Title: Future supply of boreal forest ecosystem services is driven by management rather than by climate change.

Running title: Future supply of forest ecosystem services

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Abstract

Forests provide a wide variety of ecosystem services (ES) to society. The boreal biome is experiencing the highest rates of warming on the planet and increasing demand for forest products. To foresee how to maximize the adaptation of boreal forests to future warmer conditions and growing demands of forest products, we need a better understanding of the relative importance of forest management and climate change on the supply of ecosystem services. Here, using Finland as a boreal forest case study, we assessed the potential supply of a wide range of ES (timber, bilberry, cowberry, mushrooms, carbon storage, scenic beauty, species habitat availability and deadwood) given seven management regimes and four climate change scenarios. We used the forest simulator SIMO to project forest dynamics for 100 years into the future (2016-2116) and estimate the potential supply of each service using published models. Then, we tested the relative importance of management and climate change as drivers of the future supply of these services using generalized linear mixed models. Our results show that the effects of management on the future supply of these ES were, on average, eleven times higher than the effects of climate change across all services, but greatly differed among them (from 0.53 to 24 times higher for timber and cowberry, respectively). Notably, the importance of these drivers substantially differed among biogeographical zones within the boreal biome. The effects of climate change were 1.6 times higher in northern Finland than in southern Finland, whereas the effects of management were the opposite – they were three times higher in the south compared to the north. We conclude that new guidelines for adapting forests to global change should account for regional differences and the variation in the effects of climate change and management on different forest ES.

Keywords: biodiversity; ecological modelling; Fennoscandia; Finland; forest dynamics; silviculture; SIMO forest growth simulator.

1 | INTRODUCTION

Forests provide crucial ecosystem services (ES) for society including timber, non-wood forest products (e.g., wild berries), recreation opportunities, regulation of water, soil and air quality, and climate change mitigation (Brockerhoff et al., 2017). Boreal forests represent the largest terrestrial biome (Hansen et al., 2010); they constitute around 45% of the world's stock of growing timber (Gerasimov et al., 2012), store about one-third of the global terrestrial carbon (Moen et al., 2014; Pan et al., 2011) and, despite low tree species diversity, provide habitats for a wide range of species such as saproxylic fungi and beetle species (Siitonen, 2001). The levels of ES supplied by boreal forests are highly dynamic, changing in space and over short-term periods (Snäll et al., 2021). These dynamics result from variation in both environmental conditions (e.g., climate) and management actions. Thus, a better understanding of how climate change and management will drive the future supply of ES is critical in securing high multifunctionality in boreal forests.

Forest management plays an important role in the supply of ES (e.g., Eyvindson et al., 2018; Mina et al., 2017; Morán-Ordóñez et al., 2020; Pukkala, 2016; Schwenk et al., 2012). There is no single management regime that maximizes the supply of all services simultaneously, as there are trade-offs between them (e.g., Gutsch et al., 2018; Sing et al., 2018). For example, the most severe trade-offs are found between timber production and other services (e.g., Duncker et al., 2012), such as carbon storage, bilberry and biodiversity (Pohjanmies et al., 2017). To enhance multifunctionality in boreal forests while achieving different policy and environmental targets, recent studies have highlighted the need of diversifying management alternatives across the landscape (Duflot et al., 2022; Triviño et al., 2017) and increasing the share of management regimes that are beneficial for multiple objectives simultaneously (e.g., increase the share of continuous cover forestry which maintains a multi-layered structure created by harvesting individual large trees periodically) (Blattert et al., 2022; Eggers et al., 2020; Eyvindson et al., 2021).

