerted at any place and time along the migratory route (Kubelka et al. 2021).

Insectivorous bats have long been acknowledged as key suppressors of arthropod pests in agricultural systems, and bats also control insect populations in natural ecosystems (Kunz et al. 2011). Bats have been found to utilize forests shaped by outbreaks of insect pests for foraging (e.g., Kortmann et al. 2018). Predicted future increase in outbreaks of insect pests will increase the value of the ecosystem services provided by generalist predators like insectivorous bats (Williams-Guillén et al. 2016).

Most studies of the impacts of climate change on the (a)synchrony between predator requirements and prey availability have concentrated on the breeding season (e.g., passerine birds and their prey; see above paragraph, Dunn 2004; Durant et al. 2007). However, for resident predators in the boreal forest, foraging during the non-breeding season (winter) is crucial for survival and preparation for the breeding season. Birds that depend on hoarding perishable food to survive harsh winter conditions are assumed to be susceptible to climate change (Sutton et al. 2016). For example, a long-term study of the Eurasian pygmy owl (*Glaucidium passerinum*) in Finland indicates that impacts of climate change on food-hoarding predators could be substantial, "because their 'freezers' may no longer work properly" (Masoero et al. 2020).

In a broad review of Lepidoptera ecology and climate change, Hill et al. (2021) found that most studies reported early emergence from diapause causing increasing asynchrony with host plants. In Finland, they also found that warming accelerates caterpillar development more than that of parasitoids, increasing juvenile survivorship. In contrast, climate warming may sometimes increase the synchrony between trees and their pests as documented by Pureswaran et al. (2018) in a study on the eastern spruce budworm in the boreal forests of northeastern Canada. Here, synchrony increased by up to 4.5 days for balsam fir, and up to 2.8 days for black spruce per degree increase in temperature. Another example of increased synchrony under climate warming is between temperate Geometrid moths (*Operophtera brumata* and *Agriopis aurantiaria*) and subarctic mountain birch in northern Norway, potentially explaining the northwards expansion of the outbreak range of these forest defoliators (Jepsen et al. 2011).

4.5.3 Cascades and feedbacks

The impact of altered temperature and precipitation regimes will cascade through the boreal forest ecosystem with ensuing complex interplay and feedbacks between the intensifying abiotic and biotic disturbance regimes introduced in section 2.1.3 and discussed in sections 4.3-4.5 (Seidl et al. 2017). Changing temperature and precipitation regimes might lead to reduced snow cover and a shortened period of frozen soil (Venäläinen et al. 2020). This could weaken the anchoring of forest trees, especially spruce, and thus increase the likelihood for windthrow even if wind-speed regimes remain largely unaltered. Increased amount of wind-felled trees could increase the risk for bark beetle outbreaks, especially in warm summers, which might also increase the likelihood for attacks by other insects or pathogens. The increase in dead trees resulting from such outbreaks might subsequently serve as fuel and thereby increase the likelihood or intensity of forest fires.

The importance of cascades of this kind for Norwegian forest ecosystems may also depend on management regimes and vary across forest areas. It has been suggested that removing wind-felled trees from managed forests may decrease the risk of bark beetle populations reaching critical size, and that in near-natural forests natural enemies of bark beetles may be what hinders an outbreak. However, evidence for either being effective is limited (Biedermann et al. 2019; Kaminska et al. 2021).

The community of herbivorous and granivorous (seed-eating) animals in the boreal forest include functional groups (guilds) that have specialized diets of leaves, bark, buds or seeds of conifers and dwarf shrubs. Forest grouse and crossbill species are specialized on conifer needles and seeds, respectively, and arvicoline rodents are specialized browsers of *Vaccinium* shrubs. Vegetation state transition toward a nemoralization of the forest ecosystem is likely to impact these herbivore guilds negatively, whereas other groups of species may benefit (Elmhagen et al. 2015). High amplitude small rodent cycles, which are an important driver of food web dynamics in the Scandinavian boreal forest (Boonstra et al. 2016), may be lost resulting from such nemoralization as this phenomenon does not occur south of the "Limes Norrlandicus", which is the border between the boreal and the boreo-nemoral zones in Scandinavia (Hansson and Henttonen 1985, 1988). Accordingly, recent region-wide damping of rodent cycles in the boreal forest zone have been attributed to climate warming (Cornulier et al. 2013), though others highlight that these cyclic dynamics have returned (or may not have been reduced much) in some parts of the boreal zone (Brommer et al. 2010). The damping of small rodent cycles in the boreal forest of

Fennoscandia has been accompanied by declining populations of predator species belonging to the guild that is specialized on rodent prey (Hörnfeldt et al. 2005, Kouba et al. 2021). Climate-change induced shifts in the composition of functional groups of plants and herbivores is therefore expected to also cascade to the predator level in boreal food webs (Boonstra et al. 2016).

Climate-induced changes in the community of cervids can be expected with a lower abundance of moose (mainly a boreal species) and higher abundance of red deer and roe deer (more nemoral species), which in turn may affect the plant community. The extent to which such changes may favor certain plant species above others remains unclear, but it is reasonably well established that ungulate herbivory reduces tree recruitment at local scales (also for farmed ungulates: Hegland et al. 2021). High densities and unhindered browsing by large herbivores can be facilitated by low abundances of large predators, which may therefore indirectly hinder recruitment of young deciduous trees (Angelstam et al. 2017). For example, eastern Norway recruitment of pines may be reduced by winter foraging of young saplings by moose. Ungulate herbivory may sometimes also facilitate dispersal of trees, by increasing rates of soil nutrient cycling, at least in temperate systems (Churski et al. 2017; Ramirez et al. 2018), and as such benefit many plant species and diversity in the forest floor (Hegland et al. 2013, Hegland et al. 2016) in Norway at present. There is some evidence from North America that selective browsing from ungulates have benefitted conifers at the expense of deciduous tree species (McInnes et al. 1992; Winnie, 2012). Niemelä et al. (2001) projected that the climate-induced changes in vertebrate and insect herbivore populations in southern Fennoscandia would promote the density (and biomass) of spruce, while pine and broadleaf trees would be negatively affected. In northern Fennoscandia, spruce and broadleaf trees would be promoted at the expense of pine. Herbivore impacts may counteract, or hamper, some of the direct climate effects on plant community composition in boreal forest by hindering recruitment of palatable species (4.2.11.1), a process which is similar to the slowing down of shrubification via ungulates observed in the Arctic (Bryant et al. 2014; Pecl et al. 2017; Bråthen et al. 2017).

Grouse species are characteristic for the boreal forest system and play important roles as herbivores directly or indirectly dependent on ericaceous shrubs. They are also an important food source for many species of birds of prey. Warmer summers affect densities of Eurasian capercaillie (*Tetrao urogallus* L.) and chick production of willow ptarmigan (*Lagopus* L.) in Norwegian forests negatively. This effect is likely climate induced and works via bilberry (Selås et al. 2010). The black grouse (*Lyrurus tetrix* (L.)) densities may peak at higher altitudes with lower summer temperatures (Selås et al. 2010). While earlier springs have been suspected to cause a mismatch between grouse chicks and their insect larvae food source (Ludwig et al. 2006), a long-term study in SE Norway found evidence to the contrary; Although timing of mating in black grouse and capercaillie did not advance as fast as the advancing onset of spring, the breeding success increased markedly in both of these grouse species (Wegge and Rolstad 2017). However, the abundances of grouse species are declining across their ranges which, in addition to the main cause of intensified land use through forestry practices (younger and denser forests), may be enhanced by climate change (Jahren et al. 2016). In upland Britain, the proposed mechanism for population declines in grouse and other bird taxa is the combined negative effects of drier habitats (draining of wetlands and climate change) and reduced availability of some preferred invertebrate prey taxa (Pearce-Higgins 2010). Not all of these drivers may be related to climate change.

4.5.4 Transient dynamics under climate change: forests in transition

A large percentage of the current boreal forest regions of Scandinavia are projected within this century to be subjected to climates that are consistent with boreo-nemoral or nemoral forest ecosystems (McDowell et al. 2020, Beck et al. 2018). In terms of plant functional groups, this suggests a transition from conifer to broadleaved tree dominance. For the understory, this suggests a transition from dominance of dwarf shrubs and mosses/lichens to more diverse vegetation of different functional groups of non-woody vascular plants (Moen 1999). The pace of these vegetation state transitions are expected to be substantially slower than the pace of climate change, especially for plant functional groups with long generation time, such as trees.

Assessing the leading edge of boreal range shifts with establishment into the tundra, Rees et al. (2020) analyzed data from 151 circum-arctic sites in Eastern Canada, Central and Western Canada/Alaska, Siberia, and Western Eurasia. They found an importance of precipitation rather than temperature for establishment, and that both non-growing season as well as growing season was important. Poleward latitudinal advance rates differed significantly among regions, being smallest in Eastern Canada (~10 m/year) and largest in Western Eurasia (~100 m/year). These rates were 10-100 times slower than expected if vegetation distribution remained in equilibrium with climate. See also Price et al. (2013).

Similarly, in the trailing boreal edge where temperate, broadleaf, species are expected to establish, Solarik et al. (2019) and Vissault et al. (2020) find that the limited mean dispersal distance of trees is exacerbated by unfavorable substrates and to resident boreal trees generating (strong) priority effects within the temperate-boreal ecotone, causing significant lags in temperate tree species migration into the boreal forest.

Rees et al. (2020) stress that lack of empirical evidence for swift forest relocation contradict equilibrium based assumptions and warrant caution when assessing implications of climate change. As the rate of climate change by far exceeds the speed of forest succession, trees adapted to the past climate may be effectively outside their climate zone before new species have had time to establish, with potential detrimental impacts on survival and resilience (cf. section 4.2.1). These shifts will be associated with range expansion of southern species

(4.2), range contraction of northern species (4.2), and loss of biodiversity associated with old growth forests (*q.v.*) (4.4).

The likelihood of forest transitions and shifts of biomes can be moderated by the intensity and scale of disturbance regimes. In meridional Quebec 10,000 boreonemoral forest (*q.v.*) inventory plots were sampled from 1970 to 2018. Long-term projections under the current environmental conditions indicated that moderate disturbances would promote a northward shift of the temperate forest (suggesting climatic debt, section 4.5), with disturbances reducing turnover and convergence time (Brice et al. 2020). They found that transitions were not driven by temperate tree recruitment but by mortality and growth. Overall, the results suggest that moderate disturbances can facilitate temperate-boreal forest transitions and broad-scale biome shifts (Brice et al. 2020).

Intermittent deviation from expected change trajectories can also be due to abrupt events, as exemplified by the recent large-scale outbreaks of geometrid moths in northern Norway (see section for eruptive insects, 4.2.11.2). Besides causing extensive mortality of trees, these outbreaks caused an abrupt vegetation state shift in the understory, from a state dominated by dwarf shrubs to a state dominated by graminoids (Karlsen et al. 2013).

Changes in water regimes, including precipitation and subsequent hydrological processes, play important roles in relation to disturbance and forest structure, but can vary strongly locally depending on the topography. Increased precipitation may lead to increased peat accumulation ("paludification"; Laamrani et al. 2020) in the north and west. On the other hand, especially in the south and east, lower soil moisture availability could increase the frequency and severity of forest disturbances, such as drought stress, fires and insect outbreaks, especially when combined with warmer temperatures (Brecka et al. 2018). Along gradients of increasing drought risk there is substantial turnover in species composition and forest ecosystem types (Halvorsen et al. 2020), furthermore persistent drought conditions (sometimes interacting with disease and pests) may lead to increased tree mortality (Allen et al. 2010, Singer et al. 2019) or even shifts from forest to shrub or grasslands (Brecka et al. 2018).

Overall, climate change is expected to increase the frequency and severity of disturbances, which may lead to more heterogeneous forests in a natural, unmanaged setting, as long as the disturbances are not strong enough to lead to radical ecosystem shifts (such as shifts to shrubs or to grassland). On the one hand, forest management may counteract natural processes by controlling fires, clearing stands damaged by storms, fires, or pests, and amplify natural edges and add anthropogenic edges with substantial effects on vegetation structure (Franklin et al. 2021). Conversely, others argue that perhaps forest health can be promoted through silvicultural interventions, for example species and genotype selections favouring resilient ecotypes or to maintain genetic diversity, or facilitating species migration (Parker et al. 2000). Most ecosystem responses will lag behind the velocity of climate change and the nature of such temporal mismatches leads to transient (non-equilibrium) ecosystem dynamics that may be difficult to predict (Ims and Yoccoz 2017, Turner et al. 2020, Williams et al. 2021).

It seems clear that all climatic factors considered above may affect landscape ecological patterns. However, due to complexities and uncertainties, the contributions of "single" climatic factors, and the total (potential) compound impact of climatic changes, is difficult to quantify.

4.6 Managed versus natural forests

Clear-cutting followed by re-planting is the dominant management regime in Fennoscandia. This practice results in forests that are less diverse in terms of genetics, species richness (monocultures) and vegetation structure (single tree layer) than natural forests (Aszalos et al. 2022). Trees growing from seeds under a developed canopy grow more slowly than nursery plants on a clear-cut: it can take 30 to 60 years before young trees have reached breast height (Laiho et al. 2011). Further, trees that grow in a natural forest to a larger degree compete for light, water, and nutrients, which results in more developed root systems making them more resistant to strong winds. The multi-layered structure of natural forests results in a more stable microclimate and reduction of wind speed. Overall, unmanaged forests in Fennoscandia are subjected to complex natural dynamics that create a structural diversity both within and among tree stands, resulting in forests that are very different from plantation forests (Kuuluvainen and Aakala 2010). Aszalos et al. (2022) concluded that while even-aged forestry intuitively has very low congruence with natural dynamics, uneven-aged forest management systems also produce only a portion of the complexity associated with natural disturbance effects.

There is little empirical evidence for differences in susceptibility to climate change between natural and managed forests from northern Europe. Further, while the larger part of the forests has been influenced by human activity to some degree, the management intensity is highly variable. Even so, there is no doubt that silvicultural practices affect the vulnerability of managed forests to climate change-induced stressors. When the frost and snow-free period increases, harvesting or thinning will to a larger degree take place during periods when roots are less insulated by snow and thus more exposed to damage from harvesting machinery, including when fungal spores are spreading (Solheim et al. 2013). Further, frost-free ground and more precipitation during winter mean weaker anchoring of roots during the period with highest storm intensity (Usbeck et al. 2010). Mixed stands of spruce and beech in central Europe are more resistant to anomalies in precipitation and temperature than when these tree species form monocultures (Neuner et al. 2015, Vacek et al. 2021). Moreover, simulation studies predict that monospecific spruce stands will be more vulnerable to bark beetle outbreaks and wind disturbance than forest stands that are managed to create diversity (Dobor et al. 2020, Zeng et al. 2010). Dobor et al. (2020) applied the ecosystem model iLand (Seidl et al. 2012) to investigate how interactions between climate, forest management, disturbance, and vegetation dynamics affect forest landscape dynamics when perturbed by windstorms and spruce bark beetle outbreaks. A central conclusion of their simulations is that traditional management practices, such as clearcutting in monoculture spruce forest, fail to mitigate disturbance impacts, while forestry practices that maintain forest diversity substantially reduce levels of disturbance. An earlier meta-analysis (Griess and Knoke 2011) reached a similar conclusion, as they found that mixing tree species increased resistance to windthrow and forest insect attacks (see also Jactel and Brockerhoff 2007). Dobor et al. (2020) found that monospecific forests are much more vulnerable to wind and bark beetle disturbance than species-diverse forests, and that climate change magnifies the difference in vulnerability. Their simulation imitated a typical central European spruce forest with some admixture of Scots pine, larch, fir, and beech. Norwegian forests are naturally less diverse than those in their study, but the main results of this simulation are likely to be relevant.

In Norway, as in the rest of northern and central Europe, spruce has been planted on soils that naturally would be occupied by more drought-tolerant species. Such sites are expected to be especially vulnerable to drought, but also windthrow in the near future (Spiecker 2003, Caudullo et al. 2016)

Some rare species may be threatened by both land use and climate change. Mair et al. (2017, 2018) found that for a set of highly specialized and rare fungi, forest management has the potential to compensate for negative effects of climate change by increasing the amount of protected or set-aside forests.

4.7 Red-listed species and habitats

For the Artsdatabanken (2021) assessment, climate change was assigned as a contributing factor to population declines for 38 species listed as threatened or near-threatened out of a total of 2083 red-listed forest species (Appendix III). Of these 38, the greatest representation is found across bird (9), moss (7) and vascular plant species (6), and to a lesser extent fungi and spiders (3), or lichens, beetles, flies, bees and wasps, and mammals (2) (Table 3). This contrasts with the representation found across the broader 2083 red-listed forest species where the largest groups were fungi (657 species), beetles (363), flies (224), lichens (213), and moths and butterflies (170).

For most of the 38 listed species, climate change is posited as a likely contributing factor to reduced habitat area, and increased fragmentation of populations. However, climate change is usually one of several to many factors. In the case of the birds for example, there are the additional factors of hunting and nest disturbance. A common theme for red-listed boreal forest species is that Norwegian populations are at the northern or western limits of a species distribution, and that suitable habitats in Norway are highly fragmented due either to the habitat itself being rare or to changes in zoning, agricultural or forestry practices that lead to loss or degradation of habitats.

Table 3. Numbers of forest species in each taxonomic group for which climate change is given as a threat in the Norwegian Red List. CR: critically endangered; EN, endangered; VU, vulnerable; NT; Near threatened. All threats: total threatened and near threatened red-listed species in that taxonomic group.

Taxonomic group	CR	EN	VU	NT	Total	All threats
Mosses		3	2	2	7	69
Vascular plants		1	2	3	6	116
Lichens	1	1			2	213
Fungi				3	3	657
Spiders			1	2	3	22
Beetles				2	2	363
Flies		2			2	224
Bees, Wasps		2			2	144
Mammals			1	1	2	14
Birds		2	2	5	9	25
Other groups						236
Grand Total	**1**	**11**	**8**	**18**	**38**	**2083**

The overwhelming majority of the red-listed species in Table 3 are common elsewhere: none of the red-listed species are known only from Norway. Norway has over half of the European populations for *Cassiope tretragona*, but the overall distribution of that species is circumpolar with 99% of populations found outside of Norway (Solstad et al. 2021a). The entire Norwegian population of the little bunting (*Emberiza pusilla*) was estimated to be only 30 to 100 individuals in 2015, but to be 20,000 to 60,000 individuals in Finland in 2011 (Stokke et al. 2021). The Critically Endangered lichen *Peltigera retifoveata* (Norw. *huldrenever*) has been found in only two localities in the eastern part of Norway, and the Norwegian population is estimated to be somewhere between 2 and 100 individuals (Haugan et al. 2021). However, the species has also been recorded from Finland, northern Asia, and western North America (Vitikainen 1994, Goffinet 1992). A few species seem to be rare everywhere, despite having wide species distributions, such as the moss *Tayloria acuminata* that is judged to be rare throughout Europe (Høitomt et al. 2021).

For one spider (*Zelotes puritanus* Chamberlin), one beetle (*Crepidodera lamina* (Bedel), one fly (*Brachycampta triangularis* Strobl), one wasp (*Polistes biglumis* (L.)), and one bird (the cuckoo, *Cuculus canorus* L.), climate change will likely increase habitat amount or quality. These species will be favoured by milder temperatures, by increases in broadleaf forest, or by more frequent or more extensive disturbances that increase open habitats or thin out forests.

For three species on the Norwegian red-list, the populations in Norway do contain more than 50% of all individuals in Europe. Both *Cassiope tetragona* (Arctic bell-heather, Norw. *kantlyng*) and *Rhododendron lapponicum* (Lapland rosebay, Norw. *lapprose*) are low-growing shrubs classified as Vulnerable because population declines in Norway over the next three generations (75 years) are expected to exceed 30% (Solstad et al. 2021a,b). The predicted declines are due to loss of habitat and competition from other species, triggered by climate change. The third species is a lichen, *Petigera retifoveata* (Norw. huldrenever), the only forest species that is Critically Endangered. The current habitat is relatively safe for this species; climate change could impact populations if it leads to desiccation because of high temperatures or more irregular precipitation (Haugan et al. 2021).

In general, we consider the specific habitats to have been discussed as part of the discussions about their habitat-building species and the landscape ecological processes in their respective settings. However, the list of habitat types according to the Environment Agency's mapping guidelines that was part of the ToR has been assessed, the applicable conclusions condensed on a type for type basis for the sake of easy reference, and it is found in Appendix 1.

5 Results II: Implications and consequences for the ecological condition of boreal forests in Norway

In this section, we summarize the findings from the climate change and literature review (Chapter 4) with respect to the ToR. Section 5.1 summarizes evidence for impacts of climate change and climate related variables (see 3.1.3, 3.1.4) on each of the seven characteristics of ecological condition, as defined by the Norwegian Technical System for the Assessment of Good Ecological Condition Framework (Nybø et al. 2017, see 3.1.1). Section 5.2 summarizes the role of native and alien pest and pathogen species in boreal forests. Section 5.3 summarizes the results for key tree species, different stand ages, and regions, where available. Section 5.4 discusses factors that confer resilience, resistance, and vulnerability to climate change (see 3.1.6). Section 5.5 summarizes the vulnerability of managed and unmanaged forests to climate change. Section 5.6 summarizes impacts or relevance to national biodiversity targets 1.1 and 1.2.

5.1 The ecological condition of Norwegian boreal forests in a changing climate

The ToR asks for an overview of the status of our knowledge about how the forests in Norway will develop under a changing climate. In Chapter 4, we summarized how the projected climate changes will affect abiotic and biotic aspects of boreal forests in Norway. We assessed how these climate changes and associated biotic and abiotic disturbances will impact organisms and ecological processes in the forest ecosystem. In doing so, we took an open-ended approach, in that we surveyed the literature for evidence of climate change impacts on abiotic conditions, organisms (covering a wide range of responses, from basic demographic rates to distributions), species and trophic interactions, and various aspects of ecosystem functioning. Here, we summarize this information in the context of the seven characteristics of ecological condition, following Nybø et al. (2017). This process, including how we ascribe observation-response combinations and cases thereof, is described in more detail in sections 3.3.1 and 3.3.2.

In total, our assessment uncovered information on current climate change impacts for 353 biotic and abiotic observation-response combinations, 328 of which relate to one or more of the seven characteristics of ecological condition (see 3.1.1). This comprises 496 cases of organisms by response by driver. These responses included information across a broad range of functional groups of species, including primary producers (trees, dwarf shrubs, forbs, graminoids, bryophytes, and lichens), vertebrate herbivores and granivores (ungulates, rodents, lagomorphs, birds), specialist and generalist invertebrate herbivores, insectivores (birds and bats), carnivores (birds, mustelids, fox, wolves, and bears), mutualistic fungi, viruses, and invertebrate, bacterial and fungal decomposers. These responses included changes in biomass or local abundances (biomass, growth, and densities), in phenology, in demographic rates (recruitment, mortality), in range shifts, and in population outbreaks (Figure 26). In addition, there were ecosystem-level responses, such as climate mismatches and feedbacks, along with responses reflecting nutrient cycling. We also collected information on climate responses of invasive species and pathogens (33 cases).

The largest number of responses were related to the distribution of biomass between different trophic levels (characteristic 2: 232 cases) and functionally important species (characteristic 4: 220 cases); intermediate numbers of responses were seen for primary productivity (characteristic 1: 136 cases) and landscape ecological patterns (characteristic 5: 108 cases). There were fewer responses with respect to functional group composition (characteristic 3: 77 cases), biological diversity (characteristic 6: 56 cases), and abiotic factors (characteristic 7: 54 cases). Responses can contribute to more than one ecosystem characteristic: for example, responses reflecting "climate mismatch" and "cascades" may typically impact both primary productivity, biomass distribution across trophic levels, and functionally important species.

A wide range of climate factors and climate-related disturbances were found to impact the organismal or ecosystem responses (Figure 26). The largest number of instances were for impacts of increased temperature (167 cases), both overall and in specific seasons, followed by general climate change (135 cases). Far fewer studies dealt with impacts of changes in precipitation regimes, such as increased precipitation (26 cases). We found examples of a range of climate change-related extremes, but with variable and often low numbers of responses observed for each. More frequently documented extremes included drought and heat extremes (21 and 12 cases), wind-felling (10 cases), and increased fire risk and fire intensity (33 and 7 cases). Few studies reported impacts of cold extremes (4 responses), increasing numbers of freeze-thaw cycles (5 cases), snow damage risk (2 cases), increased rain-on-snow events (1 case), and undefined climate related disturbances (9 cases for disturbance frequency, 4 for size). Evidence of impacts of more gradual climate change-related abiotic changes were also found, including decreased snow cover (17 cases), decreased frost (5 responses), altered duration of the snow season (13 cases), and CO_2 fertilization (5 cases). There was also evidence for links of climate change to pests and diseases (19 cases), alien species (1 cases), and herbivory (10 cases). Responses to increased temperature and increased precipitation were generally positive, at least in the short term. Responses to extremes were more variable, but often negative (Figure 26).

Figure 26. Summary of the negative, neutral, or positive impacts of various climatic and disturbance drivers on organismal groups within Norwegian forests. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). The figure does not include information from species categorized as alien. Interacting drivers were not explicitly included.

5.1.1 Characteristic 1: Primary productivity

Trees are the dominant primary producers in Norwegian forests, but ericaceous dwarf shrubs and to a lesser extent other vascular understory plants, bryophytes and lichens also contribute (2.2.5.1-2.2.5.6). We found consistent evidence that the primary productivity of all major plant functional types in Norwegian boreal forests will be impacted by climate change. The 136 cases across 68 observation-response combinations that reflect different aspects of primary productivity include distribution, abundance, growth and survival of major tree species (4.2.1) and understory species (4.2.2-4.2.4), along with estimates of forest productivity (4.4-4.5). Some studies also focus on the role of lags, trophic interactions, and feedbacks in affecting primary productivity (4.5). Forest management also impacts productivity: this is not a focus of our report, but is treated in section 4.6.