Climate change will strongly affect forest ecosystems during the next centuries by altering the growth, mortality and reproduction of trees (Dyderski et al., 2018; Seidl et al., 2014). Boreal forests will be particularly affected by climate change (Chen & Luo, 2015; Sánchez-Pinillos et al., 2022; Venäläinen et al., 2020) because they are expected to experience the largest increase of temperature of all forest biomes, with increases from 4°C to 11°C (Gauthier et al., 2015). On one hand, rising atmospheric CO_2 associated with climate change has a positive but uncertain effect on forest productivity and growth, although these positive trends might be transitional (D'Orangeville et al., 2018). On the other hand, rising temperature and vapor pressure deficit have mostly negative effects on forest demographic rates, but may have positive effects in cold and wet regions such as the boreal zone (McDowell et al., 2020). Moreover, several studies suggest negative impacts of climate change on the provisioning of non-wood forest ES (Breshears et al., 2011; Elkin et al., 2013; Lindner et al., 2014; Mazziotta et al., 2022) and on the biodiversity these ecosystems host (e.g., Mazziotta et al., 2015; Virkkala, 2016). In boreal forests, the impact of climate change on ES depends on the specific service, as increasing temperatures have been projected to increase harvest- and carbon-related services but decrease some cultural services such as winter sports (Holmberg et al. 2019).

Assessing the future supply of ES is crucial for promoting forest adaptation to climate change and identifying how to maximize provisioning, regulating and cultural ES as well as biodiversity under novel climatic conditions (e.g., Kellomäki, 2017). We need a better understanding of the relative importance of forest management and climate change on the future supply of ES and maintenance of biodiversity, and whether this relative importance is consistent across biogeographical zones. Several studies have investigated the joint impacts of both drivers on such supply in temperate (Gutsch et al., 2018; Thrippleton et al., 2021), mountainous (Albrich et al., 2018; Mina et al., 2017; Seidl et al., 2019) and Mediterranean forests (Morán-Ordóñez et al., 2020; Roces-Díaz et al., 2021). However, the relative importance of management regimes and climate scenarios on the future supply of a wide range of boreal ES have, to our knowledge, not been investigated.

Here, using Finland as a boreal forest case study, we first assessed the future supply of a wide range of ES using simulations of forest development. Then, we tested the relative importance of management and climate change as drivers of the future supply of these services using generalized linear mixed models. Specifically, we address the following questions: (i) How will the potential supply of ES change under different management and climate scenarios? (ii) What is the relative importance of forest management versus climate change on this potential supply? and (iii) Is the relative importance of these two drivers consistent across biogeographical zones within the boreal biome? We expect that a diversified forest management planning which includes a larger share of less intensive management regimes (i.e., no thinnings) will increase the potential future supply of non-timber ES and biodiversity (e.g., Sing et al., 2018; Triviño et al., 2017), whereas the effects of climate change will have both positive and negative effects on the supply of ES (Holmberg et al., 2019). We also expect that forest management plays a more important role than the direct effects of climate change in the potential supply of forest ES, as shown in forests in other biogeographical regions (e.g., Gutsch et al., 2018; Morán-Ordóñez et al., 2020). Finally, we expect that the importance of climate change will increase towards north as the most drastic changes are projected for higher latitudes (Ruosteenoja et al., 2016).

2 | METHODS

2.1. | Data, management regimes and simulations

Finland is the most forested country in Europe and the boreal zone (UNEP FAO and UNFF, 2009), with a forest cover of around 86% of the land area, mostly under commercial management (Vaahtera et al., 2021). Moreover, the northeastern part of Finland hosts a significant proportion of the primary forests of Europe (Sabatini et al., 2018). Finnish boreal forests are composed of approximately 50% Scots pine (*Pinus sylvestris*), 30% Norway spruce (*Picea abies*), 17% birch (*Betula pendula* and *Betula pubescens*) and 3% other broadleaved trees (Vaahtera et al., 2021). Finland is divided into four biogeographical zones; most of its area is part of the boreal zone (subdivided in south, middle and north boreal subzones) and the south coastal area belongs to the hemiboreal subzone of the temperate zone (Ahti et al., 1968) (Figure 1).

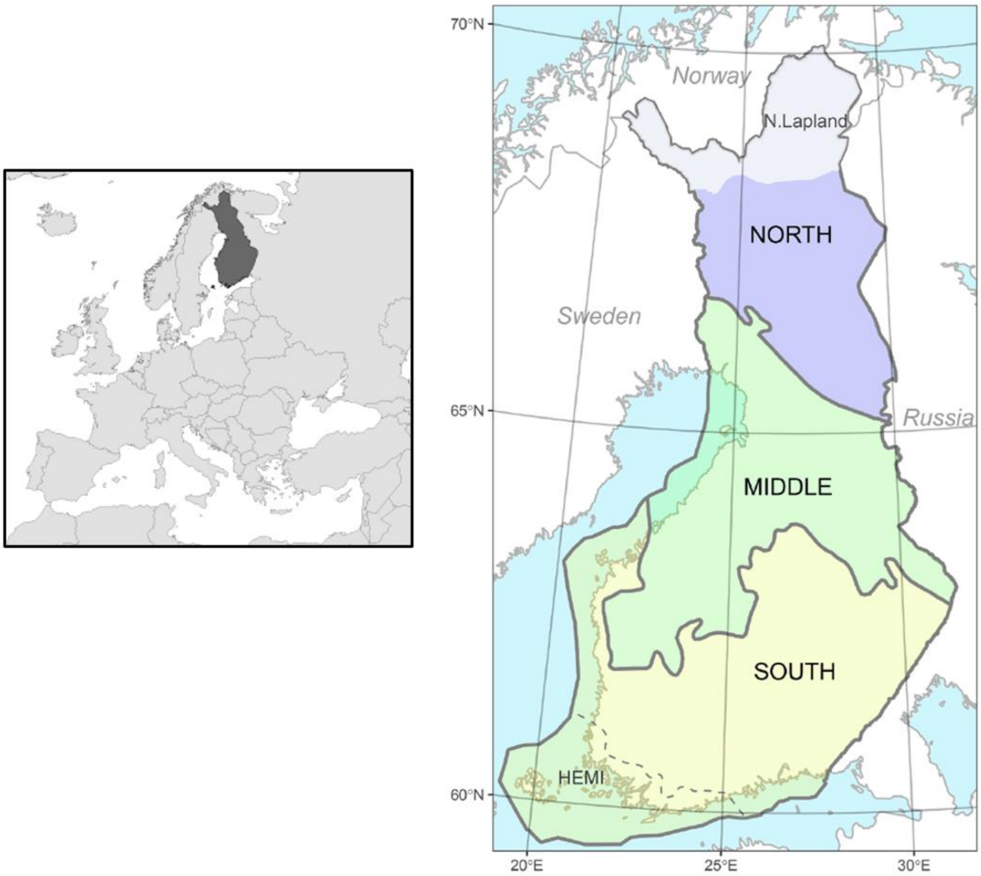

Figure 1. Location of Finland within Europe and the biogeographical zones in Finland (source SYKE open-data service).

We used a systematic sample of the Finnish Multi-Source National Forest Inventory (MS-NFI) (Mäkisara et al., 2019) as starting conditions for our simulations of forest dynamics and management over the course of one century (2016-2116). The MS-NFI data is based on satellite images, digital maps and NFI field data. The MS-NFI provides raster layers for the whole country on a large number of forest variables at a pixel resolution of 16 m, e.g., volume of the main tree species or site type, and is openly available from the National Resources Institute Finland (Luke) (http://kartta.luke.fi/opendata/valinta-en.html) (Figure 2). The MS-NFI raster layers were sampled along a systematic inventory grid following the design of the sampling scheme of the 11^{th} National Forest Inventory (NFI) which varies for different regions of Finland (for further details see http://www.metla.fi/ohjelma/vmi/vmi11-otanta-en.htm and Supporting Information Appendix S1). When a NFI plot centre overlap with a MS-NFI pixel cell, this cell was selected and treated as an individual forest plot in the simulations. In total, 52,015 forest plots representing different proportions of the country were selected for our analyses. We made this selection to accurately represent the Finnish forest conditions while keeping a reasonable computational time.