Near-term climate warming, and the associated prolongation of the growing season, is projected to increase the abundance and growth of trees in particular but also of ericaceous dwarf shrubs (4.2 and Figure 27; *well established*) and to some extent other understory vascular plants (*established but incomplete*). In contrast, bryophytes and lichens have both positive and negative responses to warming, likely linked to the relatively low optimal temperature requirements of many bryophytes in combination with decreased light availability in the understory due to increased shading by trees and ericaceous dwarf shrubs (*Figure 27, established but incomplete)*. In the longer term, as warming becomes more pronounced (4.1.1), growth responses of trees, notably spruce and birch, especially at lower latitudes and altitudes, will likely be negatively impacted both in terms of reduced growth and increased mortality (4.2.2; *well established*). Similarly, increased precipitation (4.1.2) will also increase on overstory growth and have more mixed impacts on understory plants, bryophytes, and lichens (Figure 27; *well established*).

Increased incidence and severity of climate-driven extremes (4.1.3-4.1.7) are also projected to have system-wide impacts on boreal forest primary productivity, acting especially through growth and mortality (Figure 27*, well established*). Heat extremes and droughts are projected to decrease growth and increase mortality in spruce (4.2.1.2; *well established*), pine (4.2.1.3; *established but incomplete*), and crowberry (4.2.2; *well established*)*.* Winter warm spells are expected to increase mortality in ericaceous dwarf shrubs, especially in combination with reduced snow cover (4.2.2; *established but incomplete* for bilberry, *established but incomplete* for lingonberry). Increased fire frequency and severity and increased windfelling are likely to increase mortality in spruce and pine (4.4.1; *established but incomplete*), bryophytes (4.2.4, *established but incomplete*) and to a lesser extent understory plants. Other climate related disturbances may also have similarly detrimental effects on the survival of these species (*established but incomplete*). For dwarf shrubs, a shorter snow season may promote growth, however, loss of insulating snow cover in spring and autumn may increase susceptibility to freezing events (4.2.2, *unresolved*)*.* While there is some evidence for positive effects of CO_2 fertilization on growth, these often refer to young trees; such responses may be constrained by nutrient and water availability, and weakened by extremes, suggesting the net fertilization effect is likely to be weak and to decrease in the longer term (4.4.6; *unresolved*)*.*

Increased incidence of tree pests, diseases, and herbivores under future climates is likely to decrease the abundance and increase mortality of spruce, pine, and birch, to the extent that these impacts may impede or delay the climate-driven range shifts in tree species (e.g., 4.2.1.1, 4.2.1.2, 4.2.1.3, 4.3, 4.4.1, 4.2.12.5; *well established*). These trophic interactions are evident in the involvement of ungulates, rodents and lagomorphs, carnivores and birds and bats in negative feedbacks to forest primary productivity under warming (Figure 27, *unresolved*). The resulting lags in tree and forest responses to warming and climate change are extensively documented for trees and boreal forest ecosystems across drivers, particularly temperature (4.2, 4.5.1-4.5.4, Figure 27), and they generally have positive impacts (i.e., enhancing positive climate impacts or dampening negative climate impacts) at least in the near term. Lags and asynchronies (4.5.1, 4.5.2) and feedbacks (4.5.3) in responses to near term warming and climate change more generally are extensively documented at the ecosystem level (Figure 27). While these effects are coded overall as "positive" at the ecosystem level in Figure 27, note that this does not imply increased productivity, but rather enhanced rates of ecosystem processes (i.e., both primary productivity, consumption, and decomposition, and so net impacts on forest carbon capture and storage may often be negative (see sections 4.4.1, 4.5.1-4.5.4) (*unresolved*). For more details on key tree and understory species, see section 5.4.

In summary, our assessment found evidence for a number of links between different aspects of current and projected climate change and determinants of forest productivity, notably tree growth and survival and other estimates of whole-forest productivity. Overall, this evidence suggests that in the near term (until 2050), increases in mean temperatures and growing season length will likely drive increased tree and understory plant growth and therefore increased boreal forest productivity overall (4.2, Figure 27; *well established* for trees, *established but incomplete* for understory)*.* However, increased incidence and severity of climatic extremes (drought, heat extremes, and winter warm spells, the latter especially when in combination with reduced snow cover), disturbances (fire and wind), and tree pests, diseases, and herbivores, all of which negatively impact tree and understory growth and increase mortality, may significantly offset the benefits from gradual warming (Figure 27; *established but incomplete*)*.* Trophic interactions, cascades, and lags add uncertainties. In the longer run (until 2100), climate warming is projected to reach levels where temperature growth responses in dominant boreal trees (pine, spruce and birch) will likely be negative for most of the current boreal zone in Norway (4.2, Figure 27*; established but incomplete*)*.* While there is some evidence of positive effects of CO_2 fertilization, these often refer to young trees and are likely to decline over time due to co-limitation and climate extremes (*unresolved*). Meanwhile, increased incidence and impacts of climatic extremes (drought, heat extremes and winter warm spells), disturbances (fire and wind), and tree pests, diseases, and herbivory will cause significant reductions in tree and understory growth, forest productivity, and lagged responses in forest species range shifts to track climate (Figure 27, *well established*). The negative impacts of warming on forest productivity and carbon storage can potentially be offset if the dominant boreal tree species are replaced by tree species that are better adapted to warmer climates (see 5.1.4).

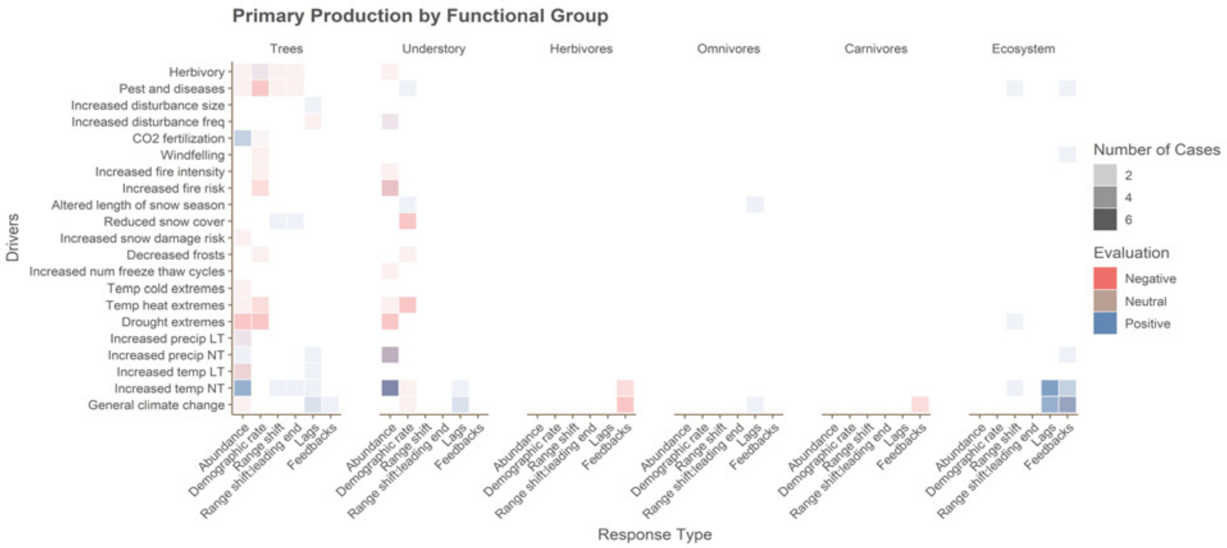


Figure 27. A summary of how climate change and disturbance drivers impact Primary Production (Characteristic 1) by organism group. Dwarf-shrubs, understory forbs and graminoids, bryophytes and lichens are combined into 'understory'. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include information from species categorized as alien. Interacting drivers were not explicitly included.

5.1.2 Characteristic 2: Distribution of biomass between different trophic levels

The total biomass of the Norwegian boreal forest ecosystem is distributed among primary producers, vertebrate and invertebrate herbivores and carnivores, and decomposers (2.3.5). Here, we summarise climate change impacts on the distribution of biomass between these trophic levels, as well as studies that assess ecosystem biomass more generally without specifying trophic level (4.21-4.2.4, 4.4.1, 4,4,2, 4.4.6, 4.5.1-4.5.4). Relatively few of the studies that we found explicitly quantify climate effects on the distribution of abundances across trophic levels, however, so our summary primarily relies on comparing the effects of drivers on abundances within the individual trophic levels. The 232 cases across 141 organism-response combinations considered for Characteristic 2 reflect the different aspects of primary productivity covered in 5.1.1 (growth and survival of major tree species (4.2.1) and of understory species (4.2.2, 4.2.3)), along with estimates of forest productivity (4.4) and bryophyte growth (4.2.4). These aspects of primary productivity were compared to those aspects related to measures of abundance (biomass, population size, demographic rates and body size) of other functional groups, including herbivores (ungulate and rodent vertebrate herbivores (4.2.8, 4.2.9, 4.4.2), herbivorous and granivorous birds (4.2.6) and bats (4.2.7), insect herbivores (4.2.11), carnivores (4.2.10), invertebrate, fungal, and bacterial decomposers (4.2.5, 4.2.11, 4.2.12, 4.4.4), and naturally occurring pests and diseases of plants and animals (4.2.11, 4.3). Several studies focus on the role of trophic interactions in affecting abundances of one or more functional groups (4.5).

The role of climate in affecting primary producers is described in the previous section, where we find that both trees and understory plants generally benefit in terms of growth from increased temperatures and precipitation, at least in the short term, but often suffer increased mortality from climate-related extremes, with impacts becoming increasingly negative with increased levels of warming (5.1.1; Figure 28; *well established*). Vertebrate herbivores such as moose, bank voles, and beavers may suffer under increased temperatures, both in terms of reduced growth and increased mortality, while red deer may benefit (4.2.9; 4.4.2; *unresolved*). A number of plant-feeding insects including bark beetles may benefit from warming, especially from increased winter temperatures (4.2.11; *established but incomplete*). Overall, insect herbivore abundance and demographic rates are often enhanced under warming (Figure 28, *established but incomplete*). Bats are predicted to decrease in abundance under warming (4.2.7; *unresolved*). Carnivores and omnivores, such as brown bears, are generally unaffected in terms of range-shifts or demographic rates, however they may suffer reduced abundance as a result of indirect effects such as reduced food availability in autumn (4.2.10, *unresolved*). However, many of these species are regulated by external pressures such as hunting, or management practices (4.2.10, *unresolved*). Some generalist species, such as red fox, are expected to increase in abundance (4.2.10, *established but incomplete*). The abundance of bumblebees is noted to be in decline, though the extent to which climate change is a contributing factor is uncertain (Figure 28, 4.2.11.3, *unresolved*). The abundance, distribution and demographic rates of native pathogens such as phytophthora generally increase under warming conditions (4.3.3, *unresolved*). Some wildlife diseases, including those transmitted by helminths, may also be further facilitated by an increase in storm activity and windfelling (4.3.5, *established but incomplete*), an increase in unfrozen ground allowing greater access to roots (4.3.5, *established but incomplete*), or increased disturbance frequencies (4.3.5, *established but incomplete*). Fungi and soil decomposer communities are also enhanced under warming, leading to increased decomposition rates (4.2.12, 4.4.4, 4.4.6, Figure 28, *well established*). This latter effect may be counteracted by reduced snow cover and associated increase in freeze-thaw cycles in the soil, which may negatively impact insect herbivores, soil arthropods, and insects leading to decreased decomposition at the whole-ecosystem level (Figure 28, 4.4.6; *established but incomplete*).

A key determinant of net outcomes on trophic structure with near term climate change and warming is trophic cascades, feedbacks, and lagged responses involving primary producers, both vertebrate and invertebrate herbivores, carnivores, and decomposers (*4.4.4, 4.4.6, 4.5.1-4.5.4*).

While there is less explicit evidence, such trophic interactions and cascades are generally affected by climate change, resulting in feedback and lags in climate change impacts on biomass distribution across trophic levels (4.4.2, -4.1.6; Figure 28, *established but incomplete*). This is because different trophic levels are affected by climate change in contrasting ways, potentially destabilizing trophic interactions and hence the trophic structure and functioning of the forest ecosystem (i.e., 4.4.4, Figure 28). The overall impacts on the forest trophic structure and functioning is difficult to predict, and since the different organisms are responding to different specific climate change drivers, many reports of lags and feedbacks sort under 'general climate change' and 'ecosystems' in our analyses.

As an example, drought extremes impede plant productivity and survival (4.2.2-4.2.4), but may simultaneously increase forest insect herbivore outbreaks (4.4.2), with negative feedbacks on plant productivity and positive impact on population sizes of carnivores and decomposers (4.4.4; Figure 28; *well established*). As another example, increased fire risk and fire severity under climate change (4.1.7) negatively impacts trees, bryophytes and lichens, some soil organisms, and impacts ecosystem functioning (4.2.1, 4.2.4, 4.5.2, 4.4.6; Figure 28, *established but incomplete*). This may have positive feedback on organism's dependent upon dead wood, such as saproxylic insects and wood decomposers overall (4.3.2, 4.4.3, 4.4.4; *established but incomplete*).

There are few documented linkages between climate-driven changes in alien species, herbivory, pests, diseases, or alien species (as drivers) and trophic structure, but again, these organisms negatively impact trees (4.2.1; *well established*) and may have positive feedbacks to saproxylic insects (4.4.2; *established but incomplete*), with knock-on positive effects on insectivorous bats (4.5.2; *established but incomplete*).

Note that while lags and feedback effects are coded as overall "positive" at the ecosystem level in Figure28, this does not imply an improvement in ecosystem functioning, but rather enhanced rates of ecosystem processes (i.e., both primary productivity, consumption, and decomposition, and so net impacts on measures of forest ecosystem functioning such as carbon capture and storage or resilience are variable, and may often be negative (see sections 4.4.1, 4.5.1- 4.5.4) (*unresolved*).

In summary, we found no studies that explicitly assessed impacts of climate change on the trophic structure of boreal forests, but we found evidence for links between different aspects of current and projected climate change and determinants of forest trophic structure. Notably, increased short-term tree growth driven especially by warming and increased precipitation (5.1.1; Figure 28, *well established*), combined with negative impacts of climate warming and extremes on survival and reproduction in many vertebrate herbivores and insectivores, including ungulate rodents, birds, and bats, less negative impacts on carnivores (all of which are driven by changes in both growing season and winter conditions, Figure 28, *unresolved – established but incomplete*), and positive responses in many plant-feeding insects, diseases, and decomposers (driven both by climate *per se* and by climate extreme and disturbance related tree mortality; Figure 28, *well established*) point to trophic restructuring of the boreal forests also in the near term (until 2050) (*unresolved)*. This trophic restructuring may be exacerbated by increased incidence and severity of climatic extremes (drought, heat extremes, winter warm spells), disturbances (fire, wind), and tree pests and diseases, which may operate through feedbacks and trophic cascades to add additional variability and uncertainties (Figure 28, *established but incomplete*). In the longer run (until 2100), climate warming is projected to reach levels where the temperature growth responses in the dominant boreal trees (pine, spruce, birch) will likely be negative for most of the current boreal zone in Norway and CO_2 fertilization effects are likely to decline (Figure 28, established but incomplete). Meanwhile, the incidence and negative impacts of climatic extremes (drought, heat extremes, winter warm spells), disturbances (fire, wind), and tree pests and diseases will increase, likely intensifying the trophic restructuring of the boreal forests towards a system where vertebrates are declining and invertebrates and especially tree pest and diseases species are increasing (*unresolved*).

Figure 28. A summary of how climate change and disturbance drivers impact "Distribution of biomass across different trophic levels" (Characteristic 2) responses across different functional groups. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include information from species categorized as alien. Interacting drivers were not explicitly included.

5.1.3 Characteristic 3: Functional composition within trophic levels

The functional composition within trophic levels comprises the distribution of relative abundances, species compositions, and functional traits within each trophic level, including primary producers, herbivores, omnivores, carnivores, insectivores, pollinators and decomposers (2.2.5). Here, we also consider mutualists, such as mycorrhizal fungal associations that are ubiquitous and functionally important in boreal systems (2.2.5.7). We found relatively little evidence in the literature for how climate impacts functional group composition within trophic levels, and our assessment of these effects thus relies on studies that document changes in community composition, relative abundances, and biodiversity within different trophic levels. The 58 organism-response combinations and 77 cases considered for this group cover forest vascular plant communities (4.4.1, 4.4.5, 4.5.4), bryophytes and lichens communities (4.2.4), bird and bat communities (4.2.6, 4.2.7, 4.5.3), mammalian herbivores (4.4.2, 4.5.3), forest insect communities, including pollinators and decomposers (4.2.11.3, 4.2.11.4, 4.4.3, 4.4.4), and soil decomposer and mutualist communities (4.2.12, 4.4.6).

Climate warming drives community turnover (via relative abundance and range shifts) from generally cold-adapted to warm-adapted species in tree communities (4.4.1, 4.4.5-4.5.4), in forest understory plants (4.2.3, 4.4.5-4.5.4) and in bryophyte and lichen communities (4.2.4, 4.4.2) (Figure 29; *well established).* These changes often incur shifts towards taller species with faster growth rates and higher carbon and nutrient capture rates, in some cases involving pronounced functional shifts, such as a shift in dominance from dwarf shrubs to grass-dominated understories, and from coniferous to deciduous trees ('nemoralization', see 4.2.3, 4.4.4, 4.4.5, 4.5.4) or even biome shifts, such as where trees colonize formerly treeless areas north of and above the current treeline (4.5.4; *well established*). For animal communities, nemoralization of the functional composition in response to climate warming has been reported for a wide range of organismal groups, including decomposers (4.2.12), various insect groups (4.2.11, 4.4.3), and mammal herbivores (4.4.2) (Figure 29, *established but incomplete*). Abundance changes may also drive feedbacks via trophic interactions, for example climate change-driven damping of small rodent cycles has led to shifts in their communities, as well as in the functional composition of the associated carnivore communities (4.5.3; *well established*). Relatively few studies explicitly attribute observed functional shifts in carnivore communities to climatic warming or other climate-related variables, however, as other drivers and notably harvesting dominate these trophic levels (4.3.2, *unresolved*). In the soil decomposer community, a shift from fungal to bacterial communities with warming, as well as functional shifts within the bacterial community in response to increased temperatures, is reported to enhance decomposition and the cycling of carbon and nutrients, and to change mycorrhizal symbioses (4.2.11, Figure 29, *established but incomplete*).

Asynchrony and lagged responses in community composition to climate change have been reported across different combinations of interactive functional groups and trophic levels within forest ecosystems (4.4.2, 4.5.2, 4.5.4 Figure 29, *unresolved*). Climate-related disturbances are reported to impact forest plant, insect, and ecosystem functional composition (4.4.1, 4.5, *unresolved*); climate-related changes in herbivory and tree pest, disease outbreaks have been reported to have minor impacts on the functional composition of understory plant, bird and forest invertebrate communities (4.2.4, 4.4.2).

In summary, the evidence collated here for climate impact on functional composition within trophic levels was relatively scarce. One recurring pattern across many organismal groups was a reported "nemoralization" towards more warm-adapted community composition within forest trees and understory plants, herbivores, and soil decomposers, various insects, and mammalian herbivores, birds, and bats, a process that is generally expected to result in faster carbon capture and cycling through the ecosystems (Figure 29, *established but incomplete*). Another recurring theme was the substantial time-lags in these functional shifts: we found reports of how vertebrate- and invertebrate herbivore communities and carnivore communities of Norwegian forests all lag substantially behind climate changes (*established but incomplete*). Such mismatches may become exacerbated in the future and thus lead to the build-up of substantial "climatic debts" in the functional composition of Norwegian forests as climate changes proceed.

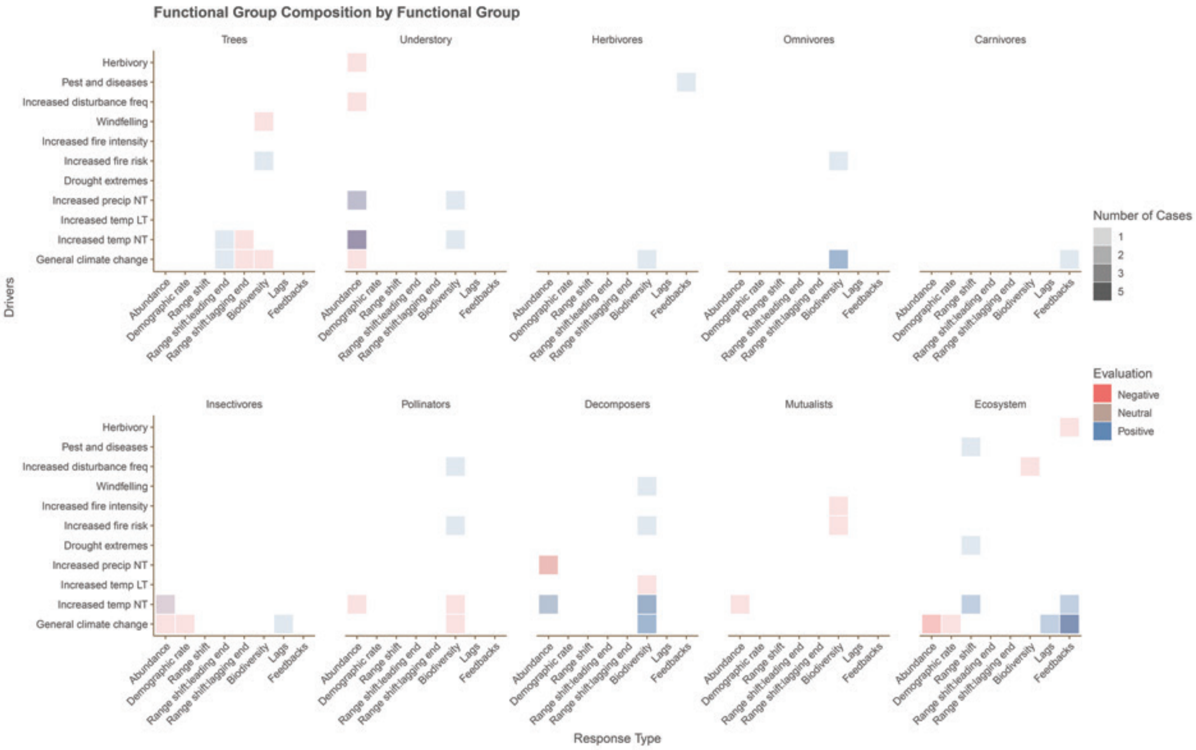


Figure 29. A summary of how climate change and disturbance drivers impact Functional Groups, specifically functional composition within trophic levels (Characteristic 3) responses across different functional groups. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include information from species categorized as alien. Interacting drivers were not explicitly included.

5.1.4 Characteristic 4: Functionally important species, habitat-building species, and biophysical structures

Forests are complex ecosystems, where many types of species play functionally important roles (2.2.5). Here, we take an organism-centered perspective for Characteristic 4, and summarise information on these species in order to understand how climate change and related factors impact them and their role in the forest ecosystem. The 135 organism-response combinations and 220 cases considered for this group cover abundances, growth, demographic rates, phenology, biodiversity and lag effects for the major tree species (4.2.1, 4.4.1), ericaceous dwarf shrubs (4.2.2), bryophytes (4.2.4), ungulate herbivores (4.2.9, 4.4.2), rodents and lagomorphs (4.2.8, 4.4.2, 4.5.2, 4.5.3), carnivores and omnivores (4.2.10, 4.4.2, 4.5.2), birds and bats (4.2.6, 4.2.7, 4.4.2, 4.5.2), saproxylic organisms (4.2.11.4), decomposers and other soils organisms (4.2.5, 4.2.12, 4.4.4), and insect herbivores (4.2.11.1, 4.3.3, 4.5.2). Several studies focus on the role of trophic interactions and feedbacks, and we summarise these findings from a functionally important species point of view (4.5.2, 4.5.3). Range shifts of organisms are not covered here, but are summarised under Characteristic 5, landscape ecological patterns (5.1.5).

A majority of the functionally important species are positively impacted by climatic warming in terms of growth and survival in the near future, but responses become more mixed and often negative as climate warming progresses (Figure 30, *well established*). Vertebrates are an exception, as many northern distributed species suffer whereas several southern distributed species remain positively affected while climate warming increases (4.2.5-4.2.12, 4.4.2, 4.5.2, *established but incomplete*). The three main tree species in boreal forests, spruce, pine, and birch, are all expected to respond to near term warming (until 2050) with increased growth, advanced phenology, and increased seed set, and spruce growth will also respond positively to increased precipitation (4.2.1.2-4.2.1.4, Figure 30, *well established).* Heat responses will negatively impact the growth of all three species (4.2.1, *established but incomplete)* as well as the mortality of spruce and pine (4.2.1.2-4.2.1.3, *established but incomplete).* Droughts will negatively impact the growth and survival of spruce and pine (4.2.1, Figure 30, *well established*). With increasing CO_2 fertilization, boreal forest trees will likely experience increased rates of growth, but also reduced longevity (4.4.6, *established but incomplete).* Warming climates will influence bud-burst timing for spruce, pine, birch and aspen (4.2.1, *established but incomplete),* and for pine and aspen this is also associated with a possible increase in risk of late-spring freezing events (4.2.1, *unresolved).* Increased risk of fire and wind-fellings are likely to increase spruce and pine mortality, and climate-related pests and diseases will increase mortality in all three key species (4.2.2, Figure 30, *well established*). Aspen, one of the less dominant but functionally important species in the rowan-aspen-willows group, may experience reduced frost hardening and dormancy, and advanced phenology in response to near term warming, along with increased mortality due to droughts (4.2.2, *unresolved*). In the longer term (until 2100), positive temperature effects will be reduced or reversed, and many climate-related negative effects will be enhanced (even though phenology may be advanced) leading to reduced growth and survival in boreal forest trees (4.2.2; Figure 30, *established but incomplete*). Changes in snow regimes, including increased snow density due to rain-on-snow events, may impact snow accumulation and increase branch breakage rates (4.4.1, *established but incomplete*). With reduced snow cover, pine in high altitude areas once susceptible to snow blight may experience reduced pressure when recruiting (4.2.1.3, *unresolved*). Importantly, the growth and mortality of these key boreal tree species will be moderated by the activities of herbivores, or plant pests and diseases, which are predicted to increase under warming climatic conditions (4.2.1.2-4.2.1.4, *established but incomplete*).