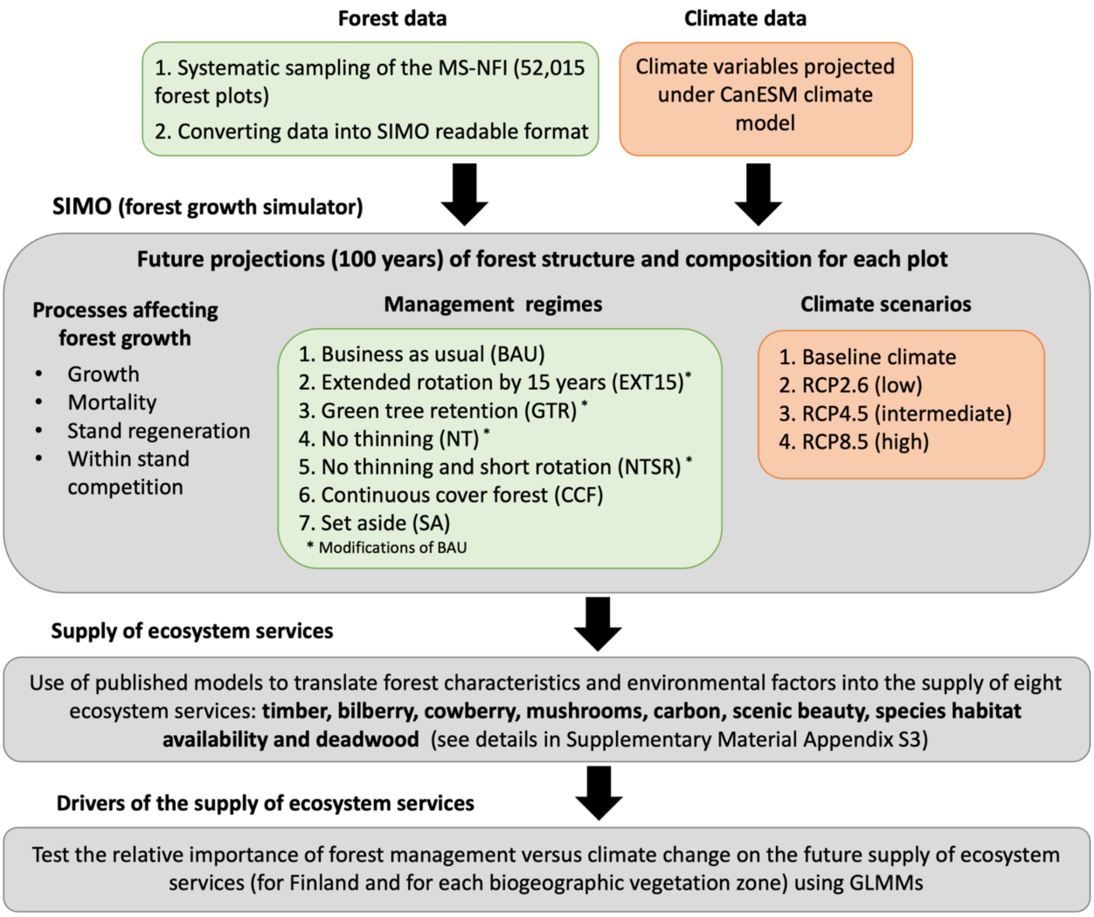

Figure 2. Flow chart showing the simulation and modelling approach used in this study.

We simulated forest development using the open-source forest simulator SIMO (Rasinmäki et al., 2009). The modelling framework in SIMO consists of over 400 equations to simulate tree growth, mortality, regeneration and within stand competition for even-aged (Hynynen et al., 2002) and uneven-aged boreal forests (Pukkala et al., 2013). Among other processes, SIMO simulates the survival and mortality of trees as a function of tree competition (which is calculated independently of the individual trees' location) and ageing. SIMO is an individual tree-based, stand-level simulator based on empirical data. The input data for SIMO contain basic environmental information (e.g., altitude, geographical location, climatic variables such as mean temperature, mean precipitation, and CO_2 concentrations) and detailed information about the forest structure and composition of each forest plot (e.g., volume of the different tree species, age, mean diameter, mean height, and basal area) (see Supporting Information Appendix S1 for further details). The impact of climate variables on forest growth dynamics in SIMO was based on climate-sensitive statistical growth and yield models. These models by means of species-specific transfer functions describe the increase in stem volume growth of trees as a function of increasing temperatures and CO_2 concentrations (Matala et al., 2005, 2006).