In the understory, ericaceous dwarf shrubs have mixed responses to warming. While warming may result in increased growth for some species, Arctic "browning" is also noted to occur throughout arctic and boreal zones, with reduced growth and higher mortality for shrub species, particularly related to shifts in snow cover, frequency of warm spells, and frost and fire occurrences (4.2.2, *unresolved*). For bilberry, increasing temperatures may increase yields if autumn temperatures aren't too high, which would reduce cold hardiness, and if snow cover persists, allowing for frost protection (4.2.2, *established but incomplete*). Bilberry flowering also may vary, with reductions occurring after warm spells in cold winters, or if premature de-hardening occurs during mild winters (4.2.2, *established but incomplete*). Lingonberry growth is likely to be enhanced by warmer temperatures and a longer growing season, provided sufficient water is available (4.2.2, *established but incomplete*). Bilberry and lingonberry recruitment may be enhanced by more frequent fires but impeded if increased fire severity removes seeds and soil, while crowberry abundance tends to decline (4.2.3, Figure 30, *unresolved*). Outbreaks of pests, such as leaf-defoliating geometrid moths may also play a role in determining the abundance of dwarf shrubs (4.2.2, *unresolved*).

Bryophytes and lichens are important plant functional groups in boreal forests, with mixed responses to climate change. Bryophytes have relatively low optimal temperatures for photosynthesis and depend on water availability. For lichens, the photobiont is usually more restricted than the fungal partner. Bryophytes and lichens have mixed responses for near–term temperature, where large and fast-growing bryophytes tend to increase with warming and increased precipitation, whereas smaller species and hair lichens tend to decrease (4.2.5; *Established but incomplete*). Bryophyte abundances decrease with fire (*well established*), and survival is decreased in response to increased freeze-thaw events (*well established*). Both bryophytes and lichen growth will be reduced under increased fire risk and intensity (4.2.5; Figure 30, *well established*).

Some herbivores, including ungulates (moose), rodents (voles, beavers, and lemmings), lagomorphs (mountain hares) and some forest birds (capercaillie, willow grouse) may suffer under a warming climate due to a combination of decreased growth, reduced recruitment, increased mortality, dampening of population cycles, and decreased population sizes (4.2.6; 4.2.8, 4.2.9; *unresolved*). Other species, notably the southern distributed red deer and roe deer, are projected to experience reduced mortality and increased growth (4.2.9; *unresolved*). Several forest birds, including capercaillie and black grouse, may experience increased chick survival (4.2.6; *unresolved).* There is much less information about other climate drivers on vertebrate herbivores, but beavers may suffer under increased precipitation, possibly due to increased flooding risk (4.2.7; *unresolved*), roe deer may experience reduced foraging capacity under deep snow conditions caused by higher levels of winter precipitation (4.2.9, *established by incomplete)* and voles and lemmings may be negatively impacted by reduced snow cover in winter, especially the loss of open spaces under the snow (4.2.7, *established but incomplete*). The mountain hare may experience lower abundances due to pressure from the alien European brown hare and its associated disease and pest burden (4.2.8, *established but incomplete*). These species-specific responses are reflected in mixed climate responses across ungulates, rodents, and birds (Figure 30).

Many different herbivorous, insectivorous, and carnivorous forest birds may suffer increased chick mortality and reduced densities under warming, whereas black grouse and capercaillie may benefit at least on the short term (4.2.6; *established but incomplete*).

The climate impacts on forest carnivores and omnivores is more mixed. Carnivorous birds may suffer decreased survival under warming (4.2.6; *Established but incomplete*). Omnivorous and insectivorous birds may advance the onset of breeding or migration times to correspond with food availability (4.2.6, *established but incomplete).* Some food-hoarding species, such as pygmy owls, may decline as a result of feedbacks, where they are unable to store harvested food over winter, if their "freezers no longer work" (4.5.2, *unresolved).* As omnivores, brown bears are projected to decrease in abundance and body mass due to the indirect impact of reduced food availability (especially bilberries) (4.2.10, *unresolved*). Smaller carnivores such as lynx or the grey wolf may change relatively little in abundance due to climate change, as their abundance and distributions are mostly controlled by management and poaching (4.2.10, *unresolved).* Predator-prey dynamics for smaller carnivores that specialize on rodent prey may be altered, depending on the extent of colour-morph mismatches with prey species (4.4.2, 4.4.3, Figure 30, *established but incomplete*).

Saproxylic insects are expected to increase in response to climate change, likely linked to increased deadwood availability *(*4.2.11.4, *unresolved*). Bark beetles generally tend to increase in recruitment and winter survival in response to warming, leading to larger and more frequent outbreaks (4.2.12; Figure 30; *established but incomplete*). Bark beetle outbreaks increase after droughts (*well established*) and windfelling (4.2.12; Figure 30; *well established*).

Some components of the soil communities may benefit from warming. Increased availability of dead wood in response to climate-related tree mortality (i.e., in response to extremes, fires, disturbances) may benefit saproxylic and decomposer fungi and invertebrates (4.2.10; 4.3.4; *unresolved*). On the other hand, fires may lead to increased mortality in these organisms (4.2.11; *well established*).

At the ecosystems scale, interactions and feedbacks between trophic levels can have wide ranging impacts on functionally important species. Large geometrid moth outbreaks result in widespread defoliation of birch trees, and subsequent shifts in understory vegetation communities from shrubs to grass; climate change is likely to increase the severity of such outbreaks (4.4.2, *established but incomplete*). Trophic cascades may also become more prevalent between small rodents and their predators, with shifts in vegetation availability dampening rodent population cycles resulting in declining predator species (4.5.3, *unresolved*).

In summary, there are many and strong but variable impacts of climate change on functionally important species in forests. The majority of the knowledge we compiled pertains to trees and forest stands, and here we see relatively consistently positive impacts of increased temperatures on abundance and a range of demographic rates (growth, survival, recruitment) in the short term (until 2050) that are considerably reduced and even reversed as warming proceeds (until 2100) (Figure 30, *well established*). Trees are generally negatively impacted by climate change-related extremes and biotic and abiotic disturbances, including changes in snow regimes, and the net effect is increased probability of reduced forest growth and survival in the longer term (Figure 30, *well established*). Ericaceous dwarf shrubs are functionally important components of the boreal forest understory, and they have mixed responses to climate warming, with increased mortality and reduced fruiting in response to winter warm spells increasing risk of 'arctic browning' (Figure 30, *well established*). Bryophytes and lichens have relatively positive responses for increases in near–term temperature, but are negatively impacted by extremes, especially fire *(well established).* Boreal invertebrate herbivores will generally benefit under warmer climates, although some species and some demographic rates may suffer (Figure 30, *established but incomplete*). For vertebrate herbivores, insectivores and omnivores a general pattern is that many species, especially among boreal forest rodents and birds, will suffer under warming, whereas many ungulates and especially more southern distributed species may benefit (Figure 30, *unresolved*). Small carnivores specialized on rodent prey may decline under warming due to cascade effects from decreased prey populations (Figure 30, *established but incomplete*). Some components of soil communities may benefit from warming, for example, the increased availability of dead wood in response to climate-related tree mortality (i.e., in response to extremes, disturbances) may benefit saproxylic and decomposer fungi and invertebrates (*unresolved*) whereas fires may lead to increased mortality in these organisms (*well established*). The many negative impacts of warming and climate-related extremes on plants translate into positive impacts on saproxylic and decomposer communities, although the evidence base is relatively limited (Figure 30, *unresolved*).

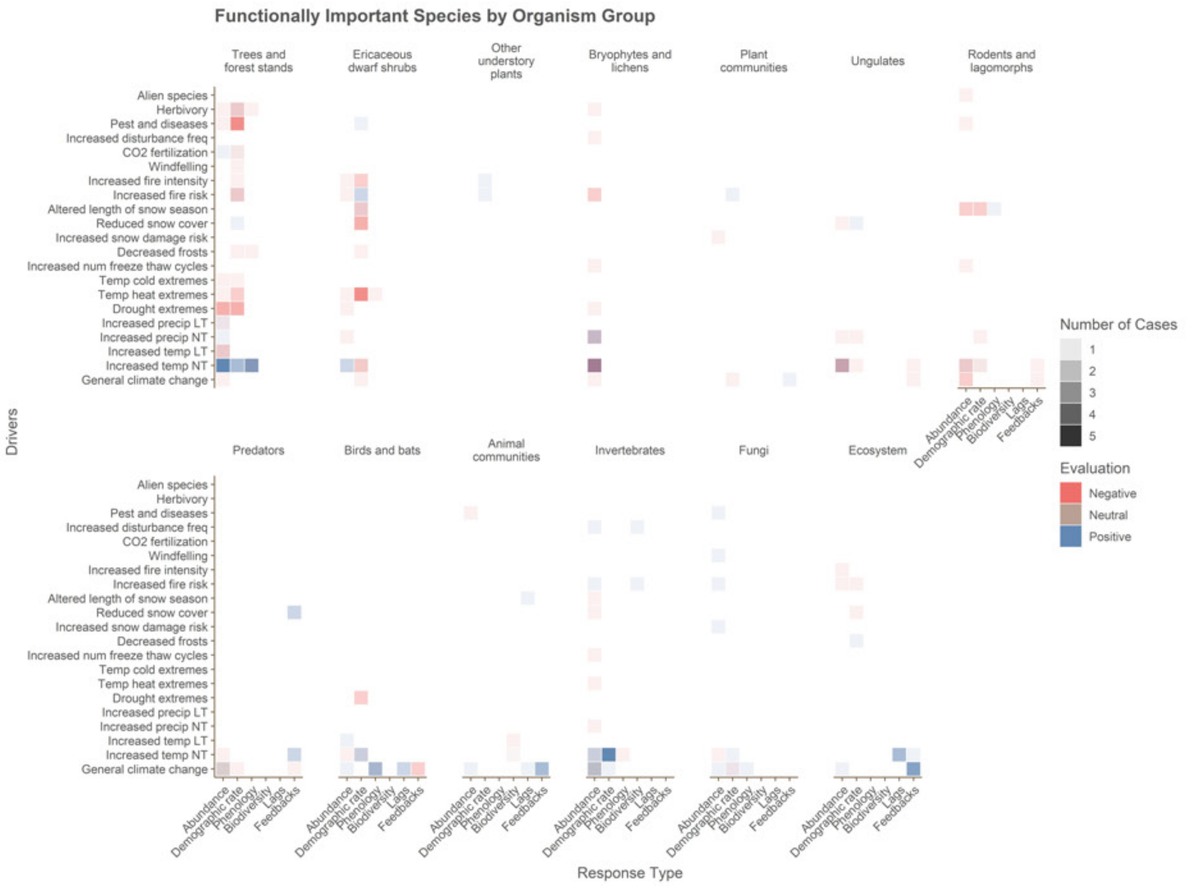


Figure 30. A summary of how climate change and disturbance drivers impact the response of functionally important species, habitat-building species, and biophysical structures (Characteristic 4) across different organism groups. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include responses involving species categorized as alien. Interacting drivers were not explicitly included.

5.1.5 Characteristic 5: Landscape ecological patterns

Landscape ecological patterns reflect the interplay between the spatial structure of landscapes (biotic and abiotic environments, habitats, corridors, barriers, and so forth), and the distributions and the dynamics of the biota inhabiting these landscapes. Here, we first summarise how climate change will impact landscape structure, then we focus on the range dynamics of biota inhabiting these landscapes.

Forests cover 37% of the land area in Norway (2.2, Bartlett et al. 2020), and this high proportion of forests suggests that there should be high connectivity within the Norwegian boreal forest biome. However, the irregular shape and outline of the country with a long coastline and many fjords, lakes, and islands (2.2.1), the wide climatic extent (2.2.2), the rugged topography (2.2.2), and the sparse and widespread human population and associated infrastructure (2.2.1) fragment the Norwegian forest landscape. The Norwegian forests also have a long history of land use and forestry, with extensive deforestation due to agriculture culminating at the end of the 18th century and extensive stand-based forestry (clearcutting) since the 1950's. This results in a very small fraction of the forests (<5%) being unaffected by logging or land use since the 1600s (2.2.1). The net result is that Norwegian forests are fragmented both in space and time, especially for species dependent on old-growth forest species or biophysical structures such as large hollow trees. Climate-related impacts on forest landscape structure include a variety of disturbances that kill or significantly alter forest stands and hence affect landscapes: increased windfelling (4.1.6); increased severity and frequency of forest fires (4.1.6); increased droughts (4.1.5); and increased herbivore (4.2.9, 4.2.11), pest (4.2.8, 4.2.9, 4.3.1-4.3.2.3) or pathogen attacks (4.3.3, 4.3.4). The increased extent and frequency of disturbances in the forest tree layer will likely lead to more forest edge and to heterogeneity in landscape features, and in reduced forest connectivity (4.5; *established but incomplete*).

These patterns and climate-driven shifts in landscape ecological patterns will impact the ability of species to adjust their ranges appropriately in response to climate change. We found 71 organism-response combinations and 108 cases describing both current and projected range dynamics (leading and lagging edges) and large scale pest or pathogen outbreaks affecting a range of boreal forest taxa and taxonomic groups. These include important boreal forest tree species (4.2.1, 4.4.1, 4.5.1-4.5.4), some understory plant communities (4.4.1), mammal herbivores (4.2.8, 4.2.9) and carnivores (4.2.10), birds (4.2.6), bats (4.2.7), invertebrate pollinators, herbivores, omnivores and insectivores (4.2.11, 4.3.1, 4.3.2, 4.4.3), fungal decomposers and pathogens (4.2.12, 4.3.3), and wildlife diseases (4.3.5).

Northwards range expansions are consistently predicted in both the short and long term for a large number of species across all trophic levels and taxonomic groups, including spruce, pine, birch, rowan, moose, red deer, wild boar, boreal birds, bats, pollinators in general, winter moths, autumnal moths, bumblebees, viruses, and fungal and invertebrate decomposers, with different levels of confidence (4.2, 4,3; Figure 31, generally *well established* for trees, *established but incomplete* in the other biota). For many of these organisms, southern range contractions are also projected, with especially strong evidence for trees. Leading edge range expansions may be limited by dispersal and habitat availability, whereas lagging edge range contractions may be exacerbated by climate extremes and disturbances, leading to projected range contraction especially in the long term (4.2.1.2 for spruce; 4.2.1.3 for pine). These trees are dominant organisms in boreal forests, and their range dynamics result in changes in forest structure and functioning, including shifts in other organismal groups and nemoralization of formerly boreal forest and expansion of forests into formerly treeless areas above and north of the current boreal forest belt (4.5.4, Figure 31, *well established*, see also 5.1.4).

These range shifts are consistently predicted to progress more slowly than the climatic warming, resulting in lagged effects and pronounced climatic debts of variable magnitude (4.5.4; Figure 31, *established but incomplete*), potentially leading to increased trophic mismatches in forest ecosystems as climate change progresses (4.5.2; *unresolved*).

There is much less evidence for impacts of climatic extremes, herbivory and pests and diseases (as drivers) on species-level landscape ecological patterns, but the evidence that exists suggests these drivers generally impede rates of leading end range shifts and thus increase climatic debts in the naturally occurring biota, especially trees (4.2.1; *established but incomplete*). For example, ungulate and rodent herbivores are widely known to limit pine, spruce, and birch from expanding their ranges northwards and upwards in altitude (4.2.1; Figure 31, well established). More positive outcomes are expected for pest and outbreak species themselves (4.2.9, 4.2.11, 4.3.1, 4.3.2-4.3.5; Figure 31, *well established*), with potential negative feedback to trees and forest communities (see Characteristics 2 and 3). As for several other characteristics, the evidence for impacts of changes in extremes is rather fragmentary, but the studies that do exist generally find negative impacts, notably for trees (Figure 31, *unresolved*).

In summary, widespread forestry practices and the complex topography, variable landscapes, and large extent of the Norwegian boreal biome render Norwegian boreal forests and their specialized forest biota quite spatially fragmented, despite the high forest cover in Norway (37%). Under climate warming, climate tracking northwards and upwards in altitude across the landscape is the major projected landscape ecological process for boreal biota. Such range dynamics are widely documented for both leading and lagging edge range limits across forest biota, including trees, ungulate grazers, rodents, birds, bats, bumblebees, moths, other invertebrates, viruses and fungi (Figure 31, *well established*). Climate-related disturbances, pests and diseases are slowing down leading edge shifts of trees in some cases (Figure 31, *established but incomplete*), and a majority of range shifts are occurring more slowly than predicted from climate change (Figure 31, *well established*). As a consequence of this, widespread "climatic debts" are occurring across boreal forest landscapes, where the species composition does not reflect today's climate and range contractions are predicted in the long term. More positive outcomes are expected for pest and outbreak species themselves, with potential negative feedback to trees and forest communities (*established but incomplete*).

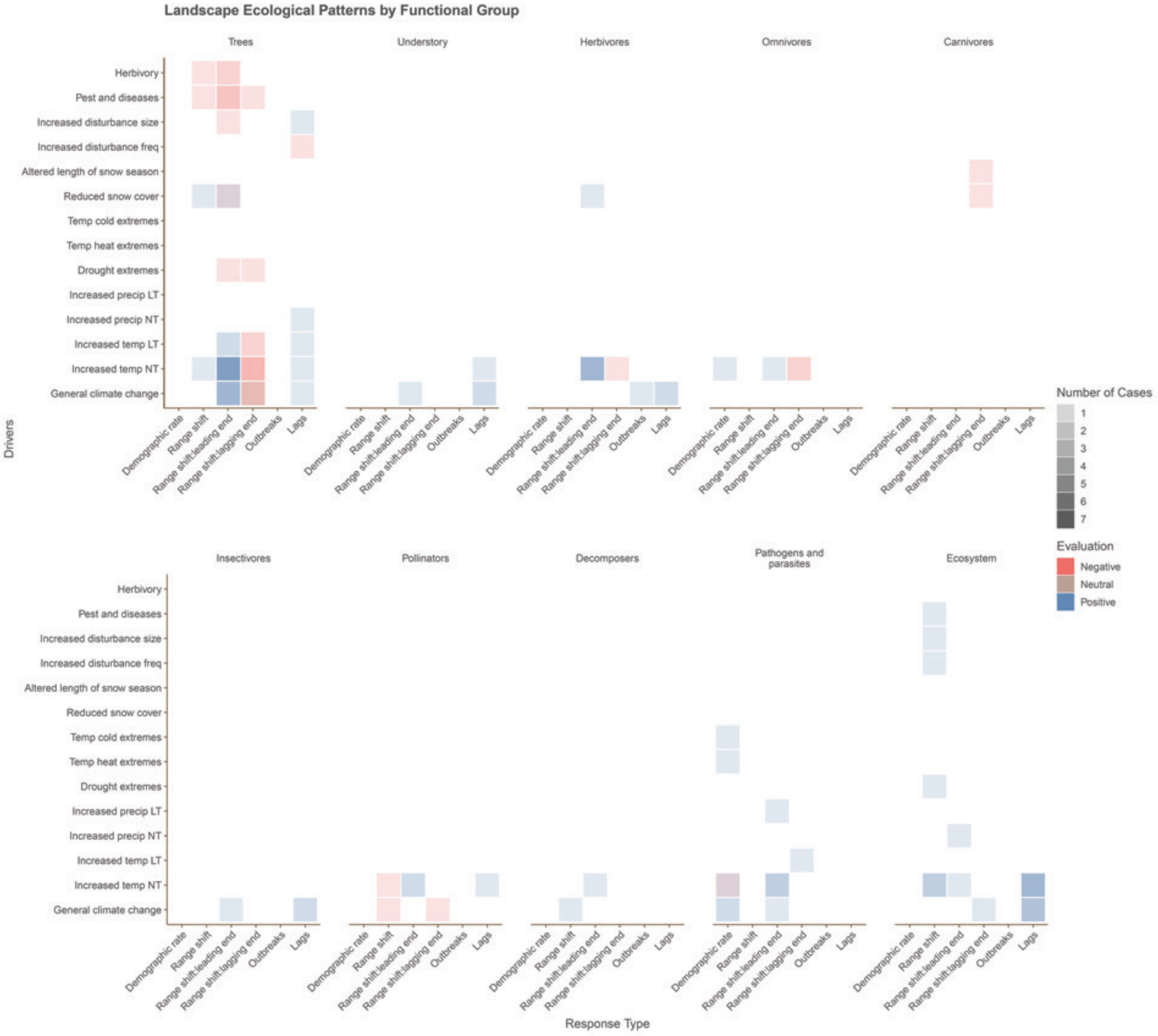


Figure 31. A summary of how climate change and disturbance drivers impact Landscape Ecological Patterns (Characteristic 5) across different functional groups. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include those species categorized as alien. Interacting drivers were not explicitly included.

5.1.6 Characteristic 6: Biological diversity–genetic diversity of ecosystems, species composition and species exchange.

Boreal forests harbor substantial biodiversity, but the evidence for climate change impacts on forest biodiversity (2.2.4), beyond what would result from range shifts (Characteristic 5) is limited. The 38 organism-response combinations and 56 cases collated for this assessment include general studies of forest biodiversity (4.3.1, 4.3.2, 34.3.4, 4.3.5, 4.3, 4.4), along with assessments of biodiversity within forest plant communities (4.2.3, 4.4.1, 4.5.1, 4.5.4), small mammals (4.4.2, 4.5.3), birds (4.2.6, 4.5.2), bats (4.2.7) forest insects (4.2.11.3, 4.4.3), saproxylic communities (4.2.11.4), soil invertebrate communities (4.2.12.1), and fungi (4.2.12.2, 4.4.4).

The biological diversities of many of these groups are positively impacted by warming, including trees (4.4.1), understory species (4.2.3), small mammals and other vertebrate communities (4.4.2), saproxylic communities and other forest insects (4.2.11, 4.4.3), soil invertebrate and fungal communities (4.2.12, 4.4.4), whereas insectivorous bats, pollinating insects, mutualistic fungi (4.2.7, 4.2.11.3, 4.2.12.2, 4.4.3), and specialized northern species across other taxonomic groups are declining in diversity (*unresolved* for most groups). This community turnover of boreal communities (nemoralization) is expected to result in increased local species richness (Figure 32) because nemoral communities are often more diverse than boreal communities, but to result in a loss of specialized northern and boreal biota. A few organismal groups are responding to increased precipitation (e.g., understory plant diversity and decomposers, 4.2.3, 4.4.4; *unresolved*).

Pests and diseases (as drivers) may decrease omnivorous bird and oligochaete worm diversity (4.2.6, 4.2.12, *unresolved*). Climate related disturbances have differential impacts on functional groups. Small-scale disturbances (wind, fire) may be important in maintaining diversity in omnivore, pollinator and decomposer communities, whereas increased disturbance frequency and size may reduce diversity in old-growth specialists communities, for example among trees, old-growth specialist insects, and ectormychorrizal fungi (4.2.12, 4.4.1, 4.4.2, 4.4.3, 4.4.4; *unresolved* in most cases).

For species dependent on mature forests, including insectivorous bats, food-hoarding birds and rodents, and saproxylic insects, negative impacts of disturbances and climate change may appear via trophic cascades (4.5.3, 4.5.4, *unresolved*). For old growth forest species, climate change may be too fast to allow these species to move across landscapes to track their increasingly fragmented habitat in the future (4.5.3, 4.5.4, *unresolved*).

In summary, the biological diversity of trees, understory species, small mammals and other vertebrate communities, saproxylic communities and other forest insects, soil invertebrate and fungal communities are expected to increase with warming, whereas insectivorous bats, pollinating insects, mutualistic fungi, and specialized northern species across other taxonomic groups are expected to decline in diversity (*unresolved* for most groups). This community turnover of boreal communities will increase local richness but result in a loss of specialized northern and boreal biota. For species dependent on mature forests, including insectivorous bats, food-hoarding birds and rodents, and saproxylic insects, negative impacts of disturbances and climate change may appear (*unresolved*). The evidence for climate change-related biodiversity change in forest is limited, especially given the high biodiversity and many specialized organismal groups found here, and the patterns are mixed.

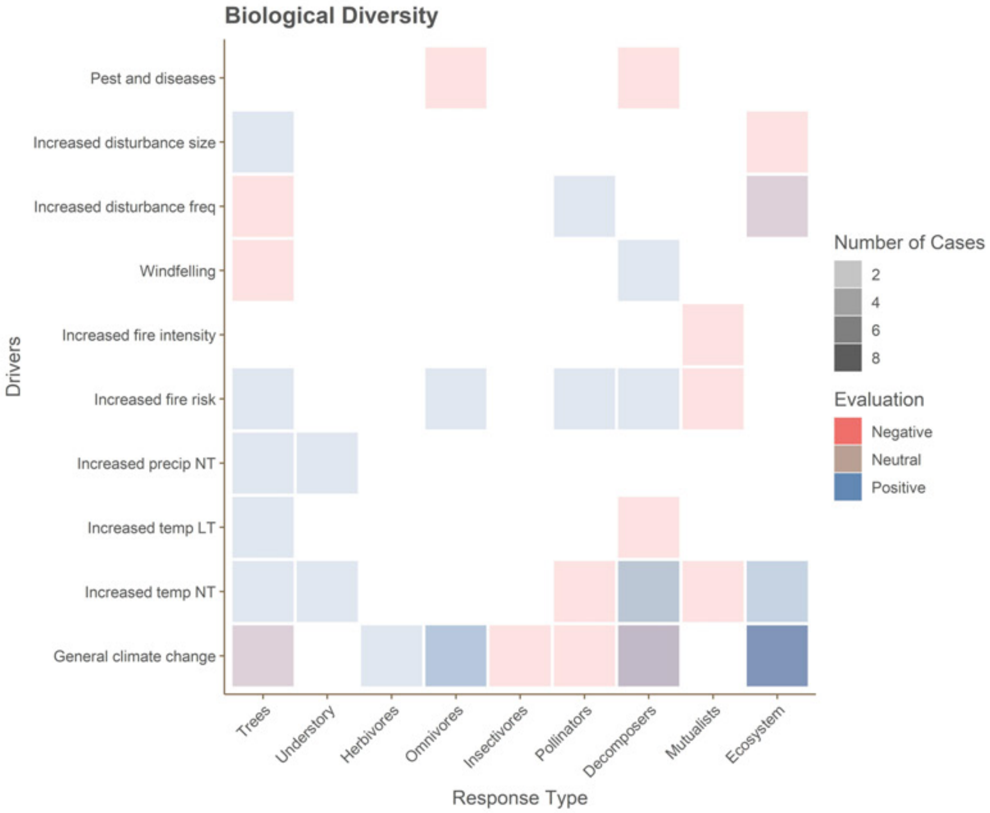


Figure 32. A summary of how climate change and disturbance drivers impact Biological Diversity (Characteristic 6) across different functional groups. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include information from alien species. Interacting drivers were not explicitly included.

5.1.7 Characteristic 7: Abiotic factors

The characteristic 'abiotic factors' refer to the abiotic components of ecosystems that may be affected by climate change. Many of the 43 organism-response combinations and 54 cases considered here are mostly related to nutrient cycling, and a few cases of lags and feedbacks, and reflect impacts on litter input and decomposition, cycling of ecosystem water-, carbon-, nitrogen, phosphorous and other nutrients; soil and ecosystem water relations (4.3.3, 4.4.4, 4.4.6, 4.5.2). Another group of responses treated here relate to whole-ecosystem consequences of asynchrony, lags, cascades and feedbacks among organismal groups (4.5.1-4.5.4).

Climate change is generally predicted to enhance rates of ecosystem nutrient cycling across a range of specific climate-related drivers (4.4.6, Figure 33, *established but incomplete*). Specifically, the literature suggests increased and more easily decomposable carbon and nutrient inputs to boreal forest soils via increased litter from trees under warming, along with faster organic matter decomposition and cycling in warmer and wetter soils (4.4.4, 4.4.6, *established but incomplete*). Increased primary productivity may lead to increased phosphorus limitation, decreasing litter phosphorus content (*established but incomplete*). These enhanced rates do not automatically indicate improved ecosystem functioning (see also Characteristic 2 and 3), for example, while there is evidence that some climatic changes may result in increased ecosystem carbon sequestration, but also to enhanced cycling and thus increased carbon loss to the atmosphere (4.4.6; *unresolved*).

Droughts may result in reallocation of biomass and phosphorus from leaves to roots (*unresolved*), and increased rain-on-snow events may increase nutrient leaching (*unresolved*). Climate-related increases in fire risk may impact soil and ecosystem carbon and nutrient dynamics via feedback from cascade effects starting with tree layer damage (*well established*). This includes increasing abundances of nitrogen, phosphorus, sulfur, aluminum, calcium, magnesium and potassium, along with increased volatilization of nitrogen and sulfur, and fly-ash loss (*unresolved*).

Whereas increased disturbance frequencies under climate change may generally decrease lags in climate responses, increased disturbance size may have the opposite effect, related to landscape ecological processes (Characteristic 5). As different biological processes and biota may vary in their response to climate change, and to specific climate change factors, climatic lags and extinction debts are likely to occur across multiple trophic levels (4.5.1, *established but incomplete).* Such mismatches are likely to result in feedbacks between trophic levels, and promote shifts in forest community compositions, ultimately affecting ecosystem function and ecosystem services (4.5.2, *established but incomplete*)*.* See characteristics 1-6 for specific comments and examples of how lagged responses and feedbacks affect the different aspects of forest ecological condition.

In summary, climate change is generally predicted to enhance rates of nutrient cycling through the forest ecosystem (*established but incomplete*). Specifically, the literature suggests increased and more easily decomposable carbon- and nutrient inputs to boreal forest soils via increased litter from trees under warming, along with faster nutrient decomposition and cycling in warmer soils leading to increased ecosystem carbon loss to the atmosphere (*well established*). Decomposers are also expected to increase in abundance and efficiency, further enhancing nutrient cycling (*well established*). Combined with changes in the soil microbial community, and less frozen ground (shorter frozen seasons, smaller extent of areas with frozen soil), increased soil respiration and decreasing soil carbon storage are likely (*established but incomplete*). Further ecosystem carbon loss may result from increases in climate-related disturbances (*well established*). Droughts may result in reallocation of biomass and phosphorus from leaves to roots (*unresolved*), and increased rain-on-snow events may increase nutrient leaching (*unresolved*). Climate-related increases in fire risk may impact soil and ecosystem carbon and nutrient dynamics via feedback from cascade effects starting with tree layer damage (*well established*).

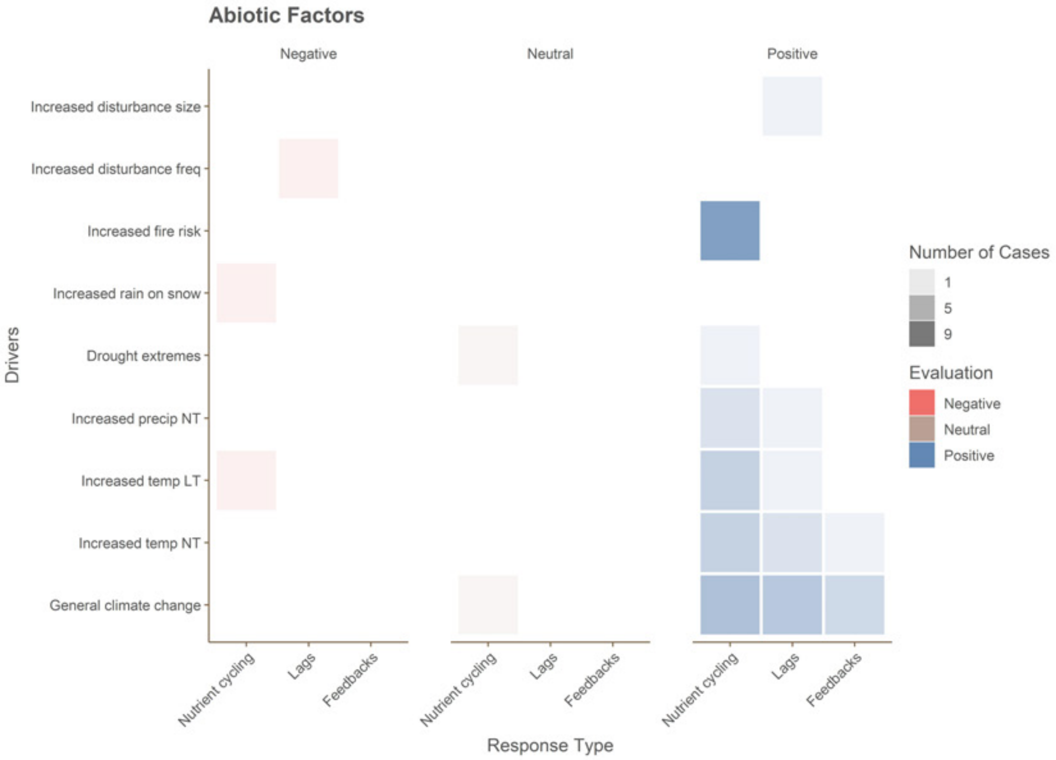


Figure 33. A summary of how climate change and disturbance drivers impact Abiotic Factors (Characteristic 7). The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). The figure does not include data from alien species. Interacting drivers were not explicitly included.

5.2 The role of pests, pathogens, and diseases

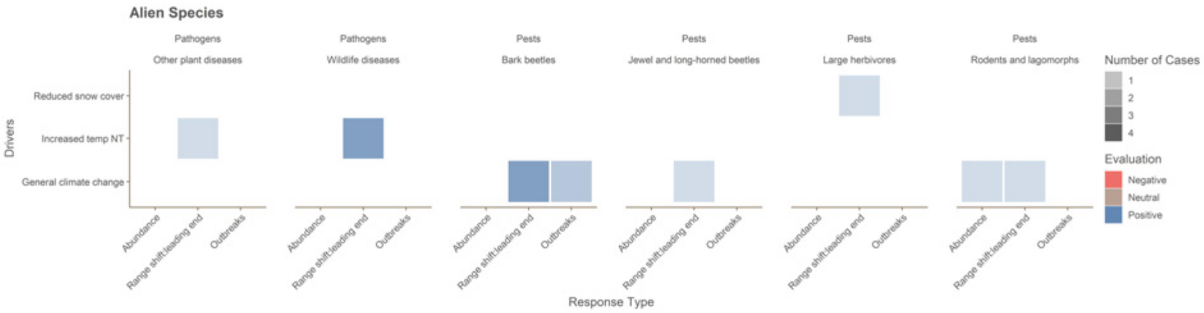


Figure 34. The impacts of climatic- and disturbance drivers on responses of alien pest and pathogen species. Results are delineated by pathogen or pest, then broad organism types. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). These alien species are not represented within the synthesis presented in 5.1.

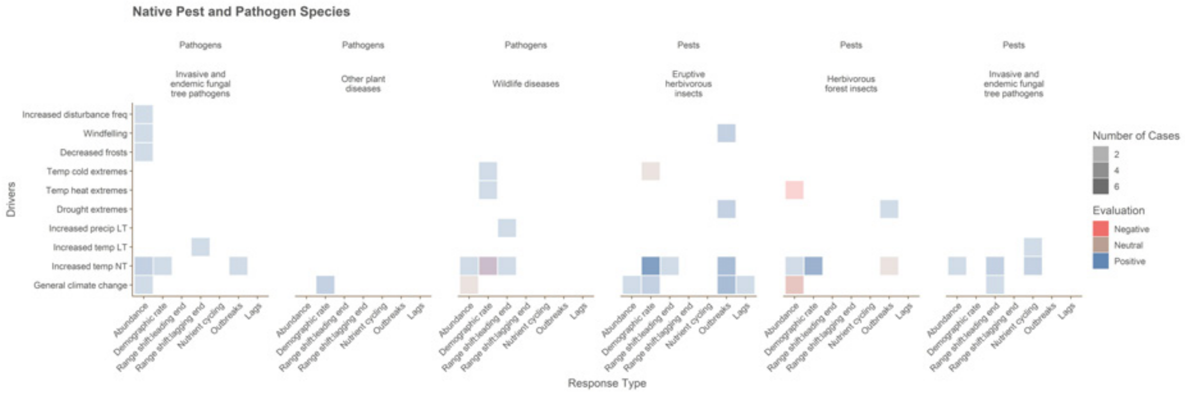


Figure 35. The impacts of climatic and disturbance drivers on responses of native pest species. Results are delineated by pathogen or pest status then broad organism types. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). NB. This does not include species identified as aliens, however, these pests and pathogen species are included in the syntheses provided in 5.1. Interacting drivers were not explicitly included.

The ToR requests that the assessment consider "other factors that may be related to climate change" and it specifically mentions pests and diseases and the establishment and spread of harmful alien species in this context. Here, we summarize information from across chapter 4 on alien or native species considered as pests or pathogens to understand how climate change and related factors impact them and their effects on the boreal forest ecosystem. For details on specific species, see especially chapters 4.2 and 4.3.

Across all pests and pathogens, there are 46 organism-response combinations for native pests and diseases (15 pathogens, 31 pests), and 25 for aliens (6 pathogens, 19 pests). Response types covered abundances, demographic rates, leading and lagging end range shifts, nutrient cycling, outbreaks and lags.

Alien pathogens include invertebrates, bacteria, and viruses affecting native plants and wildlife, and alien pests include beetles, ungulates, rodents, and lagomorphs (Figure 34). All alien pest and pathogen responses to climatic drivers are positive, implying an increase in the abundance, range, or persistence of these organisms and their impacts under future climates (Figure 34; 4.2.8, 4.2.9, 4.3; *well established*). The dominant drivers identified for change in alien pests and pathogens in boreal forests is the increase in near-term mean temperatures along with general climate change, which drive leading edge range expansions for the majority of alien pests and pathogens, increased abundance in the alien brown hare, and more frequent and severe outbreaks in alien bark beetles (4.2.8, 4.2.9, 4.3; *established but incomplete*). Reduced snow cover facilitates range expansion in wild boar (4.2.9; *established but incomplete*).

Native pathogens include invertebrates, fungi, bacteria, viruses, and native pests include invertebrate herbivores, other invertebrates, and fungi (4.2.11, 4.3.3 - 4.3.5, Figure 35). Impacts of warming and general climate change are most frequently documented, but native pests and pathogens are influenced by a range of climate drivers, including increased disturbance frequency, windfelling, decreasing frosts, increased precipitation but also increased heat extremes and droughts (4.2.11, 4.3).

The majority of native pest and pathogen responses to climatic drivers are positive, implying an increase in the abundance, range, or persistence of these organisms under future climates (Figure 35, *established but incomplete*). Impacts on native eruptive herbivorous insects, such as bark beetles and moths, are relatively well documented, and these are found to generally benefit from warming temperatures and general climate change in terms of demographic rates, range size, and outbreak frequency/size (4.2.11, *established but incomplete*). These impacts often act via climate-driven increases in reproductive rates, decreases in mortality, and decreased generation times, and outbreaks are generally enhanced when plant defenses are weakened due to e.g., wind-felling and drought extremes (Figure 35, 4.2.11, *unresolved*). Eruptive herbivorous insect demographic rates may be reduced by cold extremes (Figure 35, 4.2.11, *unresolved*). For example, winter mortality due to simply a few hours or days of intolerably cold temperatures can be what holds eruptive bark beetle or sawfly populations at harmlessly low numbers (at endemic levels). Native fungal tree pathogens follow a similar pattern to eruptive insects, generally benefiting from climatic warming and change, and from climate-related disturbances (Figure 35, 4.3.3, *established but incomplete*). Impacts on other herbivorous forest insects and plant and wildlife diseases are less well documented, and also more mixed, with some negative responses, mostly relating to climate extremes (Figure 35, see 4.2.11.1, 4.3.4, and 4.3.5 for details, *unresolved*).

5.3 Key tree species, stand ages, forest types and regions

The ToR requests that, when possible, the assessment should provide information on differences in the effects for different tree species, stand ages, and geographical regions, and that to the extent possible, an overall discussion should also be made on the significance of the expected effects for habitat types that are (near) endangered or that have central functions in forests (listed in their attachment 1). Here we briefly summarize the results from across chapter 4 and the summaries for relevant ecosystem characteristics in chapter 5.1, with respect to these issues.

5.3.1 Key tree and dwarf shrub species

Norwegian forests have key species of trees (4.2.2), ericaceous dwarf shrubs (4.2.2), other understory plants (4.2.3), and bryophytes and lichens (4.2.4). Here, we address the ToR request to summarize the primary drivers and impacts on key tree and shrub species. Across all tree species (spruce, pine, birch, rowan, and aspen) many impacts were documented as a result of near-term temperature changes (Figure 36, 5.1.1, 5.1.4). Generally, short-term warming resulted in positive impacts for abundance, demographic rates, phenology, and the leading edges of range shifts, while negative or neutral responses were documented for lagging edges of range shifts. Under long-term warming, leading-edge range shifts remained positively impacted while lagging edge ranges were negatively impacted (Figure 36, 5.1.5). Spruce and birch abundance was also negatively impacted by long-term temperature increases, while pine responded positively. Responses to increased precipitation were only documented for spruce which increased abundance, and for pine in the long-term, which declined in abundance (Figure 36, 5.1.1, 5.1.4). For the remaining climate drivers, including disturbances such as fire and temperature extremes, responses were predominantly negative with most knowledge concentrated on abundance and demographic rates in spruce and pine, and on moderating impacts of herbivory or pests and diseases (Figure 36, 5.1.1, 5.1.4).

For dwarf shrubs, impacts focused on abundance, demographic rates, and to a lesser extent phenology, and generally were attributed to a broad range of climate drivers, including temperature, drought and heat extremes, reduced snow cover, increased fire risk, and increased fire intensity (Figure 37, 5.1.1, 5.1.4). Most responses focused on bilberry, and to a lesser extent lingonberry and crowberry. Near-term warming positively impacted bilberry and lingonberry abundances. Temperature had mixed impacts on bilberry demographic rates, however, as it is sensitive to the shoulder season. For example, blueberry yield increases with warmer summers, but decreases with warmer autumns and winters, due to loss of cold hardiness and protective snow cover. Drought negatively impacts the abundance of bilberry. The impact of increased temperature extremes are mostly negative across species and response types. Reduced snow cover can negatively impact demographic rates for crowberry and lingonberry via increased spring and autumn freezing events, with mixed evidence for bilberry as a longer growing season extends growth periods. Bilberry mortality rates also increased due to reduced snow cover. Fire had both positive and negative impacts upon dwarf shrub communities, with increased fire risk promoting demographic rates for both bilberry and lingonberry, while they suffer under increased fire intensity, though to a lesser extent for bilberry. Crowberry abundance decreases under fire.

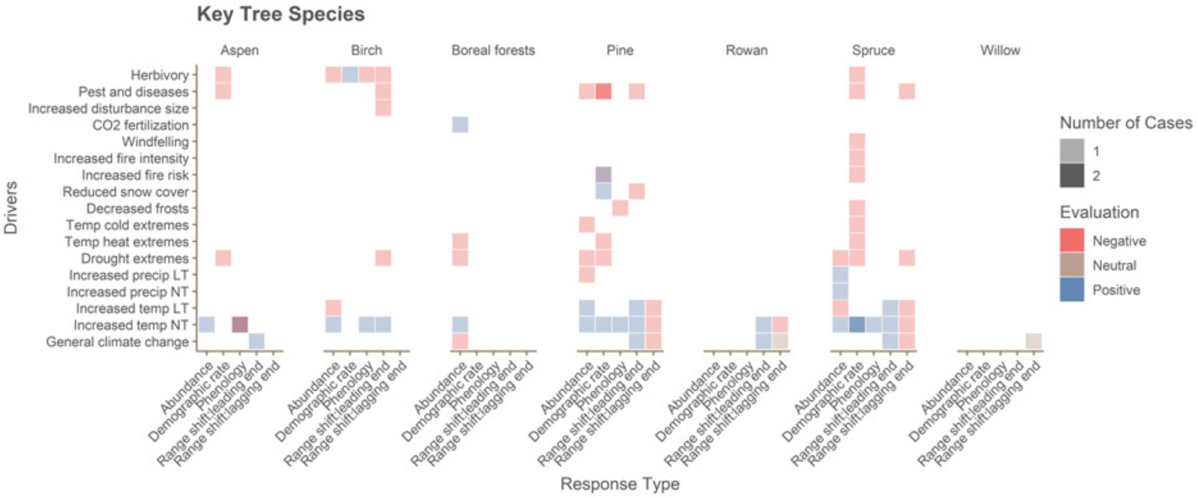


Figure 36. The impacts of climatic and disturbance drivers on responses of key tree species in Norwegian Forests. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). NB. This does not include species identified as aliens. Interacting drivers were not explicitly included.

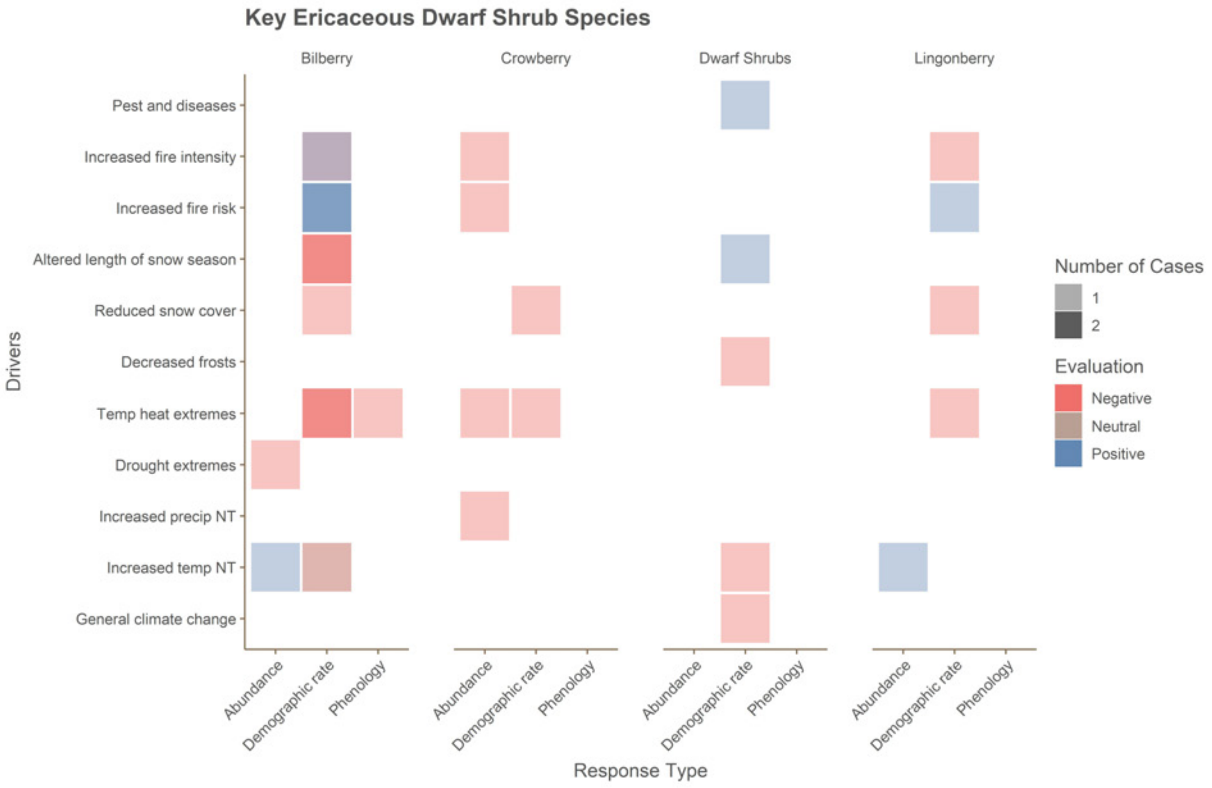


Figure 37. The impacts of climatic and disturbance drivers on responses for key tree species in Norwegian Forests. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). As multiple climate drivers may influence a given response type, and be either positive or negative, overlapping evaluations may be displayed (by muted shades). NB. This does not include species identified as aliens. Interacting drivers were not explicitly included.

5.3.2 Key forest types and regions

Some findings from Chapter 4 are of particular relevance for specific habitat types: Old-growth habitat types (C1, C10-C14, C21-C22, see Appendix 1) are vulnerable to increased disturbance frequencies (section 4.1). This is not because of particular susceptibility to fire, wind, or outbreaks (rather the contrary), but for the simple statistical reason that if the current frequency of disturbance has an average chance p of functionally destroying a habitat, the proportion P of habitat expecting to reach age T intact is an exponential decay function of the disturbance rate. This means that the higher the disturbance rate, the smaller the part of the habitat will be over a certain age when the overall landscape is at age equilibrium. The implication is that climate-change induced increased disturbance will decrease the coverage of habitat types that are defined by a long time period since the last major disturbance i.e., 'old-growth' habitat types.

The deciduous habitat types (C13-C22) are generally expected to expand their ranges northwards and towards higher altitudes, following the changes in habitat-forming tree species distributions (section 4.2.2). However, the old types (C13-C14, C21-C22) are subject to the same processes as other old habitat. While they may be less subject to bark beetle outbreaks, other pests and diseases (Chapter 4.3) are relevant for deciduous habitat building species, and forest fires and similar easily spill over, especially where the deciduous habitats form small patches in a matrix of drought susceptible spruce and pine forests. Whereas considerable stand replacement is expected to occur, no old (age >120-160 years) new deciduous habitat will form in previously needle-leaved stands over the less than 80 years that form the scope of this report.

Old spruce habitats (C10, C12-C12.4) are obviously particularly vulnerable, as they are old - type habitats consisting of the habitat-building tree species expected to see the strongest increase in mortality and disturbance rates. To a lesser extent this also goes for old spruce forests (C11-C11.4).

Forest types on landscapes particularly prone to drought stress (C7.3, C9) form another particularly vulnerable group as they must be expected to have little buffer against the increased risk of summer drought. One of these, Olivine forest (C9) is listed as Endangered (EN) on the red list for habitat types (Framstad 2018). See also Appendix 1 for red list status and summary.

5.4 Factors that confer resilience, resistance, and vulnerability to climate change

The ToR for the present assignment asks for "a summary of factors that can contribute to resilience to climate change, linked to the same seven characteristics from Nybø et al. 2017". In the context of forest ecosystems, Thompson et al. (2009) defined "resilience as the capacity of a forest to withstand (absorb) external pressures and return, over time, to its pre-disturbance state". When viewed over an appropriate time span, a resilient forest ecosystem is able to maintain its "identity" in terms of taxonomic composition, structure, ecological functions, and process rates. Thompson et al. (2009) also specified the characteristics that are believed to confer forest ecosystem resilience (Box 1) and which management actions likely foster resilience under climate change (Box 2). While these characteristics and recommendations are also broadly applicable to Norwegian boreal forest ecosystems, we include some further comments that appear specifically relevant to the Norwegian context.