We simulated forest dynamics for 100 years into the future (2016-2116), separated in 5-years sequences. This 100-year simulation allows the full rotation length of the standard, even-aged forestry. Each forest plot was simulated under 28 alternative scenarios that resulted from combination of seven management regimes and the climate change scenarios.

For each forest plot, we simulated up to seven management regimes: rotation forestry with final clear cut as business as usual (*BAU*) following the official Finnish forest management recommendations for rotation forestry, which tend to favor actions that lead to monospecific forests (Äijälä et al., 2014); four regimes that represent modifications of BAU; continuous cover forestry aiming for uneven-aged and more diversely structured forests; and set aside with no management actions (see Table 1 for further details). Management is based on decision rules which depend on site type, height of the dominant tree species and age of the forest stand. For BAU, a final clear cut is conducted when the dominant tree height is larger than 14-16 meters and the age is 70-90 years. After the final clear cut, the stand is prepared and artificially regenerated (either by planting or seedling trees) (Äijälä et al., 2014). The four modifications of BAU represent alternatives that seek to enhance forest multifunctionality as they either increase the size of the trees or promote a more natural self-thinning mortality of trees, with consequent higher accumulation of deadwood. For example, no thinning regimes (NT and NTSR) are expected to improve the habitat of species dependent on deadwood and dense forests (Tikkanen et al., 2012). The specific set and total number of simulated regimes for each forest plot depended on the initial conditions and characteristics of the plot. For example, forest plots with reduced growth may not meet the threshold conditions of some of the management regimes, resulting in fewer applied management regimes than plots with high wood productivity. Forest management is not allowed in protected areas, so these were excluded from our analyses.

Table 1. Description of simulated forest management (adapted from Mönkkönen et al. (2014) and Eyvindson et al. (2018)).

Management regime	Acronym	Description
Business as usual	BAU	Even-aged rotation forestry with final clear cut; 1–3 thinnings; final clear cut with green tree retention level 10 trees/ha (Äijälä et al. 2014).
Extended rotation by 15 years	EXT15	BAU with postponed final clear cut by 15 years.
Green tree retention	GTR	BAU with 30 green trees retained/ha at final clear cut.
No thinning	NT	BAU without thinnings; trees grow slower due to increased competition and final clear cut is often later than with thinnings.
No thinning with short rotation	NTSR	BAU without thinnings and final clear cut done 20 years earlier.
Continuous cover forestry	CCF	Large trees are periodically removed (thinnings from above using basal area threshold of 16–22 m^2/ha). The minimal time between thinnings is 15 years. No final clear cut (Pukkala et al., 2013).
Set aside	SA	No management actions.

Regarding the four climate change scenarios, we considered a baseline climate scenario (which assumes that the mean climatic conditions for the period 1996-2014 will be held constant over the 100-year simulation period), and three alternative greenhouse forcing scenarios, termed Representative Concentration Pathways (RCPs): RCP2.6, RCP4.5 and RCP8.5. In Finland, the annual mean temperature is projected to increase by 1.9, 3.3 and 5.6°C by the 2080s under the RCP2.6, RCP4.5 and RCP8.5 scenarios, respectively, compared to the reference period of 1996-2014 (Ruosteenoja et al., 2016; Venäläinen et al., 2020). The mean annual precipitation is expected to increase by 6%, 11% and 18% under these RCPs by the 2080s, respectively. The changes are projected to be larger during the winter than during the summer months. During the potential growing season (April-September), the mean temperature is expected to rise by about 1-5°C and precipitation by 5%-11%, depending on the RCP scenario (Ruosteenoja et al., 2016).