Box 1. Forest ecosystem attributes essential to resilience and robustness (modified from Thompson et al. 2009)

- Forest resilience is an emergent ecosystem property conferred at multiple scales by biodiversity; i.e., genetic diversity, functional species diversity, and ecosystem diversity (beta diversity) across a forest landscape. Resilience is necessary to maintain desirable ecosystem states under variable environmental conditions.
- Most natural forests are highly resilient ecosystems, adapted to various perturbations and disturbance regimes. However, the system will shift to a different state that may or may not be less resilient if disturbance exceeds the capacity of the forest to recover, which is unlikely to provide the former level of ecosystem services.
- Complex forest ecosystems are more productive and provide more services than those with low species richness. Productive forests dominated by mature trees are stable ecosystems.
- There is niche differentiation among functionally important species (e.g., trees) in a forest, as well as competition, leading to complexity and variability within and among forest ecosystems and their processes. Some of this variability is caused by small local changes in site conditions across a forest.
- Redundancy of functional species is common in natural forest ecosystems and is directly related to ecosystem resilience. Redundancy provides insurance against changing environmental conditions, and species with limited functions under one set of conditions may become driver species under an altered set of conditions.
- Diverse forest systems are more stable (within defined bounds) than less diverse systems and this is partly related to a robust regional species pool and the beta diversity among ecosystems. However, even high diversity is no guarantee for ecosystem resilience once climate conditions move beyond those experienced by most of the component species.
- Although a forest may change states in response to disturbances, ecosystem functions may not necessarily be highly altered, suggesting that the ecosystem is ecologically resilient, even though the forest community structure may have changed. However, ecological resilience is unlikely in a forest with reduced redundancy due to intensive forestry.
- There is a negative relationship between species diversity, landscape diversity, and the capacity of a forest system to be invaded, especially by pests and diseases.
- Not all parts of a forest ecosystem are equally resilient to disturbances, including those arising from climate change. The result of disturbances will depend on tree species composition, natural disturbance regime, and moisture, temperature, and edaphic conditions.

Box 2. Forest management principles to foster resilience and stability under climate change (modified from Thompson et al. 2009)

- Maintain genetic and species diversity in forests using natural stands as benchmarks.
- Maintain stand and landscape structural complexity using natural forests as models and benchmarks.
- Maintain connectivity across forest landscapes by reducing fragmentation and expanding protected area networks.
- Maintain functional diversity (and redundancy) and eliminate conversion of diverse natural forests to monotypic or reduced species plantations.
- Reduce non-natural competition by controlling invasive species and reduce reliance on non-native tree crop species for plantation, afforestation, or reforestation projects.
- Reduce the possibility of loss of resilience by apportioning some areas of assisted regeneration with trees from regional provenances and from climates of the same region that approximate expected conditions in the future.
- Maintain biodiversity at all scales (stand, landscape, bioregional) and of all elements (genetic, species, community) and by taking specific actions including protecting isolated or disjunct populations of organisms, and populations at margins.
- Ensure that there are national and regional networks of scientifically designed, comprehensive, adequate, and representative protected areas. Build these networks into national and regional planning for large-scale landscape connectivity

5.4.1 Resilience, resistance, and vulnerability with respect to the seven characteristics of ecological condition

The summary of climate change impacts on the seven characteristics of ecological condition in boreal forests (5.1) reveals patterns and responses of relevance to forest resilience, resistance, and vulnerability to climate change. In particular, the rapid rate of current climate changes and the variable projections for specific drivers (4.1) in combination with species-specific and response type-specific climate impacts (4.2) along with pronounced trophic interactions, lags and feedbacks (4.3-4.5), sets the stage for loss of resilience and/or resistance and generally increased vulnerability of the biodiversity and functioning of the forest ecosystem as climatic changes progress into the future.

For the **primary productivity** of boreal forests **[Characteristic 1; 5.1.1]**, despite short-term increases in productivity due to increased temperature and precipitation, in the longer term (until 2100), climate warming is projected to reach levels where growth and range sizes of the dominant boreal trees (pine, spruce, and birch) will likely be reduced for most of the current boreal zone in Norway. Meanwhile, the negative impacts of climatic extremes, disturbances, pests, diseases and herbivores will become more pronounced, causing significant reductions in tree and understory growth with negative impacts on forest productivity and **functionally important species**' **[Characteristic 4; 5.1.4]** ability to track their climatic ranges, resulting in climate lags and mismatches that may confer threats to forest resilience and increased vulnerability*.* The net impact of these extremes is likely to vary over time and between species. Spruce-dominated forests are likely to be more vulnerable to fire, even though pine-dominated habitats have higher fire risks. Broadleaf-dominated forests are less at risk. In the forest understory, ericaceous dwarf shrubs may have little resistance to declining snow cover, whereas many bryophytes and lichens are vulnerable to increased temperature, and due to extremes, especially fire*.* Many boreal birds, rodents, and ungulates may be vulnerable to climatic warming and especially climate extremes, whereas invertebrate herbivores and more southern-distributed ungulates, such as deer, may be more resilient. Trophic interactions and cascades are generally likely to decrease resistance and increase vulnerability to climate change. For example, small carnivores which specialize on rodent prey may decline under climate change due to cascade effects from decreased prey populations and disrupted population cycles. Negative impacts of warming and climate-related extremes on plants may translate into positive impacts on herbivore, saprophyte and decomposer communities.

Under climate warming, species distributions following their climate zones across the landscape is the major projected **landscape ecological process [Characteristic 5; 5.1.5]** for boreal biota. Such range dynamics are widely documented across forest biota, including trees, birds and bats, ungulate and rodent grazers, bumblebees, moths, other invertebrate groups, and viruses and fungi. As current range shifts are generally not keeping up with the changing climate, vulnerability is expected to increase and resistance increase as climate change progresses. These effects are likely exacerbated by climate-related disturbances, pests, and diseases which may slow down range shifts of some species. More positive outcomes are expected for pests and other species prone to sudden population bursts (outbreaks), which are generally more resilient to climate variability and disturbances, with potential negative feedback to trees and forest communities. Important mechanisms that limit tree establishment and slow down their range expansion tracking climate zones, leading to increased vulnerability over time, include herbivores consuming young plants, poor landscape connectivity, and a lack of mutualistic or symbiont species, such as pollinators or mycorrhizal fungi.

Climate-change-related changes in **biodiversity [Characteristic 6; 5.1.6]** will entail increased richness of trees, understory species, small mammals and other vertebrate communities, saproxylic communities and other forest insects, soil invertebrate and fungal communities, whereas insectivorous bats, pollinating insects, mutualistic fungi, and specialized northern species across other taxonomic groups are expected to decline. The replacement of boreal- and cold-adapted species with more warm-adapted species could increase resilience in terms of ecosystem functioning and species richness per se, which is expected to result in increased local species richness among trees, small mammals and other vertebrates, saproxylic forest insects, soil invertebrates, and fungal communities because nemoral forests are often more diverse in these taxonomic groups than boreal communities. However, this replacement may result in increased vulnerability for specialised boreal biota, such as those reliant upon mature forests, as they are less resilient to climate change. Increased incidence of pests and diseases may further lead to a loss of stability in tree- and bird biodiversity.

Substantial and asynchronous time-lags in **functional composition within trophic levels [Characteristic; 5.1.3]** may create temporal mismatches and increase species' vulnerability to climate change. For example, mismatches may occur between plants and their pollinators or birds and their insect prey, and cause feedbacks, decreasing resilience, and increasing vulnerability of the forest ecosystem as climate changes proceed. These climate-driven but variable changes across forest biota may change the **trophic structure [Characteristic; 5.1.2]** of the boreal forests. These effects may be exacerbated by climatic extremes (drought, heat extremes, winter warm spells), disturbances (fire, wind), and tree pests and diseases, and feedbacks and trophic cascades may add variability and uncertainties. In the longer term, we may see a trophic restructuring of the boreal forest ecosystems with an overall decline in vertebrate herbivores, birds, bats, and to some extent carnivores, and increase in invertebrates, tree pests, and diseases*.*

The impact of climate change upon ecosystem nutrient cycling **[abiotic factors, Characteristic; 5.1.7]** will depend upon the resilience of boreal forest systems. Climate change is predicted to enhance rates of ecosystem nutrient cycling specifically via increased and more easily decomposable carbon- and nutrient inputs to boreal forest soils via increased litter from trees under warming. Additionally, faster nutrient decomposition and cycling in warmer soils will lead to increased carbon loss to the atmosphere. With decomposers also expected to increase in abundance and efficiency, nutrient nutrient cycling will be further enhanced. Combined with changes in the soil microbial community, and less frozen ground, increased soil respiration and decreasing soil carbon storage are likely consequences. Further ecosystem carbon loss may result from increases in climate-related disturbances, such as fires.

5.4.2 Landscape complexity and geographical regions

Structural complexity and diversity at multiple levels of organization and spatial scales confer resilience (Box 1). As noted in 2.3.2, the rugged topography of Norway produces a high degree of landscape complexity, with relatively narrow belts and small-scale patchworks of edaphic and bioclimatic conditions. This topographical forest landscape complexity makes it less likely that disturbances and extreme events, like pest organism outbreaks, droughts, storms, and forest fires exert large scale effects throughout the landscape. That is, such topographic complexity is likely to harbor climatic refugia for biota even under profound region-scale climate change. Moreover, owing both to topography and to steep maritime - continentality gradients, the bioclimatic context of Norway may act to buffer landscape to regional scale impact of climate change on biodiversity (Graae et al. 2018). This is because species do not need to relocate over long distances to find conditions that are within their climate envelopes. However, this also implies that local ecosystems may be displaced relatively fast, with some cold-adapted ecosystems disappearing, and new ecosystems appearing (Jansson et al. 2015).

The Norwegian forest range bioclimatically from the ecotone between nemoral and southern boreal forest in the south to the ecotone between northern boreal forest and arctic tundra in the high north. Forest compositions are expected to be most resilient to climate change in the central part of species ranges (Chapin et al. 2004). Conversely, ecotones are expected to be especially prone to fast climate-driven state shifts (Risser 1993). This means that the ecotones toward alpine and arctic tundra and nemoral forest are likely change hotspots. The profound vegetation state changes due to the recent spread of insect pest outbreak across the birch forest-arctic tundra transition zone in Eastern Finnmark is consistent with these expectations (see Section 4.4.2). It is also noteworthy that climate change is projected to vary considerably across the national-scale climate gradient in Norway with the most profound changes taking place in the ecotone between the boreal and Arctic biomes in the northeastern part of the country (Pedersen et al. 2021).

In a warmer climate with more extreme drought events, fire frequencies and burnt-over areas are expected to increase (4.1.7). At the same time, we expect more fire-resilient tree species (pine and deciduous) to replace the more fire-sensitive spruce in many locations. The replacements will be particularly evident in geographical areas that will gradually become too warm and too dry for spruce (4.2.1, 5.1.1, 5.1.4). Over time, the increase in the abundance of more fire resistant tree species, in combination with a decrease of the more fire sensitive spruce, will shape the fire regime of Norwegian forests and contribute to landscape complexity.

5.5 Vulnerability of managed and natural forests to climate change

The ToR requests an assessment of resilience, robustness, and vulnerability factors of importance for forest management and adaptation. Here, we summarize our findings with relevance to these issues. In the context of drought, resilience refers to the capacity of a forest to return to pre-drought growth conditions, while resistance refers to the ability to withstand a drought during its occurrence (Vanhellemont et al. 2019). Functional- and structural diversity is suggested to play an important role in forest resilience and resistance to drought (Vanhellemont et al. 2019) (4.2, 4.3, 4,6). Most results suggest that the typically heterogeneous (in terms of age, size, and species composition) relatively open, and with little or no management impact are more drought resistant or resilient than homogeneous, dense, and heavily managed forests (4.2.2., 4.6). There are also studies indicating that mixed forests more effectively utilize available soil water than monospecific ones, which may increase resilience to short-term droughts, but not to longer-term or more extreme or longer-term droughts (4.2.2). Simulation studies further suggest that dense, homogeneous and monospecific forests are more vulnerable to storms, snow-load and pest attacks (4.3, 4.6). Lastly, increasing the areas of set-asides and protected forests will increase the resilience of the wood decomposer community to environmental perturbations and thus make the diverse invertebrate and fungal decomposer communities less vulnerable to climate change (see also 4.6).

Impacts on the resilience and vulnerability of functionally important species such as trees and dwarf shrubs are likely to have cascading impacts on ecosystem functioning and stability, and as shown above, the habitat-forming tree and dwarf shrub layers are vulnerable to climate extremes. Mature spruce trees are rarely exposed to physiological drought under present Norwegian climatic conditions. However, increased mortality has been observed and will be expected in the future after extreme events and on shallow, well-draining soils during droughts (4.2.2, 5.1.4). Thus, drought resistant species on well drained soils are likely to improve resistance. In Norway, as in the rest of northern and central Europe, spruce has been planted on soils that naturally would be occupied by more drought-tolerant species. Such sites are expected to be especially vulnerable to drought events in the near future. Mature pine is considered as highly resilient to drought under Norwegian conditions, and typically occupies drier sites. However, seedlings and young trees are not as robust, suggesting that extreme drought years may limit establishment (4.2.2, 5.1.4).

5.6 Biodiversity goals

The ToR requests that "An overall assessment should also be made of the vulnerability factors of importance for forest management and adaptation, including achieving the national biodiversity targets 1.1 and 1.2". Below, we describe our approach and results for each of these targets.

Biodiversity target 1.1. states that ecosystems *should be 'in good condition'*, and to address this, we synthesize the relative importance of different climate and climate-related drivers in impacting the ecological condition of boreal forests across all the seven characteristics of ecological condition. As detailed in section 5.1, our literature searches reveal both positive, negative, and neutral impacts of climate change and climate-related abiotic and biotic factors on boreal forest ecosystems.

The majority of the positive impacts (n=286) relate to increased abundances, enhanced population growth, leading edge range expansions, lags in climate responses, and enhanced feedbacks under near term climate warming and/or general climate change (Figure 38). There is also evidence for enhanced nutrient cycling in response to fires. Negative impacts (n=189) relate to reductions in abundances, especially in response to near-term warming but also in response to a wide range of climate drivers, along with impaired range shifts and feedbacks (Figure 38). Few studies document neutral impacts (N=21).

As a result, there are striking differences in the most important climate drivers for positive and negative climate change responses (Figure 39). Positive impacts are primarily driven by warming and general climate change, which increase primary productivity, enhance the abundance of many functionally important species and functional groups, and drive changes in landscape ecological patterns, especially via leading edge range expansions towards higher elevations and latitudes.

In contrast, negative impacts are primarily driven by various kinds of climate extremes (including drought, temperature extremes, freeze-thaw cycles, and frost) and climate-associated disturbances (fire, snow, wind). These extremes and disturbances lead to reduced primary productivity via decreased plant growth and increased mortality, the loss of many functionally important species, and changes in biomass distribution across trophic levels. Increased fire risk and fire intensity under climate change also have predominantly negative impacts, especially on primary productivity and functionally important species. Overall, warming and climate change dominate the positive impacts for each ecosystem characteristic (i.e., >60%), whereas for negative impacts, a much wider range of impacts are documented and especially extremes and disturbances play a larger role (Figure 39) (see section 5.1 for details).

These results imply that gradual climate changes, such as warming or increased precipitation, will have substantial and important impacts, including structural, functional and biodiversity changes. These gradual temperature and precipitation shifts are not likely to be immediate threats to ecosystem functioning, however, and may result in a net increase in forest productivity and increased biodiversity of some organismal groups, at least in the near term (c.f., 5.1). In contrast, the increased frequency and intensity of weather extremes under climate change and climate-related disturbances (see 4.1) are likely to incur negative impacts that are often system-wide and generally lead to loss of ecosystem functioning and resilience.

The importance and role of pests, pathogens, parasites and diseases negatively impacting the ecological condition of forests is likely to be of increasing importance in the future (section 5.2), as are changes in herbivory and other trophic interactions. Because climate extremes and disturbances are inherently difficult to predict and disentangle from the general effects of warming (section 4.1), and compounding effects associated with time lags, asynchrony, trophic interactions and cascades (section 4.5), climate change will entail increased risks of unexpected loss of forest biodiversity and ecosystem functioning.

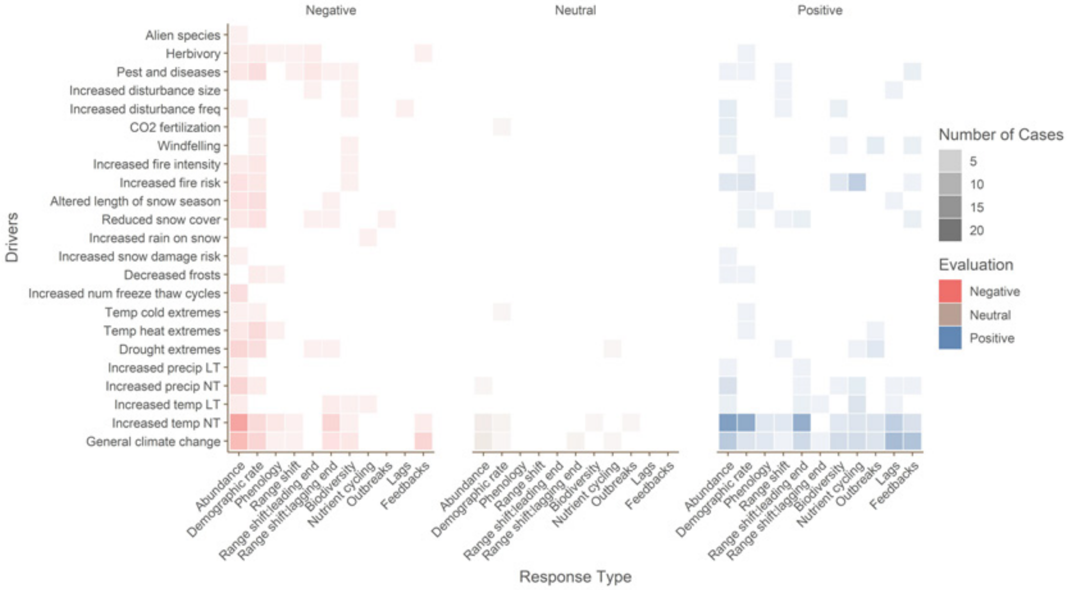


Figure 38. Summary of the negative, neutral, or positive impacts of various climatic and climate related disturbance drivers on different types of organismal and ecosystem responses for Norwegian boreal forests. The impacts of some climate drivers are assessed both near term (until 2050, NT) and long term (2100, LT). The figure does not include information from species categorized as alien. Interacting drivers were not explicitly included.

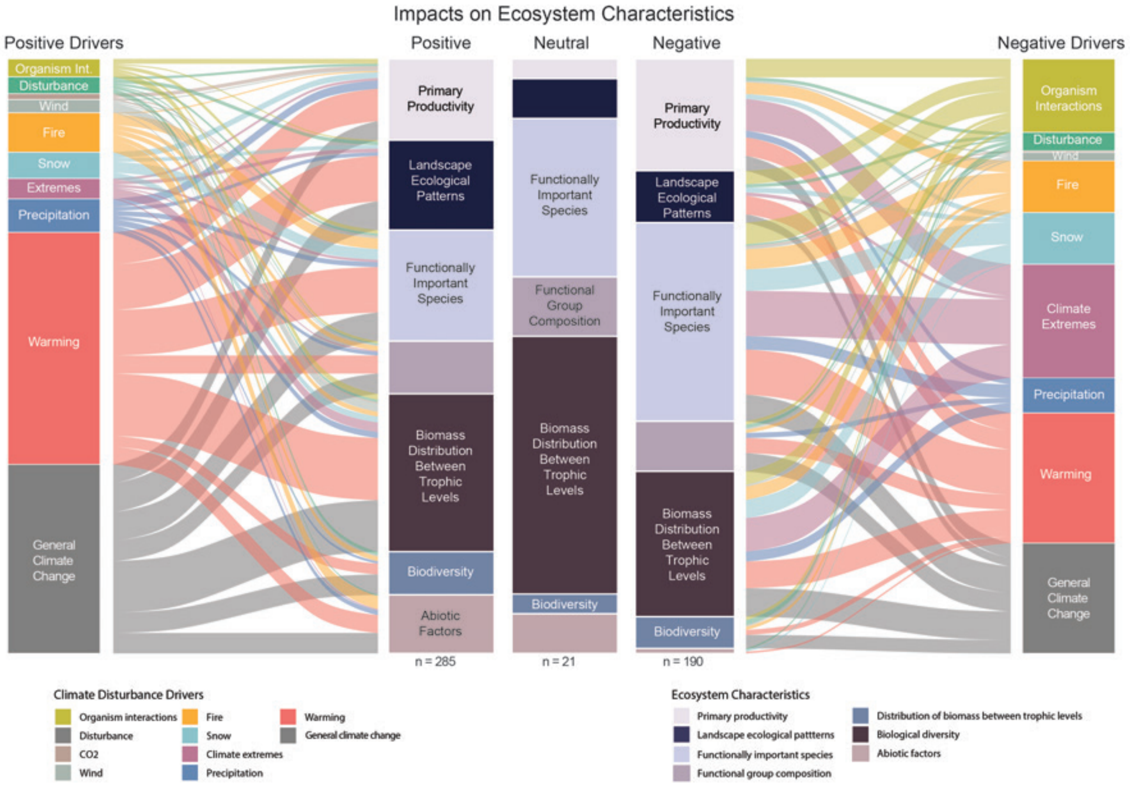


Figure 39. A summary of the amount of evidence for positive (left) and negative (right) and neutral (centre) impacts of climate change related drivers on the ecological condition of Norwegian boreal forests. Ecological conditions are represented by the seven ecosystem characteristics of the Norwegian ecological conditions Framework. The center column summarizes ecosystem characteristics for which null (neutral) impacts were documented. Climate change related drivers are aggregated into nine major classes reflecting gradual climate change, climate extremes, and climate-related disturbances. The height of each driver class or ecosystem characteristic within the respective bars represents the relative weight of evidence from the scientific literature reviewed related to that specific driver class or ecosystem characteristic. The flows represent the relative body of evidence that a specific climate driver class has a positive or negative influence on a specific ecosystem characteristic (no attribution provided for the null responses). Note that positive, negative, and null impacts were evaluated separately in this figure. Sample sizes under each bar plot represent the overall weight of evidence within the report. NB. To avoid double-counting, impacts of long-term temperature and precipitation change are not counted in addition to short term temperature and precipitation in the aggregations of drivers. Alien species are not included. Interacting drivers were not explicitly included. Importantly, the weight of evidence provided reflects the methodologies used for literature selection and aggregation (see 3.3 and 3.1), for example, literature highlighting species specific insights may generate more climate-response combinations and cases than literature referencing impacts on boreal forests more broadly.

Biodiversity target 1.2) states that "*no species and habitats should be eradicated and the development of endangered and near endangered species should be improved*". We examined the Norwegian Red list of Species (Artsdatabanken 2021) for information on climate change as a threat to forest species (section 4.7). To date, climate change is identified as a specific threat to only 38 out of the total of 2083 forest species on the red-list. It should be kept in mind that few localities are known for many of these species, at least in part due to under-reporting, and that the habitat requirements and ecology of most of these species are not well known. Given how poorly known many red-listed species are, the severity of predicted climate change effects is usually given as "unknown" in the expert reports. A common theme for these 38 red-listed species is that climate change is just one among several threats (4.7), and that the Norwegian populations make up a small fraction of their global distribution so that the species may not be threatened throughout their range (4.7). Also, suitable habitats for many threatened forest species are often highly fragmented due either to the habitat itself being rare, or to changes in zoning or agricultural or forestry practices that lead to loss or degradation of habitats. Species-level detail is provided in 4.7. In addition, southern range limit contractions of northern and alpine species is projected for a range of taxa, including trees, (section 5.1.5), which will lead to local extinctions and more generally range contractions in boreal and northern species not currently classified as red-listed.

In general, threatened forest habitat types are subject to the general changes in disturbance regimes, extreme events, community range shifts, as described throughout this report. While specific data is lacking, threatened habitats are by definition rare, and therefore, threats due to landscape ecological processes (low connectivity, slow ecological dynamics, fast climatic changes; see chapter 4 and summaries elsewhere in chapter 5) should generally be at least as problematic for these forests and their biota as for forests in general. Appendix I lists these nature types individually, based on the assignment letter from the Norwegian Environment Agency, and augmented with a qualitative indicator of main expected effects of particular relevance for that nature type.

6 Data gaps and uncertainties

6.1 Knowledge gaps that should be given priority

The ToR "request that a review be made of knowledge deficiencies, with an assessment of which knowledge gaps should be given the highest priority in the years to come." The evidence for climate change impacts on the ecological condition of forest collated for this report covered a wide range of organisms, ecological characteristics, and climate change-related factors, as summarized in chapter 5. The analysis with respect to the questions posed in the ToR revealed combinations of climate drivers, characteristics of ecological condition, organismal groups, functions, and systems for which have limited evidence, some of these limited our ability to answer the ToR (Figures 38, 42). Some of these knowledge gaps are especially detrimental for our ability to assess climate change impact on the future dynamics, diversity and condition of forest ecosystems. Here we point to three general sets of such knowledge gaps, and identify specific research and knowledge priorities within each set. The lists are not in order of priority or importance.

Set 1: Knowledge related to characteristics of ecosystem functioning

Across all organismal groups and trophic levels, we find that the existing knowledge is largely related to impacts on abundance, demographic rates, and ranges of dominant species, with less information on climatic thresholds, ecosystem functioning, and ecological interactions (Figure 42). This points to knowledge gaps regarding:

- Impacts of climate and climate-related drivers on biodiversity, biotic interactions, and species and ecosystem functioning (Characteristics 2, 3, 6, and 7) including the magnitude and consequences of time-lagged and asynchronous shifts within and between organismal groups.
- Factors that confer forest ecosystem resilience, resistance, and vulnerability, and therefore limited ability to predict and mitigate threats by managing for reduced forest vulnerability in a changing climate. This includes the role of land-use and forestry in affecting resilience to climate change.
- How climate change, and especially changes in climate extremes, will impact ecosystem carbon stocks and dynamics. In particular, we lack understanding of how climate change impacts the contributions and interactions between the primary producers (both trees and understory), consumers (insect and vertebrate herbivores) and the soil decomposer and mycorrhizal symbiont communities in controlling the net ecosystem carbon uptake and emissions.

Set 2: Knowledge related to specific drivers and causal relationships

- Knowledge on the role of climate extremes and climate-related disturbances as drivers of ecological condition in Norwegian forests, which are particularly important as we find that they exert strong and predominantly negative impacts on the ecological condition of boreal forest systems.
- Some functionally important organismal groups are underrepresented. In particular, knowledge about the climate change impacts on understory vegetation, including dwarf-shrubs, bryophytes and lichens, and key decomposer and mutualist communities, and their role and functioning in impacting forest condition under climate change.
- Impacts of climate change on functionally important insect species, especially considering their diverse roles in Norwegian forest ecosystems, and to what degree changes observed align with the ongoing global loss of insect biodiversity and biomass.
- Animal- and plant diseases that can have large ecological impact but do not affect humans or economically important species. In general, fungal pathogens in plants are much more studied than bacteria (including phytoplasmas), oomycetes, nematodes, and viruses.

Set 3: Knowledge gaps related regional and system context-dependencies

- Insights as to how local adaptation, or regional variation in responses, may impacts species’ resistance or resilience to climate change
- We could benefit from more co-ordinated, long-term, ecosystem-based research/monitoring efforts for integrating field-based data with regional- and national-level knowledge systems (e.g. species distribution maps, soil conditions, climate forecasts, remote sensing and modeling tools) so as to develop realistic, and robust predictions for species beyond primary producers
- There is a general lack of empirical knowledge about forest ecosystem transition and succession on the scales and time frames relevant for current climate changes, calling for more comprehensive and ecologically informed assessment and monitoring.

More specific information on the knowledge gaps and needs are given in the sections below.

6.2 Forest response models and studies

Tree-growth forestry models and observational studies are much used in the literature, for good reasons, but often have different limitations and point to different conclusions when assessing the implications of climate change to forest growth, recruitment, mortality and productivity.

Though frequently used, even major forest model systems, like the Swedish planning model system HEUREKA (Fahlvik et al. 2014), suffer from serious shortcomings when used to predict the effects of climate change:

- Model error within data range is usually accounted for, but far greater concerns appear when using models to extrapolate effects of climate change out of observed data range. Particularly since model functions tend to be parameterized and developed for conditions where the trees are found naturally or profitably grown. Thus the models extrapolate growth functions beyond the warranted data range, and often do not include tipping points where a positive effect biomes negative or vice versa.
- Moreover, being models of growth, these models may inadequately or not at all include effects of stress and extreme events on mortality risk. This is particularly exacerbated when models use the mean of climate-related variables by using average temperatures or degree-days as their climate input without taking variances into account. Essentially, the frequency at which heat or drought exceeds a tolerance limit may have a much greater impact on forest dynamics than degree days extrapolated to a growth response.
- Lastly, using HEUREKA as an example, important risks and uncertainties are either not included (like fire or pests), or given misleadingly simplistic (temperature and drought) or inappropriate (storms) representation (SLU 2019, Skytt et al. 2021). Some factors are notionally included, such as autumn and spring phenology being influenced by temperature (Keenan et al. 2014), but may fail to include interactions. For instance by ignoring that temperature is not the only seasonal cue, and as day length is not affected by climate warming, potential asynchrony in these functionally paired cues may arise (Hänninen and Tanino 2011; Way and Montgomery, see also the section on phenology).

Models simulating growth and production of economically important forest trees are useful in forestry planning under known conditions, but the ability of growth models to conclude about forest dynamics under climate change should be taken with considerable skepticism and be evaluated and validated against observations individually. Experimental studies on single species, on the other hand, have other limitations. The larger part of experimental studies is carried out on seedlings or juvenile trees, while mature trees are usually subject to retrospective tree-ring studies. Moreover, effects of temperature on growth of mature trees are often studied together with effects of precipitation, as these two climatic factors are tightly connected. Many experimental studies do not take variance and extreme values into account. For practical reasons, experimental studies also tend to exclude larger-scale effects like fires, pest outbreaks, and interspecific competition. Still, they can provide relevant information on physiological responses on the scale of individual plants. Lastly, the problems with observational studies are the lack of control groups and the problem of inferring causality. Observation-based research on long-lived species such as trees are often practically restricted to be correlational studies of events that have happened, often as results of surveillance programs that may not have been designed to address all the parameters one may wish for fifty years into it.

Better process-based models and experiments are needed to accurately predict climate-induced changes in phenological patterns (Delpierre et al. 2016, Hänninen et al. 2019). Assessing the theoretical framework against observations or experiments for phenological match/mismatch on population dynamics, habitat distribution, connectivity, community composition etc., remains an important challenge (Kharouba and Wolkovich 2020).

Future species ranges as a consequence of climate change are most commonly predicted by use of species distribution models (SDMs) (Urban, 2015). SDMs are correlational models of low structural complexity that rely on the statistical relationship between species occurrence and local climate. These models have often been criticized for relying on over simplistic assumptions and neglecting critical biological processes involved in species' responses to a rapidly changing environment (Moullec et al. 2022), however, very few alternatives are available.

The Norwegian SiTree framework (Antón-Fernández and Astrup 2022) for single-tree simulations can handle stand-level dynamics (or larger given enough computing power) on an individual-tree basis. While it is subject to the same risks and problems as other models, it may also represent a promising way forward due to it being functionally modular. That is, the functions describing the different vital rates and demographic processes, and how they respond to the environment, are not just parameterized for each model run but can be specified by the user. Thus, nothing in principle stops the framework from being developed into a set of functions that capture major effects of soil type, competition and climate well enough to be validated against a wide range of climates and attain good predictive capabilities even for strong medium to long-term climate change.

6.3 Climate models and uncertainty in projection

Most of the energy retained by increasing atmospheric greenhouse gas concentrations is absorbed by the world's oceans. The year 2021 set a new record for ocean heat content, meaning it was on average the warmest ocean temperatures recorded by humans (Cheng et al. 2022). The North Atlantic temperature plays an important role for regional temperature and precipitation in Norway, and is heavily influenced by the Gulf Stream. Current temperature regimes are maintained by a heat influx from large-scale circulation of warmer air and seawater that gives parts of Norway considerably more rain and less seasonally variable temperatures than is typical for the main areas of the boreal zone. The Gulf stream has a circulation pattern carrying most heat towards Scandinavian coasts, making its volume, direction, and temperature of great regional importance for the Norwegian climate (Ketzler 2020). However, understanding the exact influence of the Gulf stream, and how it will respond to climate change, is a major challenge when predicting future climate conditions in northern Europe in general and Norway in particular (Collins et al. 2018). The North Atlantic Ocean shows a warming trend for the entire instrumental record, with a strongly increasing rate of warming from around 2000, especially in the Gulf Stream region. However, there is an exception in the form of a cooling region south of Greenland (Seidov et al. 2017), which may signal a slowdown of the Atlantic meridional overturning circulation and reduced oceanic heat transport into the region (Keil et al. 2020). The further developments of the oceanic heat transport and the corresponding effects on Norwegian climate are uncertain and contentious. Should major changes occur to the oceanic heat transport, the climate projections for Norway will have to be strongly revised.

Even more importantly, the ToR mentions thresholds for abrupt changes in biodiversity or other characteristics, and such tipping points are likely an inherent part of the climate system. A growing number of publications warn of tipping points and tipping point cascades that are not represented by current models and simulations, but where a moderate warming may initiate a set of self-reinforcing mechanisms leading to considerably stronger warming than the anthropogenic emissions alone would cause. Such tipping point cascades are not accounted for in current models that couple emissions to impacts but may explain otherwise poorly predicted shifts in earth’s climate history (Lenton et al. 2019, Brovkin et al. 2021, Wunderling et al. 2020, Klose et al. 2020, Pereiro and Viola 2018). If tipping points were better understood, models embracing them could improve predictions about the consequences of climate change and perhaps make possible effective intervention (Pearce 2007, Lenton 2020, Sharpe and Lenton 2020, Swingedouw et al. 2020, Wang and Hausfather 2020).

Inadequate knowledge of the climate system’s sensitivity and of the likely variability in future climate change, as well as limitations in the climate models, lead to uncertainties in the projections for any emissions scenario. Notably, the upper values of the temperature confidence interval would represent an extremely dramatic shift in climate regimes. Should the more pessimistic projections come true, it is unlikely that mitigation measures can compensate for central functions, like global food security (Tomter and Dalen 2018), let alone for impacts on biodiversity levels of ecosystem services.

More research should consider forest shifts interacting with land-use changes that result from implementing climate change measures, as well as other land-use changes forecasted by integrated RCP-SSP scenarios. As an example SSP1xRCP2.6, SSP3xRCP4.5 and SSP5xRCP8.6, from Land-Use Harmonization2 (see the IPCC AR6 (2021) and Hurtt et al. (2020).

The position of tipping points or other thresholds that lead to abrupt changes in ecosystems may be notoriously difficult to predict because they are often caused by extreme events and unknown synergistic interactions among multiple drivers (e.g., compound disturbances and depend on spatial and temporal contingencies; see Turner et al. 2020).

Global atmospheric CO_2 concentrations had a median value of 200 ppm and never exceeded 300 ppm between 800,000 years ago and the year 1500. This suggests that today's atmospheric CO_2 levels of about 420 ppm (and rapidly rising) represents a level of climate influence, heat energy balance, and atmospheric composition that is new to written history, to modern life with agriculture, and to our experience as a species. This is a sobering perspective when considering long-term temperatures and greenhouse gas concentrations that necessarily impacts our ability to extrapolate into the future.

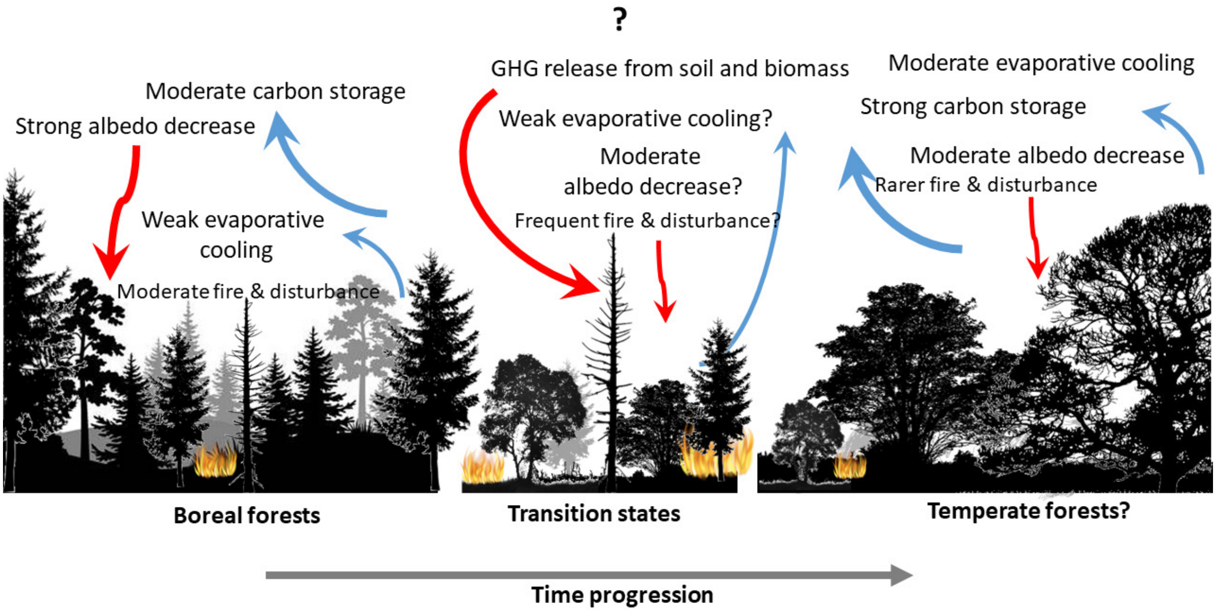


Figure 40. As boreal forests undergo nemoralization towards more hemiboreal and temperate states not only their carbon cycles and carbon sequestration changes, but also their resistance to large-scale disturbances like fires, their evapotranspiration and, not the least, their albedo. All of which link back to regional and global climate. However, where these factors have been studied for established forest

systems of each type, we in practice know little of the transition phases under large-scale, extremely rapid climate change. This adds its own level of uncertainty to climate models, as the boreal vegetation zone is big enough to have substantial feedback effects, positive and negative, on the global climate.

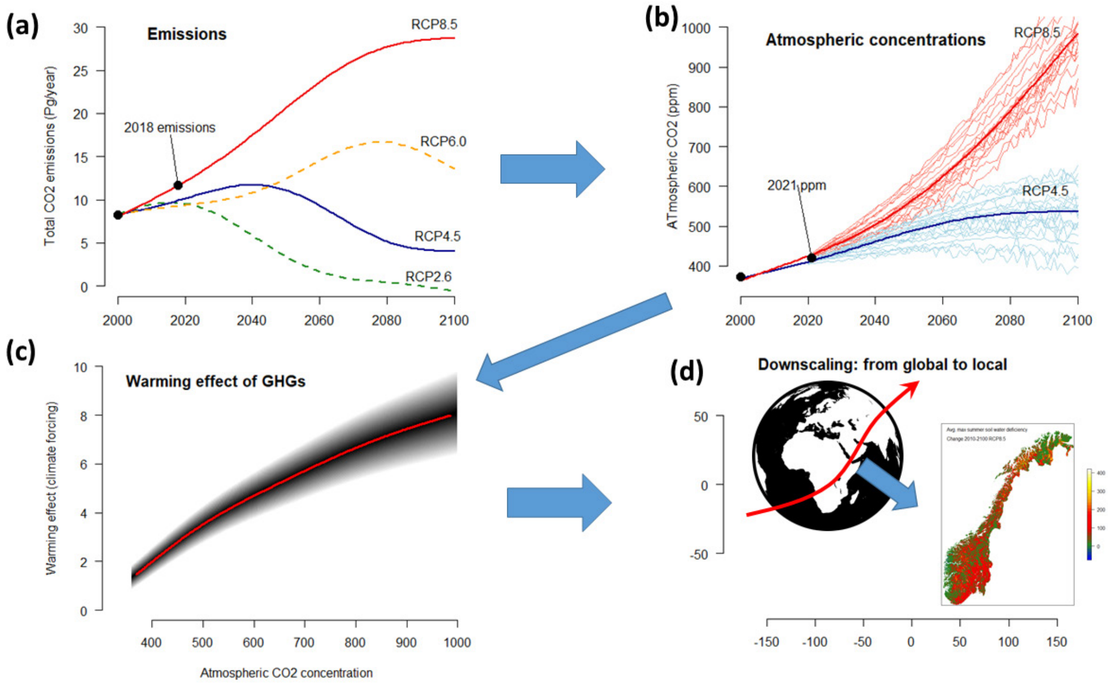


Figure 41. Different sources of uncertainty in climate projections. (**a**) First, we do not yet know what the GHG emissions that result from the next century of politics, technology and economy. (**b**) Second, even for a given level of human emissions, we do not exactly know the resulting greenhouse gas concentration once the human-made emissions meet the natural cycles releasing, breaking down and sequestering them. (**c**) Third, for a given level of atmospheric GHG concentrations, the effect on climate is somewhat uncertain even for the best of modern models, due to the complexity of the system and feedback between the different components. (**d**) Lastly, taking a global climate model and downscaling the results to get highly detailed predictions about the climate for specific regions and landscapes introduces local effects of topography, weather and small-scale variation not necessarily captured by the global model. Therefore, the neat-looking trajectories that often are presented in publications in reality come with both systematic and random sources of variation and error that can have substantial effects on biotic systems that are often disproportionately affected by extreme values.

6.4 Uncertainty and possible biases in assessing ecological conditions

Ecosystem characteristics can be assessed based on indicators, which are direct or indirect measures (proxies or surrogates) of state variables (like population sizes or nutrient concentrations) or drivers of change (Lindenmayer and Likens 2011). Since the publication of the Ecological Condition Framework (Nybø et al. 2017), considerable efforts have been invested in development and communication of methodological frameworks (Jakobsson S. et al. 2021, Töpper et al. 2019, Jepsen et al. 2020, 2022). Biomass distribution across trophic levels as measured by different types of autotrophic and heterotrophic organisms is poorly known due to lack of measurement and monitoring data. In the recent assessment of the ecological condition of the forest ecosystem in Norway (Framstad et al. 2021), two proxies were used as indicators of the biomass in different trophic levels: (1) population densities of moose and red deer, and (2) population densities of brown bear, lynx and wolf, representing herbivores and predators, respectively. The population densities of the assessed herbivore species are estimated to be close to the assumed natural levels, whereas the population densities of the assessed predators are far below natural levels. Primary producers, decomposers, and microbiota were not included in the assessment of ecological condition, but it was mentioned that Normalized Difference Vegetation Index (NDVI) and the volume (m^3 ha^{-1}) of trees in could reflect the size and trends of the biomass of the primary producers. The NDVI values show a slight increase during the last decade, and the volume of living trees has increased during the last 15 years (Framstad et al. 2021).

This report is tasked to provide a comprehensive, ecosystem-level review of climate change impacts on Norwegian forests based on published scientific literature. A fundamental challenge is that studies are scattered geographically (different ecological contexts), and differ in methodology (observational, experimental, modeling) and in themes (different components and processes are mostly considered separately). Assembling such bits and pieces *post hoc*, may lead to an unknown degree of "synthesis errors". This error could be remedied if there were more empirical studies that by research or monitoring design were *a priori* ecosystem-based (Lindenmayer et al. 2018, Ims and Yoccoz 2017). Presently, there are no ecosystem-based studies in Norway that adequately encompass the seven ecosystem characteristics requested by the ToR of the present assignment.

6.5 Further data gaps

Direct responses:

We find, presumably for practical reasons, far more studies on direct effects of heat, moisture etc. on major functional groups than on interactions and indirect effects of multiple factors (Figure 42). This includes very variable availability of growth response, recruitment and survival studies across species and groups (Figure 38).

How the growth and reproduction of conifers respond to past changes in environmental factors seems fairly well understood, but we lack knowledge for many deciduous tree species, such as the ecological important rowan, aspen and willows, as well as many of the hardwood species. There is thus a need for more research on the response of non-commercial species to climate and climate change.

Likewise, functionally important plant species of the understory, like bilberry, lingonberry, and crowberry, have been studied to some extent in relation to climatic factors. However, almost all studies are from relatively high altitudes or from northern boreal or arctic-alpine regions. There is thus need for more long-term studies on the abundance and phenology of these plant species and their interactions, also towards their lower or more southly distribution limits, where the species are likely to first experience sub-optimal conditions under continuing climate change.

Direct impacts of climate variables and climate change effects on animal growth, reproduction and phenology except for cervids and some other mammals are understudied in comparison with plant responses. Also, the important link between plants and animals in the context of plant-herbivore, plant-pollinator or other plant-animal interactions like forage quality may need more attention in climatic research in northern forest systems. Of particular importance for insect- or disease outbreaks is climate effects on the nutritional quality and on the amounts or quality of herbivory-induced chemical defenses in plants.

Biodiversity:

Nationally red-listed species are of particular conservation concern. Generally, while many species associated with forests are listed as threatened to a lesser or greater degree, there is insufficient knowledge about their physiology, behavior and ecology. This lack of knowledge gives high uncertainties on how their populations will respond to climate change (Akcakaya et al. 2006). We have discussed potential impacts on biodiversity of climate regime-induced changes in stand-replacing disturbances, such as wildfires, droughts, extreme weather events like strong windstorms, insect outbreaks, and tree diseases. However, the impacts of changes in any one of these single factors on biodiversity cannot be predicted with any certainty because different types of disturbance interact with each other in complex ways (Simberloff 2010).

Even in a well-studied country like Norway, there is an extensive diversity of undescribed fungi and other components of the soil community, making it difficult to generalize their roles and interactions within the forest biome, and their responses to and effects on climate change. However, empirical observations based on the functionally important state of the growing mycelia would give more direct evidence of how climate change affects forest fungi. Hence, we see a need for long-term monitoring programs that include DNA-based analyses of microbial organisms. We also call for more experimental studies testing causal relationships between climate factors and fungal growth and survival, with cascading effects on vegetation and carbon dynamics.

Fungal pathogens in plants are much more studied than bacteria, oomycetes, nematodes, and viruses. There appears to be a general lack of knowledge about the plethora of possible pathogens affecting mammals, birds, insects and other animals, so the selection mentioned here should be regarded as examples, not an overview. Research tends to focus on the plethora of pathogens that affect both humans and animals (zoonotic), or livestock, and thus diseases that only affect wild species of little commercial interest are likely mostly undescribed.

Interactions, cascades, and indirect effects:

Uncertainty pervades predictions about forest insect dynamics, due to complexity, incomplete understanding, unstable relationships, or lack of data (Dukes et al. 2009; Cooke and Carroll 2017). However, because the dynamics of forest insect outbreaks depend strongly on the availability and susceptibility of host trees, such outbreaks will not be driven by climate alone but will be strongly influenced by forest management (Ji et al. 2011, Murdock et al. 2013, Ciesla 2015, Scheller et al. 2018). Changes in forest disturbance regimes can feedback on climate through effects on water and carbon flux in forest ecosystems (Ayers and Lombardero 2000).

An example of a potential climate change impact on biotic interactions for which we still lack knowledge is the potential temporal or spatial mismatches between flowering plants and their mutualist pollinators like bumblebees (Hegland et al. 2009, Kerr et al. 2015). These are inherently difficult to study and to estimate consequences on fitness from climate change. Such studies require a mix of long-term observations and experimental assessments.

Specific points:

Comparative studies are necessary to test several proxies like tree-ring responses or context-dependency of charcoal functions used to address historical fire frequencies across a variety of boreal forest ecosystems (Makato and Koike 2020).

Several research groups have felt that the literature on animal responses to fire is taxonomically biased and incomplete when it comes to documenting fire and landscape characteristics and demographic processes (see Volkmann et al. 2020).

Pollinators are a functionally important species group that are clearly under global pressure, and as such would benefit from more attention in Norwegian environmental monitoring.

There are surprisingly few studies available in the international literature on large mammalian boreal predators' responses to climate change, particularly beyond just increasing mean temperatures.

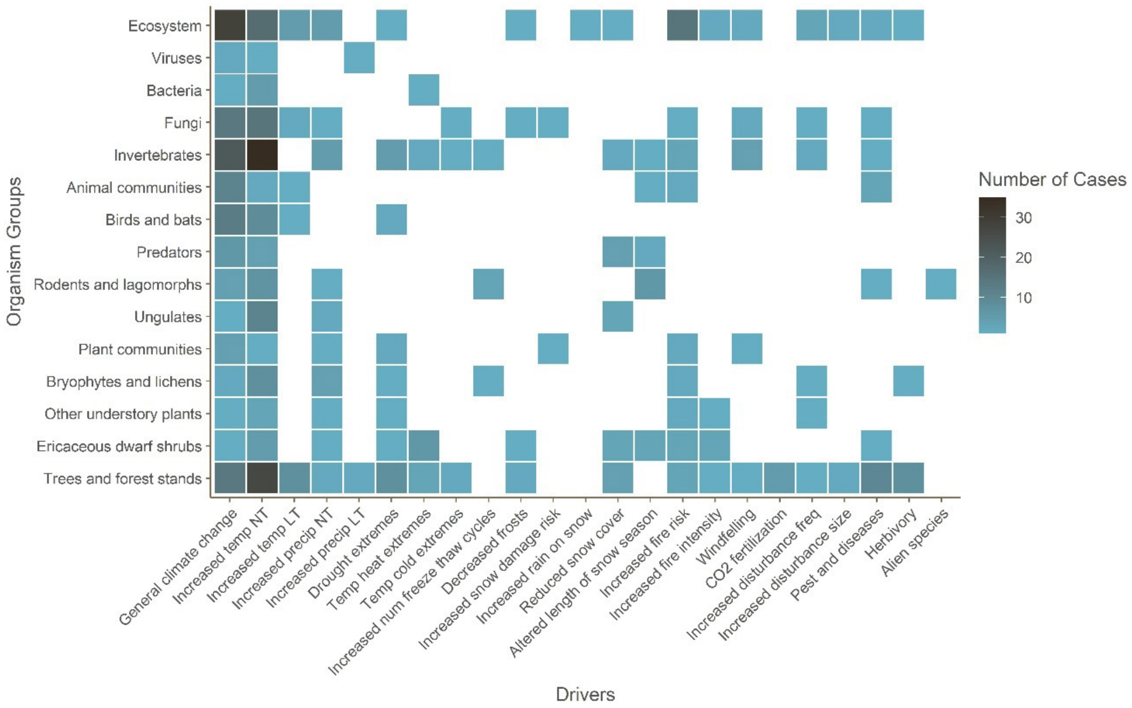


Figure 42. The body of evidence in this report, given as the number of cases from the literature in which a relationship between a specific climate change related driver and the response of a specific organismal group was recorded. The drives include climatic changes and climate change-related disturbances and biotic factors, as reported in the literature. Note that each cell may include information on a broad range of response types of the organismal group to the specific driver (such as changes in growth, demographic rates, biodiversity, or functioning), and that the total cases per cell includes both positive, negative, and neutral response of the particular organismal group to the specific driver. A scientific paper may include information on one or more driver-response cases. Empty cells (or low number of cases) are indicative of knowledge gaps in the reviewed literature. Temp" = temperature. "precip" = Precipitation, "NT" = Near-term changes (until year 2050). "LT" = long-term changes (until year 2100). Interacting drivers were not explicitly included.