For this study, we selected the climate variables driving forest growth and decomposition dynamics for mineral soils (using Yasso07 model): mean and amplitude of temperature, CO_2 concentration and precipitation. The climate variables were downscaled to a 0.2° X 0.1° longitude-latitude grid by a quantile-quantile type bias correction algorithm for temperature (Räisänen & Räty, 2013) and parametric quantile mapping for precipitation (Räty et al., 2014). Gridded harmonized meteorological data by Aalto et al. (2013) were used. For the baseline climate scenario, we used 5-years mean values over the period 1996-2014 (Lehtonen et al., 2016), and for the three future climate change scenarios (RCP2.6, RCP4.5 and RCP8.5) we used 5-years mean values from one General Circulation Model, the Canadian Earth system model CanESM2 (Von Salzen et al., 2013). Initially, we considered and compared data from five global circulation models (GCMs): CanESM2, CNRM-CM5, GFDL-CM3, HadGEM2-ES and MIROC5, sourced from the fifth phase of the Coupled Model Intercomparison Project (CMIP5; Meehl et al., 2009; Taylor et al., 2012) for whole of Finland (Supporting Information Appendix S2). Then, we focused only on CanESM2 as the differences among GCMs were very small and we preferred to reduce the complexity of the analyses (Supporting Information Appendix S2).

2.2. | Ecosystem services

We estimated the potential of Finnish boreal forests to provide a wide range of forest ecosystem services (including provisioning, regulating and cultural ones) that are relevant in Finland (Saastamoinen et al., 2014): (i) timber; (ii) bilberry; (iii) cowberry; (iv) mushrooms; (v) carbon storage; (vi) scenic beauty; (vii) habitat availability for key vertebrate species; (viii) deadwood (Table 2; Supporting Information Appendix S3). We used already published models (see Table 2; Supporting Information Appendix S3) to link the potential supply of forest services to the forest's structural characteristics and environmental factors, as projected by SIMO under the 28 scenarios resulting from the combination of forest management regimes and climate change scenarios (Figure 2).

The most important provisioning service, from an economic perspective, is timber harvest. The forest sector generated 9 billion euros in 2018 which represented 4.5% of the Finnish gross domestic product Vaahtera et al., 2021). We calculated the total amount of harvested log and pulp timber extracted during thinnings and final harvesting (m^3 ha^{-1}). Forests play a significant role in the Finnish way of life, and the enjoyment of forest's benefits by citizens is supported by the traditional everyman's right which allows picking wild berries and mushrooms or hiking even in private forests. The wild berry and mushroom yields harvested from Finnish forests annually can reach tens of millions of kilos annually (Saastamoinen et al., 2014). Here, we used output data from the SIMO projections (e.g., site type, dominating tree species, stand age, stand basal area; Table 2) constituting explanatory variables in the models to predict the yields (kg ha^{-1}) of three forest collectables goods: bilberry (*Vaccinium myrtillus*) (Miina et al., 2009, 2016), cowberry (*Vaccinium vitis-idaea*) (Miina et al., 2016; Turtiainen et al., 2013), and marketed mushrooms (including *Boletus edulis*, *Lactarius spp*. among others) (Tahvanainen et al., 2016).

Table 2. Ecosystem services studied. See Supporting Information Appendix S3 for detailed information of each service.