7 Relation to the IPCC Sixth Assessment Report (2021-2022)

The United Nations Intergovernmental Panel on Climate Change (IPCC)'s Sixth Assessment Report (AR6) consists of studies by three Working Groups (WG) reporting on the following topics:

- The Physical Science Basis (WGI) -published 2021
- Impacts, Adaptation and Vulnerability (WGII) -published February and March 2022
- Mitigation of Climate Change (WGIII) -to be published late 2022.

WGI of AR6 was published in time to be integrated into this report, and is therefore referred to where relevant in the chapters dealing with the physical science of climate change. Note that the AR6 introduces the Shared Socioeconomic Pathway (SSP) as a nomenclature for future scenarios of greenhouse gas emissions. It is a more flexible system for inclusion of socioeconomic effects and feedbacks, and meant to replace the Representative Concentration Pathway (RCP) system introduced by the AR5 in 2014. However, practically all available studies and data are based on the RCP scenarios, meaning we still refer to the RCP scenarios throughout. For a rough conversion, consider RCP8.5 as encapsulated by SSP5.8.5, and RCP4.5 by SSP2.4.5.

WGII was published just as this report was being finalized, not in time to be incorporated but in time to be assessed for consistency. While the IPCC assessments deal with global warming levels (GLWs) and regional effects on coarser scales than is the focus of this report, they ultimately build on the same body of published research. As independent selections from the same literature the findings should be consistent. Thus, the main findings of AR6 WGII most relevant for Norwegian forests are summarized below and their consistency with the results (Chapter 4) of this report is addressed. The AR6 WGII has been summarized verbatim to the extent practicable.

WGIII is not yet published and so will not be addressed further here.

7.1 Summary of IPCC AR6 WGII relevant for climate change on current boreal forests

7.1.1 Summary of large-scale changes by end of 2021

The polar regions are experiencing impacts from climate change at magnitudes and rates that are among the highest in the world, and will become profoundly different in the near-term future (by 2050) under all warming scenarios. In the Arctic, accelerated sea-ice loss, increased permafrost thaw and extreme high temperatures have substantially impacted marine, freshwater and terrestrial sociological-ecological systems. Multiple physical, ecological and societal elements of polar regions are approaching a level of change potentially irreversible for hundreds of years, if not millennia. Evidence of borealization of terrestrial and marine systems is emerging, and cascading impacts are on-going and widespread yet challenging to quantify fully due to complexity and lags in ecological expression of change. Warming substantially exceeding the global average has already been observed for the northern parts of the temperate and boreal zone and is projected to continue.

<u>Consistency:</u> Some of the more dramatic changes at high latitudes have been increasingly evident since the Hanssen-Baue report of 2015. But they were expected, and we have drawn on enough updated climate data (including AR6 WGI) for this to be incorporated in our assessment, both for forests north of the Arctic circle, and regarding leading-edge borealization of current arctic (tundra) biomes.

Changes that are detected in boreal forests and consistent with, but not formally attributed to climate change, include increased wildfire in Siberia, long-lasting smoldering belowground fires in Canada and the United States, tree mortality in Europe, and post fire shifts of boreal conifer to deciduous broadleaf tree species in Alaska. In the tundra and boreal forest, where wildfire has naturally been infrequent, burned area showed statistically significant increases of ~50% year^{-1} across Siberia, Russia, from 1996 to 2015 and 2% year^{-1} across Canada from 1959 to 2015. Wildfire burned ~ 6% of the area of four extensive Arctic permafrost regions in Alaska, USA, eastern Canada, and Siberia from 1999 to 2014. In boreal forest in the Northwest Territories, Canada, and Alaska, USA, the area burned by wildfire increased at a statistically significant rate of 6.8% year^{-1} in the period 1975-2015, with smoldering belowground fires that lasted through the winter covering ~1% of burned area in the period 2002-2016. While burned area was correlated to temperature and reduced precipitation in Siberia and to lightning, correlated with temperature and precipitation in the Northwest Territories and Alaska, no attribution analyses have examined relative influences of climate and non-climate factors.

Consistency: We find the increased wildfire tendencies associated with warm summers to be reflected in Norwegian data and find reason to believe, like most studies, that Norwegian fire impact will increase, though likely less than in the Siberian boreal forest.

From 1930 to 1960, boreal forest growth became limited more by precipitation than temperature.

Consistency: While we did no formal comparison of effect strength for Norway, and heat still plays a role for growth in Scandinavia, the pattern of increasing relative water impact seems consistent.

7.1.2 Observed effects on forest vital rates and ranges by end of 2021

Since the publication of AR5 in 2014, more studies confirm rapid changes in Arctic terrestrial and freshwater systems including increased permafrost thaw, changes to tundra hydrology and vegetation (overall greening of the tundra, regional browning of tundra and boreal forests), coastal and riverbank erosion. Biome shifts and structural changes within ecosystems have been detected at an increasing number of locations, including upward shifts in the forest/alpine tundra ecotone, northward shifts in the deciduous/boreal forest ecotones, increased woody vegetation in sub-Arctic tundra. Climate change continues to alter vegetation and attendant biodiversity, with divergent regional trends across the Arctic due to disparities in local conditions and changes in growing seasons. Warming facilitates woody vegetation growth in northeastern Siberia, western Alaska, and northern Quebec, as well as a northward expansion of shrub vegetation and sub-Arctic and boreal species. Plants display more stable distributions at low rather than at higher mountain altitudes. Microclimatic variability in some locations can buffer warming impacts.

Consistency: While no areas of Norway have still been designated as having gone through a biome shift, changes in species composition along ecotones, a rising treeline and so on are reported. We have not reported generic stability differences over altitudes, and note that microclimates may buffer but also be vulnerable to warming impacts.

Across Europe, rates of tree mortality in field inventories from 2000 to 2012 were highest in Spain, Bulgaria, Sweden, and Finland, positively correlated to maximum winter temperature and inversely correlated to spring precipitation. Tree mortality in Austria, the Czech Republic, Germany, Poland, Slovakia, and Switzerland doubled from 1984 to 2016, correlated to intensified logging and increased temperatures.

Consistency: The same studies of tree mortality underlie our projections for the future as the climate zones currently experiencing increased mortality of spruce starts including Norway.

7.1.3 Observed effects on interactions, phenology, cycles and communities by end of 2021

Observed changes impact structure, functioning and resilience of ecosystems, and ecosystem services such as climate regulation. Degrading vegetation survival, habitat for biodiversity, water supplies, carbon sequestration, and other key aspects of the integrity of ecosystems and their ability to provide services for people. In western North America, increasing temperatures have allowed bark beetles to move further north and higher in elevation, survive through the winter at sites where they would previously have died, and reproduce more often.

Consistency: This overview is consistent with effects discussed here. The northward expansion of the outbreak range of geometrid moths in northern Norway with devastating impacts on the northern boreal birch forests represents an analogue to the North American bark beetle case.

In western North America, some insects that were previously innocuous have become important agents of tree mortality.

Consistency: This has not yet been seen in Norway to the best of our knowledge, but the future possibility been mentioned here

Pests insect infestations related to higher temperatures have caused extensive mortality of Norway spruce across nine European countries. Forest insect pests have expanded northward, and severity and outbreak extent has increased in northern North America and northern Eurasia, due to warmer winters reducing insect mortality and longer growing seasons favouring more generations per year. Increases in forest insect pests have contributed to tree mortality and changes in carbon dynamics in temperate and boreal forest areas.

Consistency: Similar effects on spruce have not yet been observed in Norway, but is much discussed and found to be a likely future consequence here too. However, the northwards outbreak range expansion of geometrid moth in northern Norway, concurrently with increasing temperature in this region, has caused large-scale mortality of birch stands, abrupt shifts in understorey vegetation and cascading food web impacts.

Declines in pollinator ranges in response to climate are occurring for many groups in Europe, with observed shifts to higher elevations of southern and lower elevation in northern species resulting in higher pollinator richness in Northern Europe. Lags in responses to climate change suggest current impacts on pollination have not been fully realized.

Consistency: Pollinator decreases are observed and discussed here too. The effect of lags (climate debts) are discussed for many groups and systems as a whole.

The timing of many processes, including spring leaf unfolding and autumn senescence and flight dates changed in response to changes in seasonal temperatures, water and light availability (very high confidence), resulting e.g. in earlier arrival dates for many birds and butterflies. Greatest growing season lengthening in plants has been detected in Western, Northern and Eastern Europe, but shortening in parts of Southern Europe driven by later senescence, increasing population growth for butterflies and moths and birds, and residence time for migrant birds.

Consistency: These effects on phenology are all discussed in this report, except bird residency time which was not discussed specifically by us.

European temperate and boreal forests, wetlands and peatlands hold important carbon stocks. Effects of warming and increasing droughts on soil moisture, respiration and carbon sequestration have been detected across European regions. CO_2 has increased net primary productivity and caused substantial changes to temperate and boreal forest ecosystems, including biome shifts and increases in wildfire, insect pest outbreaks, and tree mortality, all at a global mean surface temperature increase of 0.9º C above the pre-industrial period.

Consistency: This summary reflects effects discussed in this report, though we did not initially elaborate the point that all the changes observed so far have not only occurred at less than one degree of warming, they are not all yet realized due to response lags.

7.1.4 Medium confidence or unattributed

Interacting with climate change are non-climatic hazards, such as habitat loss and fragmentation, over-exploitation, water abstraction, nutrient enrichment, and pollution, all of which reduce resilience of biotas and ecosystems (very high confidence). Peatlands in NEU and EEU and other historically important cultural landscapes in Europe are overexploited for forestry, agriculture, and peat mining. Forests in WCE were impacted by the extreme heat and drought event of 2018, with effects lasting into 2019 and losses in conifer timber sales in Europe. Northward shifts of tree species distributions are documented in Northwestern

Europe but not consistently detected. Vegetation changes detected but found to be more caused by land use and land management changes than climate change include upslope and poleward forest shifts in Europe following abandonment of timber harvesting or livestock grazing, changes in wildfire in Europe affected by fire suppression, fire prevention, and agricultural abandonment, and forest species composition changes in Scotland due to nitrogen deposition from air pollution, as well as boreal and temperate forest area increases likely caused by forest plantations and regrowth in Asia and Europe between 1982 and 2016 and in Canada between 1984 and 2015. Pollinators are also declining due to lack of suitable habitat, pollution, pesticides, pathogens and competing invasive alien species.

Consistency: This summary is consistent with this report.

Extirpation, e.g. local losses of species, have been observed in response to climate change in Europe. Strong climate-induced declines have been detected in thermosensitive taxa, including many freshwater groups, insects, amphibians, reptiles and birds. The loss of native species, especially specialized taxa, is changing biodiversity; however overall biodiversity could remain stable because losses may be compensated by range shifts of native and the establishment of non-native species.

Consistency: This summary is consistent with this report, though we do problematize the biodiversity aspects for forests in greater detail and with regards to species identity, not just number of species.

7.1.5 Projected effects on forest vital rates

Risks for terrestrial ecosystems will increase with warming with high impacts at > 2.4ºC GWL and very high impacts > 3.5ºC GWL. Land use changes will increase extirpation and extinction risk. In Northern Europe, biodiversity vulnerability is projected to be lower than in Southern Europe, as new climate and habitat space is becoming available. Warming < 1.5ºC GWL might limit risks to biodiversity, while 4ºC GWL and intensive land use may lead to a loss of suitable climate and habitat space for most species. There is a high agreement between observations and projections of tree death in temperate and boreal forests, with current projections indicating this trend will continue.

Consistency: This summary is consistent with this report, except we do not point out specific levels of warming for risk delineation. We do however find that warming is expected to have largely positive effects on spruce growth and demographic rates in colder parts of Norway where it has available nutrients and water within ca. 1.5 ºC warming, but negative effects over increasingly large areas dominating beyond 2 ºC.

Temperate and boreal forests possess greater diversity of physiological traits related to plant hydraulics, so they are more buffered against drought than tropical forests. Nevertheless, in temperate forests, drought-induced tree mortality under RCP8.5 could cause the loss of half of northern hemisphere conifer forest area by 2100. In the western United States, one-tenth of forest area is highly vulnerable to drought-induced mortality under RCP8.5 by 2050.

Consistency: This summary is consistent with this report, except we indicate loss of biome rather than loss of conifer trees, as that is what we have data for, and it is unclear how the Norwegian landscape will interplay with forestry and conifer physiology to allow persistence despite climate debt.

7.1.6 Projected effects on range shifts and communities

As a consequence, boreal tree species are expected to move northwards (or upwards) into regions dominated by tundra, unless constrained by edaphic features, and temperate species are projected to grow in regions currently occupied by southern boreal forest. In both biomes, deciduous trees are simulated to increasingly grow in regions currently dominated by conifers. These simulation results have been supported by observational examples. Climate change increases risks of biome shifts on up to <15% for <2ºC warming and to <35% of global land at ≥4ºC warming. Changes in distribution are projected for major tree species in all European regions at 1.7°C GWL, with economic implications for managed forests. The longer growth season in Northern and Western Europe will support the establishment of invasive species.

AR6 attributes to anthropogenic climate change observed changes in upslope and poleward boreal and temperate biome shifts at sites in Asia, Europe, and North America, range shifts of plants; earlier blooming and leafing of plants; poleward shifts in tree-feeding insects; increases in insect pest outbreaks; and thawing of permafrost that underlies extensive areas of boreal forest. Under high warming scenarios, models indicate poleward shifts of boreal forest into treeless tundra across the Arctic, and upslope shifts of montane forests into alpine grassland.

In Arctic tundra, boreal forests, northern peatlands, including permafrost areas, climate change under scenarios of 4ºC temperature increase could triple burned area in Canada, double the number of fires in Finland, increase lightning-driven burned area 30 to 250%, push half of the area of tundra and boreal forest in Alaska above the burning threshold temperature, and double burned area in Alaska. Area at high risk of biome shifts from climate change and land use change combined can double or triple compared to climate change alone.

Novel ecosystems, with no historical analogue, are expected to become increasingly common in future.

Consistency: This summary is consistent with this report, except we do not quantify effects of land use change.

Risks emerging from climate change for phenology are uncertain, given asynchrony between species, taxa and trophic responses and the complexity of phenological events and their cues (medium confidence). Spring events may continue to occur earlier, but reduced chilling may decrease this temporal shift. Projections for autumn are mixed, with continuing delays or earlier onset of leaf senescence, but reduced chilling may also decrease these developments.

Consistency: This summary is consistent with this report.

Forest expansion in boreal regions results in net warming, possibly influencing cloud formation and rainfall patterns. These changes are affecting climate, pollination and soil protection services. If not managed through increased reforestation/revegetation or peatland restoration, future climate change impacts will progressively limit the climate regulation capacity of European terrestrial ecosystems, especially in Southern Europe. Predominantly positive CO_2 fertilization effects at current warming will change into increasingly negative effects of warming and drought on forests at higher temperatures. In Northern and Eastern Europe, peatlands are projected to shrink with 1.7°C GWL, and become carbon sources at 3°C GWL, peat bogs to lose 50% carbon at 2°C GWL, and blanket peatland to shrink or regionally disappear. Thawing of Arctic permafrost from a projected temperature of 4ºC and resulting wildfire could release 11-200 Gt carbon that could substantially exacerbate climate change.

Consistency: This summary is consistent with this report, notably with regards to effects of CO_2 *fertilization. However, we do not address peatlands specifically, as they are beyond the scope of this report.*

Projected climate impacts on pollinators show mixed responses across Europe, but are greater under >3°C GWL. Increasing homogenisation of populations may increase vulnerability to extreme events. Geographic changes to the climatic niche of pollinators are similar to insects, with mixed trends, depending on group and location. In Northern Europe, species richness may increase for some groups, with unclear trends for bumblebees. Future land use will have important effects on pollinator distribution as habitat fragmentation in densely populated Europe decreases opportunities for range shifts and micro climatic buffering.

<u>Consistency</u>: This summary is consistent with this report. We also discuss the potential role of microclimate buffering on topographically heterogeneous Norwegian landscape in facilitating upslope but slowing northward range shifts.

7.1.7 Resilience, robustness, and feedbacks

Some boreal forests have proven resilient to disturbances, including to recent unprecedented rates of insect attacks. Reforestation, either natural or anthropogenic, leads to summer cooling and winter warming of the ground, while forest thinning or removal by fire has the reverse effects and deepens the upper layer free of permafrost where it exists.

<u>Consistency</u>: This is consistent with this report except we do not discuss seasonal effects on permafrost dynamics due to its sparse occurrence in forested regions of Norway.

However, there is an increasing body of literature that has found continued, longer-term responses of ecosystems to climate change, so-called 'committed changes,' that arise from lags that exist in many systems. Many processes in ecosystems take more than a few decades to quasi-equilibrate to environmental changes. Therefore, trends of changing vegetation cover identified in simulations of transient warming continue to show up in simulations that hold climate change at low levels of warming. Such changes, which could tip ecosystems into an alternative state, could also be triggered by a 'warming overshoot' – if global warming were to exceed a certain threshold, even if mean temperatures afterwards decline again.

Even if warming achieved by 2100 remained constant after 2100, such committed responses continue to occur. In one study the opposite was found for boreal forest cover, which showed a strong committed increase. The committed changes in vegetation composition correspond to large committed changes in terrestrial carbon uptake and losses, and would plausibly also appear in other ecosystem functioning and services. These studies point to the importance of having not only a multi-decadal but also a multi-century perspective when exploring the impacts of political decisions on climate change mitigation taken now. Even if climate-warming targets are met, published evidence so far suggests that fundamental changes in some ecosystems are likely as these correspond to well-understood ecosystem physiological responses that trigger long-term changes in composition.

<u>Consistency</u>: Unfortunately, we have not been able to find sufficient literature to address this with respect to Norwegian forests specifically, and have not discussed the theoretical or general reasons for believing slow process time lags and tipping points between multiple stable states will be important in Norwegian forest and landscape dynamics. However, we

have no reason to believe we are somehow particularly exempt from this general picture and should perhaps have emphasized this more clearly.

Restoring natural fire regimes: Some natural ecosystems are adapted to burning, such as savannas and boreal forests. Where fire has been suppressed or non-native species of trees planted in more open habitats, there is a risk that potential fuel accumulates, which can result in larger and hotter fires. Solutions can include restoring natural fire regimes.

Consistency: This has not been mentioned as a potential mitigation strategy for Norway, as forest fires have been rare enough since establishment of the current boreal forest biome here that fire-driven ecologies here are of limited extent and thus probably of less relevance. With the expected increase in forest fires, maintaining a sufficient fire regime to allow local species to persist seems unlikely to be a problem in Norway.

Reforestation of formerly forested land can help to protect and recover biodiversity and can be one of the most practical and cost-effective ways of sequestering and storing carbon. It can also restore hydrological processes, improving water supply and quality and reducing risks of soil erosion and floods.

Consistency: This has not been mentioned to any particular degree as reforestation is the general practice already in Norway and no great deforested areas exist except where other forms of land use have taken over. However, should climate-driven disturbances open large areas of forest, assisted reforestation obviously needs to be considered.

Expanding the nature reserves would help species conservation; to facilitate species movements across climatic gradients, increase of landscape connectivity can be elaborated by setting up habitat corridors between nature reserves and along elevational and other climatic gradients. Assisted migration of species should be considered for isolated habitats as mountain summits or where movements are constrained by poor dispersal ability. Introducing seeds of the species to new regions will help to protect them from the extinction risk caused by climate change.

Consistency: This has not been mentioned in any great detail specifically, but is consistent with findings and is a question of strategies and priorities.

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9 Appendices

9.1 Appendix I

Net effects on the list of habitats summarized overall trends in the knowledge base emerging form literature searches

Table A1:

Overview of ecosystems and habitat types according to the Environment Agency's mapping guidelines (the English translation of EA mapping units is highly unofficial, as no official translation exists at present. It is thus only to give the English reader a qualitative idea of what is meant).

EA mapping units:

https://www.miljodirektoratet.no/ansvarsomrader/overvaking-arealplanlegging/naturkartlegging/naturtyper/

Corresponding NiN major ecosystem type (Halvorsen et al. 2020), https://www.biodiversity.no/Pages/135568/Red_List_for_Ecosystems_and?Key=1489754979

and Redlist status https://artsdatabanken.no/rodlistefornaturtyper?Key=1545304342

An assessment of climate effects for each type:

+/- Effects vary between individual species in the type, or between locations or over time in ways that makes the net effect unpredictable or ambiguous.

-/(+) Some species or locations of this nature type may see increasing abundance or distribution, but most effects seem likely to decrease ecological conditions and/or abundance of the nature type.

- The clear majority of climate change effects seem to be detrimental for the conditions and/or occurrence of this nature type.

-– This nature type seems particularly vulnerable to several major effects of climate change, with no realistic compensatory range shifts o.s.

English translation	EA mapping unit	Norwegian name	NiN major ecosystem type	Redlist status	Net	Particular climate change related effects
Boreal forest	NL	Skog	Forest (T4)	NL	-(-)	Major type. See in main text for effect summaries. In general these also apply to land cover types listed below.
Hollow oaks	C1	Hule eiker	NL	NL	-	Increased loss rate from windfellings and fires. Increased range, but centuries to establish and form.
Alluvial forest	C20	Flomskogsmark	Forest (T30)	VU	+/-	Increased precipitation, but also increased need for drainage and risk of flooding
Old low herb spruce forest	C10	Gammel lågurtgranskog	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Spruce disfavoured by climate.

Old pine forest	C11	Gammel furuskog (-)	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Spruce disfavoured by climate.
Old pine dominated natural forest	C11.1	Gammel furudominert naturskog	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Pine disfavoured by climate.
Old pine forest w. old trees	C11.2	Gammel furuskog med gamle trær	Forest (T4)	NL	- -	Old forests are subject to increased loss rates not balanced by regeneration rates. Pine disfavoured by climate. Fire vulnerable
Old pine forest w. fallen dead trees	C11.3	Gammel furuskog med liggende død ved	Forest (T4)	NL	-/(+)	Old habitat loss vs. regeneration imbalance. Transient effect of more dying trees. Pine disfavoured by climate. Fire vulnerable.

Old pine forest w. standing dead trees	C11.4	Gammel furuskog med stående død ved	Forest (T4)	NL	-/(+)	Old habitat loss vs. regeneration imbalance. Transient effect of more dying trees. Pine disfavoured by climate.
Old spruce forest	C12	Gammel granskog (-)	Forest (T4)	NL	- -	Old forests are subject to increased loss rates not balanced by regeneration rates. Spruce disfavoured by climate.
Old spruce dominated natural forest	C12.1	Gammel grandominert naturskog	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Spruce disfavoured by climate.
Old spruce forest w. old trees	C12.2	Gammel granskog med gamle trær	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Spruce disfavoured by climate. Fire vulnerable.

Old spruce forest w. fallen dead trees	C12.3	Gammel granskog med liggende død ved	Forest (T4)	NL	-/(+)	Old habitat loss vs. regeneration imbalance. Transient effect of more dying trees. Spruce disfavoured by climate.
Old spruce forest w. standing dead trees	C12.4	Gammel granskog med stående død ved	Forest (T4)	NL	-/(+)	Old habitat loss vs. regeneration imbalance. Transient effect of more dying trees. Spruce disfavoured by climate.
Old low herb willow-rowan forest	C13	Gammel lågurtselje-rogneskog	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates.
Old low herb aspen forest	C14	Gammel lågurtospeskog	Forest (T4)	NL	-	Old forests are subject to increased loss rates not balanced by regeneration rates.

Lime-rich birch forest	C15	Kalkbjørkeskog	Forest (T4)	NL	-/+	Birch competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Moist rich deciduous forest	C16	Frisk rik edellauvskog	Forest (T4)	NT	+/-	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Moist low herb deciduous forest	C16.1	Frisk lågurtedellauvskog	Forest (T4)	NT	+/-	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Moist lime-rich deciduous forest	C16.2	Frisk kalkedellauvskog	Forest (T4)	NT	+/-	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.

Low herb deciduous forest	C17	Lågurtedellauvskog	Forest (T4)	VU	-/(+)	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Low herb oak forest	C17.1	Lågurteikeskog	Forest (T4)	VU	+/-	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Low herb beech forest	C17.2	Lågurtbøkeskog	Forest (T4)	VU	+/-	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Low herb elm-linden-hazel forest	C17.3	Lågurtalm-lind-hasselskog	Forest (T4)	VU	-/(+)	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease

						likely more prevalent.
Lime-rich deciduous forest	C18	Kalkedellauvskog	Forest (T4)	EN	-/(+)	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Lime-rich linden forest	C18.1	Kalklindeskog	Forest (T4)	EN	+/-	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Lime-rich hazel forest	C18.2	Kalkhasselskog	Forest (T4)	EN	+/-	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.

Tall perennial deciduous broadleaf	C19	Høgstaude edelløvskog	Forest (T4)	VU	-/(+)	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Harvested forest	C2	Høstingsskog	Forest (T4)	NT	-/(+)	Decidious trees favored. Limited distribution vulnerable to disturbance. Elm disease likely more prevalent.
Old tall perennial grey alder forest	C21	Gammel høgstaudegråorskog	Forest (T4)	NT	-	Old forests are subject to increased loss rates not balanced by regeneration rates.
Old poor deciduous forest	C22	Gammel fattig edellauvskog	Forest (T4)	NT	-	Old forests are subject to increased loss rates not balanced by regeneration rates. Elm disease more prevalent.

Boreal rainforest	C3	Boreal regnskog	Forest (T4)	VU	-	Limited distribution, vulnerable to disturbance, no room for range shift
Boreonemoral rainforest	C4	Boreonemoral regnskog	Forest (T4)	VU– Vulnerable	-	Limited distribution, vulnerable to disturbance, no room for range shift
Lime-rich spruce forest	C5	Kalkgranskog	Forest (T4)	VU	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species.
Moist lime-rich spruce forest	C5.1	Frisk kalkgranskog	Forest (T4)	VU	-	Limited distribution, vulnerable to disturbance, disfavored habitat building species.
Moist lime-rich pine forest	C5.2	Frisk kalkfuruskog	Forest (T4)	VU	-	Limited distribution, vulnerable to disturbance, disfavored habitat building species.

Tall perennial spruce forest	C6	Høgstaudegranskog	Forest (T4)	NT	-	Limited distribution, vulnerable to disturbance, disfavored habitat building species.
Lime rich and herb pine forest	C7	Kalk- og lågurtfuruskog	Forest (T4)	VU	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species.
Low herb pine forest	C7.1	Lågurtfuruskog	Forest (T4)	VU	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species.
Chalk pine forest	C7.2	Kalkfuruskogn	Forest (T4)	VU	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species.

Drought exposed chalk spruce forest	C7.3	Tørkeutsatt kalkgranskog	Forest (T4)	VU	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species. Vulnerable to drought.
Rich sand pine forest	C8	Rik sandfuruskog	Forest (T4)	NT	- -	Limited distribution, vulnerable to disturbance, disfavored habitat building species. Vulnerable to drought.
Olivin forest	C9	Olivinskog	Forest (T4)	EN	-/(+)	Very limited distribution defined by geology, as such vulnerable to disturbance. Very vulnerable to drought.
Rich spruce marsh forest	E11.2	Rik gransumpskog	Wetlands (V2)	EN	-	Limited distribution, vulnerable to disturbance, disfavored habitat building species.

Rich alder marsh forest	E11.3	Rik svartorsumpskog	Wetlands (V2)	VU	-/+	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Springwater-deciduous forest	E11.4	Kilde-edellauvskog	Wetlands (V2)	VU	-/+	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.
Rich willow beach forest	E14.1	Rik vierstrandskog	Wetlands (V8)	VU	-/+	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.

Salt-impacted black alder beach forest	E14.3	Saltpåvirket svartorstrandskog	Wetlands (V8)	NT	+/-	Decidious trees competitively favored. Limited geological distribution suggest vulnerability to disturbance.

9.2 Appendix II

Search strategy for published literature

Two index databases were searched:

- Web of Science Core Collection on the Web of Science platform, consisting of the Science Expanded, Social Sciences, Arts and Humanities and Emerging Sources citation indices. The field Topic (TS) was used, which searches the Publication title, Abstract, Author keywords and Keywords Plus®.
- Biological Abstracts on the Web of Science platform. The field Topic was used, which searches in Title field, Foreign Title field, Abstract field, Major Concepts field, Concept Code(s) field, Taxonomic Data table, Disease Data table, Chemical Data table, Gene Name Data table, Sequence Data table, Geographic Data table, Geologic Time Data table, Methods and Equipment Data table, Parts and Structure Data table and Miscellaneous Descriptors field. This thus covers the major concepts, taxonomic and geographic subject headings the database.

As both databases are on the same platform, the same syntax was used for both (Table A1). The strategy aims to find publications containing search terms from three thematic elements: Forests/tree species of interest (searches 1-8, 14-21), climatic factors (searches 9-11) and ecological variables (search 12). The two forest searches are respectively to focus on research geographically close to Norway (searches 1-8) and on other regions of the world/boreal forests generally (searches 14-21). Elements from the search strategy of Savilaakso et al. (2021) were used in development of the forest search.

Sets #13 and #23 from each database were exported on 21/04/2021, resulting in an larixEndNote library of 23 527 items. A deduplication procedure based on Bramer et al. (2016) was carried out, after which 18 223 items remained. For reviews (export of sets #23 and #24, 23/04/2021), the total library consisted of 1890 items, of which 1432 remained after deduplication.

The set of 1432 reviews was screened for relevance by two reviewers independently, based on the titles and abstracts using Rayyan (www.rayyan.ai). After title and abstract screening, 523 reviews remained (83 of which were found through the search in Biological Abstracts but not Web of Science).

Table A1. Search strategy used in Web of Science and Biological Abstracts

	Search	Results in WoS	Results in Bio. Abs.	Notes
1	TS = (“forest*” OR “tree*” OR “taiga” OR “plantation$” OR “deciduous” OR “gymnosperm*”)	797 001	731 393	General forest/tree terms
2	TS = (“norway” OR “norwegian” OR “swed*” OR “finland” OR “finnish” OR “estonia*” OR “latvia*” OR “lithuania*” OR “european russia” OR “western russia” OR “nordic” OR “fennoscan*” OR “scandinavia*” OR “north* europ*”)	370 676	185 995	Countries/regions where most forest types /trees are of interest
3	#1 AND #2	28 014	26 793	
4	TS = (“boreal forest*” OR “montane forest*” OR “picea abies” OR “norway spruce” OR “european spruce” OR “betula pubescens” OR “pinus sylvestris” OR “scots pine” OR “larix” OR “larch” OR “fir” OR “abies” OR “sorbus” OR “populus” OR (“salix” AND “tree$”) OR ”conifer*”)	125 923	198 498	Forest types and species
5	TS = (“norway” OR “norwegian” OR “swed*” OR “finland” OR “finnish” OR “estonia*” OR “latvia*” OR “lithuania*” OR “european russia” OR “western russia” OR “nordic” OR “fennoscan*” OR “scandinavia*” OR “north* europ*” OR “slovakia*” OR “hungar*” OR “poland” OR “polish” OR “ukrain*” OR “czech republic” OR “romania*” OR “germany” OR “german” OR “switzerland” OR “austria” OR “austrian” OR “tatra mountain*”)	1 205 249	472 082	Countries where only certain forest types /species are of interest
6	#4 AND #5	24 118	26 529	
7	#3 OR #6	36 379	36 695	
8	#7 NOT TS = (“kelp forest*”)	36 319	36 648	Exclusion of marine forests
9	TS = (“climat*” OR ((“global” OR “anthropogen*”) NEAR/3 (“warm*” OR “heating”)) OR (“emissions” NEAR/5 “scenario*”) OR (“elevat*” NEAR/3 (“CO2” OR “carbon dioxide” OR “greenhouse gas*”))	651 366	474 097	Climate change terms

	OR ‟global change”)			
10	TS = (‟temperature*” OR ‟rain” OR ‟rainfall” OR ‟precipitation” OR ‟humidity” OR ‟snow” OR ‟subnival space*” OR ‟subnivean space*” OR ‟frost” OR ‟permafrost” OR ‟freeze thaw*” OR ‟wind” OR ‟winds” OR ‟flood*” OR ‟fire$” OR ‟wildfire*” OR ‟drought” OR ‟heatwave*” OR ‟heat wave*” OR ‟windstorm*” OR ‟storm$” OR ‟extreme weather” OR ‟arctic vortex” OR ‟atlantic gyre” OR ‟NAO index”)	4 380 887	1 394 917	Climate variable terms
11	#9 OR #10	4 715 357	1 640 803	
12	TS = (‟ecological condition*” OR ‟condition assessment*” OR ‟ecosystem condition typolog*” OR ((‟ecosystem*” OR ‟forest$” OR ‟landscape” OR ‟vegetation”) NEAR/5 (‟function*” OR ‟structure” OR ‟characteristic$” OR ‟management” OR ‟dynamic*” OR ‟model*” OR ‟connectivity” OR ‟complexity” OR ‟health”)) OR ‟MODIS” OR ‟SPOT vegetation” OR ‟PROBA V” OR ‟PROBA vegetation” OR ‟landsat” OR ‟resilience” OR ‟resilient” OR (‟climat*” NEAR/5 (‟sensitivity” OR ‟resistance” OR ‟toleran*”)) OR ‟population size*” OR ‟population structure” OR ‟population dynamic*” OR ‟colonisation” OR ‟colonization” OR ‟establishment rate$” OR ‟extinct*” OR ‟mortality” OR ‟survival” OR ‟reproduction” OR ‟propagation” OR ‟recruitment” OR ‟replacement rate” OR ‟species abundance*” OR ‟competition” OR ‟cone formation” OR ‟seed production” OR ‟seed crop$” OR ‟germination”	11 480 560	16 848 028	Ecological terms

	OR ((“tree” OR “natural*”) NEAR/3 “regenerat*”) OR “tree death” OR “dieback” OR “defoliation” OR “leaf toughness” OR ((“discoloration” OR “discolouration”) NEAR/3 “foliage”) OR (“nutrient” NEAR/3 “foliage”) OR “crown condition” OR “crown architecture” OR “vapour pressure deficit” OR “vapor pressure deficit” OR “windthrow” OR “growing conditions” OR “growth rate$” OR “annual growth” OR “tree growth” OR “photosynthetic capacity” OR “C/N ratio*” OR (“uptake” NEAR/3 (“nutrient*” OR “carbon” OR “nitrogen” OR “nitrate” OR “phosphorous”)) OR (“drought” NEAR/3 (“toleran*” OR “stress”)) OR (“stress” NEAR/5 (“factor*” OR “response*” OR “limit*”)) OR ((“ecophysiological” OR “physiological”) NEAR/5 (“response*” OR “limit*”)) OR “phenolog*” OR “seasonality” OR “dormant” OR “dormancy” OR “growing season*” OR “bud burst” OR “biomass” OR “primary produc*” OR “productivity” OR “canopy cover” OR “leaf area index” OR “NDVI” OR “vegetation index” OR (“forest” NEAR/3 “composition”) OR “old growth” OR “dead wood” OR “deadwood” OR “woody debris” OR “decompos*” OR “leaf litter” OR “plant litter” OR (“vegetation” NEAR/5 (“chang*” OR “composition” OR “shift$”)) OR “succession*” OR “disturbance” OR “gap formation” OR “state shift$” OR “insulari*” OR “fragmented” OR “fragmentation” OR ((“range” OR “ranges”) NEAR/3 (“expan*” OR “contract*” OR “limit” OR “limits” OR “shift*”))			

	OR ((“northern” OR “distribution”) NEAR/3 “limit$”) OR “timberline” OR “forest line” OR “treeline” OR ((“forest*” OR “stand”) NEAR/5 (“extent” OR “boundar*”)) OR (“landscape” NEAR/5 (“pattern*” OR “ecolog*” OR “charactertistic*”)) OR “species distribution*” OR “community effect*” OR “biological diversity” OR “biodiversity” OR ((“divers*” OR “composition” OR “richness”) NEAR/5 (“genetic” OR “species” OR “taxonomic” OR “function*” OR “communit*”)) OR “essential biodiversity variables” OR “threatened” OR “endangered” OR “red list*” OR “generalist*” OR “specialist*” OR “pioneer$” OR “habitat-forming species” OR “keystone species” OR “key species” OR “ecosystem engineer*” OR ((“species” OR “plant”) NEAR/5 (“invasive” OR “introduc*” OR “non-native” OR “non-indigenous” OR “alien” OR “exotic” OR “naturalised” OR “naturalized”)) OR “endemic$” OR “functional group*” OR “functional type*” OR “ground layer” OR “field layer” OR “vascular plant$” OR “bryophy*” OR “lichen*” OR “moss” OR “mosses” OR “ericaceae” OR “vaccinium” OR “pollinator*” OR “bees” OR “bee” OR “seed dispers*” OR “endophyte*” OR “trophic structure*” OR “trophic level*” OR “trophic network*” OR “food web*” OR “carnivore*” OR “predator*” OR “predation” OR “mesopredat*” OR “detritivor*” OR “saprotroph*” OR “saproxylic” OR “herbivor*” OR “frugivor*” OR “grazer*” OR “scavenger*”			

	OR ((“fauna$” OR “animal*” OR “avian” OR “mammalian”) NEAR/5 (“chang*” OR “composition” OR “abundance” OR “communit*” OR “diversity”)) OR “bird$” OR “woodpecker*” OR “picidae” OR “owl$” OR “grouse” OR “tetrao” OR “phasianidae” OR “nesting” OR “mammal$” OR “ungulate*” OR “deer” OR “rodent*” OR “amphibian*” OR ((“microbial” OR “microbe$” OR “bacteria*”) NEAR/5 (“activity” OR “composition” OR “abundance” OR “communit*” OR “diversity”)) OR “mycorrhiza*” OR “ectomycorrhiza*” OR “mycelia” OR “mycelium” OR “mycelial network*” OR “fungi” OR “fungal” OR “polypore$” OR “rhizosphere” OR “gadgil effect*” OR (“soil” NEAR/5 “respiration”) OR (“soil” NEAR/5 (“biota” OR “organism*” OR “microorganism*” OR “microbes” OR “microbial” OR “bacteria*” OR “animal*”)) OR “mesofauna*” OR “microfauna*” OR “insect*” OR “invertebrate*” OR “arthropod*” OR “microarthropod*” OR (“risk*” NEAR/5 (“abiotic” OR “biotic”)) OR “pest” OR “pests” OR “disease*” OR “pathogen*” OR “parasite*” OR “outbreak*” OR “bark beetle*” OR “Dendroctonus valens” OR “Ips typographus” OR “root rot” OR “Heterobasidion” OR “cytospora” OR “canker disease” OR “rhizosphaera” OR “needle cast” OR “blue stain fung*” OR “pine wood nematode*” OR “Bursaphelenchus xylophilus” OR “birch dieback disease” OR “Melanconium betulinum” OR “Anisogramma virgultorum” OR “Marssonina betulae” OR “dutch elm disease” OR “Pityogenes chalcographus” OR “Ophiostoma spp” OR “Autumnal moth” OR “Dendrolimus pini” OR “Lymantria monacha” OR “Bupalus piniaria” OR “Panolis flammea” OR “Diprion pini” OR “Hymenoscyphus fraxineus” OR “Ips ametinus” OR “Agrilus planipennis” OR “Monochamus spp” OR			

	“Sphaeropsis sapinea” OR “Ophiostoma novo-ulmi” OR “Diplodia sapinea” OR “chemical defence*” OR “chemical defense*” OR “phenolic compound*” OR “phenolics” OR “terpenes” OR “carbon based defence*” OR “carbon based defense*” OR “tannin*” OR “secondary metaboli*” OR “hydrology” OR (“soil$” NEAR/5 (“mineralisation” OR “mineralization” OR “nitrogen” OR “nitrate” OR “carbon” OR “phosphorous” OR “ph” OR “organic matter” OR “condition*” OR “propert*” OR “structure”)) OR “ellenberg” OR (“runoff” NEAR/5 (“carbon” OR “nitrogen” OR “phosphorous” OR “nutrient*”)) OR “nutrient cycl*” OR “nutrient flow” OR (“carbon” NEAR/3 (“cycl*” OR “flux” OR “sequest*” OR “storage”)) OR “ecosystem carbon” OR “methane cycl*”)			
#13	#8 AND #11 AND #12	10 947	11 303	Sets exported
#14	TS = (“taiga”)	2 916	3 638	General forest/tree terms
#15	TS = (“forest*” OR “tree*” OR “plantation$”)	784 863	671 962	General forest/tree terms
#16	TS = (“boreal” OR “subboreal” OR “hemiboreal” OR “boreonemoral” OR “canada*” OR “canadian” OR “russia*” OR “siberia*”)	564 123	279 513	Countries/zones/forest types of interest
#17	#15 AND #16	39 922	39 699	
#18	TS = (“picea abies” OR “norway spruce” OR “european spruce” OR “betula pubescens” OR “pinus sylvestris” OR “scots pine” OR “larix” OR “larch” OR “fir” OR “abies” OR “sorbus” OR “populus” OR (“salix” AND “tree$”) OR “conifer*” OR “deciduous” OR “gymnosperm*”)	138 279	224 888	Trees

#19	TS = (“boreal” OR “subboreal” OR “hemiboreal” OR “boreonemoral” OR “canada” OR “canadian” OR “russia*” OR “siberia*” OR “montane” OR “high elevation”)	580 255	295 551	Countries/zones/forest types of interest
#20	#18 AND #19	15 945	24 556	
#21	#14 OR #17 OR #20	45 310	48 303	
#22	#11 AND #12 AND #21	19 376	17 910	
#23	#11 AND #12 AND #21 **Refined by: DOCUMENT TYPES:** (REVIEW) [Web of Science] #11 AND #12 AND #21 **Refined by: LITERATURE TYPES:** (LITERATURE REVIEW) [Biological Abstracts]	890	388	Sets exported
#24	#13 **Refined by: DOCUMENT TYPES:** (REVIEW) [Web of Science] #13 **Refined by: LITERATURE TYPES:** (LITERATURE REVIEW) [Biological Abstracts]	424	188	Sets exported

Search strategy for reports

Supplementary sources were searched in April 2021. The total number of results found by the searches is reported below. Search results were scanned for relevant titles and abstracts.

Norwegian reports and grey literature

Google Scholar was used for a broad Norwegian search. The following search string was used, with ca. 3420 results:

klimaendring|klimaendringer skog|trær|taiga|tajga|gran|bjørk|furu|lerk|rogn|osp|selje

The first 100 results were screened to find relevant works, which were added to the literature set.

Search of relevant institutional archives was also done via their Brage repositories. In these archives, search options are relatively limited, and precision is reduced by search terms found in the full text. For this reason, search strategies varied slightly between archives, and for some, only a certain number of results pages were examined under the assumption that the most relevant results are higher in the list.

Archives of Norwegian Institute for Nature Research (NINA) was searched at https://brage.nina.no. The whole collection was searched with the following options:

- Search 1 (30 results)
    - Keywords: *climat* (forest* OR tree* OR taiga OR spruce OR birch OR pine OR larches OR rowan OR popular OR willow)*
    - Filters: Type contains *report;* Language contains *eng*
- Search 2 (222 results)
    - Keywords: *klima* (skog* OR barskog OR lauvskog OR løvskog OR trær OR taiga OR gran OR bjørk OR furu OR lerk OR rogn OR osp OR selje)*
    - Filters: Type contains *report*

Archives of the Center for International Climate and Environmental Research (CICERO) were searched at https://pub.cicero.oslo.no/. The whole collection was searched with the following options:

- Search 1 (218 results)
    - Keywords: *climat* (forest* OR tree* OR taiga OR spruce OR birch OR pine OR larches OR rowan OR popular OR willow)*
    - Filters: Type contains *report*
- Search 2 (62 results)
    - Keywords: *klima* (skog* OR barskog OR lauvskog OR løvskog OR trær OR taiga OR gran OR bjørk OR furu OR lerk OR rogn OR osp OR selje)*
    - Filters: Type contains *report*

Archives of Norwegian Institute for Bioeconomics (NIBIO) were searched at https://nibio.brage.unit.no. The whole collection was searched with the following options:

- Search 1 (17 results)
    - Keywords: *skog* OR barskog OR lauvskog OR løvskog OR trær OR taiga OR gran OR bjørk OR furu OR lerk OR rogn OR osp OR selje*
    - Filters: Type contains *report;* Title contains *klima*
- Search 2 (53 results)

    - Filters: Type contains *report;* Title contains *skog*
- Search 3 (1687 results)
    - Keywords: *klima* (skog* OR barskog OR lauvskog OR løvskog OR trær OR taiga OR gran OR bjørk OR furu OR lerk OR rogn OR osp OR selje)*
    - Filters: Type contains *report*
- Search 4 (148 results)
    - Keywords: *climat* (forest OR forests OR tree* OR taiga OR spruce OR birch OR pine OR larches OR rowan OR popular OR willow)*
    - Filters: Type contains *report;* Language contains *eng*

Swedish and Finnish reports

Archives of the Swedish Forest Agency (Skogsstyrelsen) were browsed year by year:

- Reports 2021: https://www.skogsstyrelsen.se/om-oss/rapporter-bocker-och-broschyrer/
- Reports 2020: https://www.skogsstyrelsen.se/om-oss/rapporter-bocker-och-broschyrer/rapporter-2020/
- Reports 2019: https://www.skogsstyrelsen.se/om-oss/rapporter-bocker-och-broschyrer/rapporter-2019/
- Reports 2018: https://www.skogsstyrelsen.se/om-oss/rapporter-bocker-och-broschyrer/rapporter-2018/
- Reports 2017: https://www.skogsstyrelsen.se/om-oss/rapporter-bocker-och-broschyrer/rapporter-2017-och-tidigare/
- Reports 2016 and earlier: https://shop.skogsstyrelsen.se/sv/publikationer/

Archives of Natural Resources Institute Finland (Luonnonvarakeskus) were searched via the organisation's repository Jukuri, at www.luke.fi/en/publications-archive. This includes publications archived from the Finnish Forest Research Institute (Metla), which was integrated in 2015.

- Search 1 (44 results)
    - Search coverage: Whole repository

    - Keywords: *climat* (forest* OR tree* OR taiga OR spruce OR birch OR pine OR larches OR rowan OR popular OR willow)*
    - Filters: Language contains *eng*; Publisher contains *Finnish;* Journal Not contains *Silva fennica*

The filters were added to limit found publications to English, and to grey literature published by the Finnish Forest Research Institute and the Finnish Society of Forest Science. Silva Fennica was removed as this journal is covered by the Web of Science literature search.

Canadian Forest Service reports:

To find reports from the Canadian Forest Service, a search was carried out using the advanced search functions on the website of "Natural Resources Canada" at https://cfs.nrcan.gc.ca/publications/advanced. All monographs were searched, while series were filtered to find those linked to research rather than public information. All series containing the words "report" or "research" were included, as well as those pertaining to the themes of this report.

- Search 1 (106 results)
    - Keywords: *climat**
    - Publication type: *monographs*
- Search 2 (130 results)
    - Keywords: *climat**
    - Publication type: *series;* Series: All containing the following were selected: *Informational Report, Internal report, Technical Report, File Report, Interim Research Report, Joint Report, Forestry Report, Forestry Technical Report, COFRDA Report, FRDA Report, USDA General Technical Report, FIDS Report, Rapport RIMA, Forest Health Pest Report, Miscellaneous Report, Multigraphed Report and Leaflet, Research Notes, Bi-monthly-Research Note, CFS Research Notes, Exotic Forest Pest Advisory, Frontline Policy Perspective, Department of Forestry Publication, Mountain Pine Beetle Working Paper, R&D Technical Note, NODA/NFP Document, Science-Policy Notes, Working Paper, State of Canada's Forests, Pest Forum, Forest Health and Biodiversity News, CCFM Criteria and Indicators, Sustainable Forest Management Network Research Notes, Canadian National Vegetation Classification, Remote Sensing in Canada.*

9.3 Appendix III

The 38 forest-associated species on the Norwegian Red List for Species for which climate change is a specified threat. Caegories: CR, critically endangered; EN, Endangered; VU, vulnerable; NT, near threatened. (**https://www.biodiversity.no/Pages/135380/Norwegian_Red_List_for_Species**) **.**

Group	Scientific name	Category 2021	pos/neg climate	Primary threats to populations
Mosses	*Anastrophyllum joergensenii*	EN	negative	land use change, climate change
Mosses	*Brachydontium trichodes*	EN	negative	watershed management, climate change
Mosses	*Isopterygiopsis alpicola*	EN	negative	Current and future climate change
Mosses	*Anastrophyllum donnianum*	VU	negative	land use change, climate change
Mosses	*Tayloria acuminata*	VU	negative	habitat loss
Mosses	*Buxbaumia viridis*	NT	negative	forest management, climate change
Mosses	*Hymenoloma compactum*	NT	negative	Current and future climate change
Vascular plants	*Cystopteris sudetica*	EN	negative	forest management, climate change
Vascular plants	*Cassiope tetragona*	VU	negative	Intraspecific competition; climate change

Vascular plants	*Rhododendron lapponicum*	VU	negative	Intraspecific competition; climate change
Vascular plants	*Dryas octopetala*	NT	negative	Intraspecific competition; climate change
Vascular plants	*Luzula parviflora*	NT	negative	Intraspecific competition; climate change
Vascular plants	*Pulsatilla vernalis*	NT	negative	forest management, climate change
Lichens	*Peltigera retifoveata*	CR	negative	firewood extraction; removal old or hollow trees
Lichens	*Heterodermia speciosa*	EN	negative	forest management, land use changes, other human activities, climate change
Fungi	*Helvella hyperborea*	NT	negative	forest management
Fungi	*Mycena latifolia*	NT	negative	land use changes, invasive species
Fungi	*Rhodoscypha ovilla*	NT	negative	forest management, watershed management
Spiders	*Arctobius agelenoides*	VU	negative	forest management, climate change

Spiders	*Aculepeira lapponica*	NT	negative	habitat loss, climate change
Spiders	*Zelotes puritanus*	NT	postiive?	land use changes, climate change (could be favourable)
Beetles	*Altica brevicollis*	NT	negative	forest management, land use changes
Beetles	*Crepidodera lamina*	NT	positive?	loss of habitat, but milder climate is favorable
Flies	*Brachycampta triangularis*	EN	positive	Future climste change affects on broadleaf forests
Flies	*Coelosynapha loici*	EN	negative	Future climate change; recreation, tourism
Bees, wasps	*Bombus distinguendus*	EN	negative	land use changes, invasive species, climate change
Bees, wasps	*Polistes biglumis*	EN	postiive?	increased habitat area?
Birds	*Anser fabalis*	EN	negative	many factors including climate change
Birds	*Bubo bubo*	EN	negative	Land use changes
Birds	*Emberiza pusilla*	VU	negative	loss of habitat, also climate change

Birds	*Melanitta nigra*	VU	negative	many factors including climate change
Birds	*Apus apus*	NT	negative	forest management, climate change affects on prey
Birds	*Cuculus canorus*	NT	negative	Land use changes; climate change affecting prey
Birds	*Lullula arborea*	NT	positive?	loss of habitat, but milder climate is favorable
Birds	*Pernis apivorus*	NT	negative	climate change affecting prey; forest management
Birds	*Tringa totanus*	NT	negative	loss of habitat, also climate change
Mammals	*Eptesicus nilssonii*	VU	negative	forest managemenet, land use changes, other human activities
Mammals	*Lepus timidus*	NT	negative	climate change; predation; hunting; iinvasive species