Ecosystem service	Description	Most relevant predictors	Units	Type	References
Timber	Extracted log and pulp wood during thinnings and final harvesting	Stand basal area, stand age, site type	$m^3\ ha^{-1}$	Provisioning ES	Rasinmäki et al. (2009)
Bilberry	Yield of bilberry (*Vaccinium myrtillus*)	Site type, dominating tree species, regeneration method, altitude, stand age, and stand basal area	$kg\ ha^{-1}$	Provisioning & Cultural ES	Miina et al. (2009, 2016)
Cowberry	Yield of cowberry (*Vaccinium vitis-idaea*)	Site type, dominating tree species, temperature sum, altitude, stand age, and stand basal area	$kg\ ha^{-1}$	Provisioning & Cultural ES	Turtiainen et al. (2013); Miina et al. (2016)
Mushroom	Yield of marketed mushrooms	E.g., for cep are stand basal area and stand age	$kg\ ha^{-1}$	Provisioning & Cultural ES	Tahvanainen et al. (2016)
Carbon storage	Carbon in biomass Carbon in mineral soils (Yasso07 model) Carbon in peatlands	Stand age and tree species composition Litter fall, temperature, and precipitation	$m^3\ ha^{-1}$	Regulating ES	Lehtonen et al. (2004) Liski et al. (2005); Tuomi et al. (2009; 2011) Ojanen et al. (2014)
Scenic beauty	An index based on forest age, density and tree species composition	Stand age, stem density and tree size and species composition	ha^{-1}	Cultural ES	Pukkala et al. (1988, 1995)
Habitat availability	An index combining the habitat suitability models of six indicator vertebrate species	Stand age and tree species composition	ha^{-1} (range 0-1)	Biodiversity indicator	Mönkkönen et al. (2014)
Deadwood	Volume of 5 categories of deadwood	Stand age and tree species composition	$m^3\ ha^{-1}$	Biodiversity indicator	Mäkinen et al. (2006)

We assessed climate regulation as the total amount of carbon stored within forest biomass and soil (m^3 ha^{-1}). The carbon stored within forest biomass includes living wood, dead wood, extracted timber and the residuals left after harvesting. Soil carbon was evaluated using two models. For mineral soils, we use the Yasso07 model (Liski et al., 2005; Tuomi et al., 2009, 2011), and for peatland soils were the carbon flux models by Ojanen et al. (2014). Almost all Finns (96%) engage in some form of recreational outdoor activities, mostly in forests (Sievänen & Neuvonen, 2011), which have well-known effects on the physical and mental health and wellbeing of people (Wolf et al., 2020). The cultural or aesthetic value of the forest was estimated using an index (ha^{-1}, no unit) which assess the scenic beauty of forests based on their structural characteristics such as stand age, number of stems per area and tree size and species composition according to previous studies from Pukkala et al. (1988, 1995).

As biodiversity indicators, we used a measure of species habitat availability (habitat suitability index) and deadwood volume. The habitat suitability index (ha^{-1}, no unit) combines the habitat availability of six key vertebrate species of boreal forests: capercaillie (*Tetrao urogallus*), flying squirrel (*Pteromys volans*), hazel grouse (*Bonasia bonasa*), long-tailed tit (*Aegithalos caudatus*), lesser-spotted woodpecker (*Dendrocopos minor*) and three-toed woodpecker (*Picoides tridactylus*). These species were selected to represent a wide range of habitat types as well as social and economic values including game birds, umbrella and threatened species. The models included in the habitat suitability index were taken from Mönkkönen et al. (2014) and were based on literature and expert opinion about the habitat requirements of the focal species. Deadwood is a critical resource in boreal forests (Stokland et al., 2012) and an indicator of forest biodiversity (Lassauce et al., 2011). Intensive forestry in Fennoscandia has decreased the amount of deadwood to a small fraction of its pristine levels (Siitonen, 2001). Thus, the amount of deadwood is considerably higher in natural old-growth forests than in managed production forests.

2.3. | Estimate of the potential future forest attributes and supply of ES

We first analyzed the projected changes over time of different forest attributes related to forest structure and composition and for each combination of climate and forest management scenario. The selected attributes represent some of the most relevant predictors of the different ES (Table 2).

To estimate the potential supply of the ES, we calculated their cumulative supply after the 100-year time horizon (values were summed up over all simulation years and averaged across all forest plots in the study area and by biogeographical regions – see details further below) for each service under each management regime and climate change scenario. We also estimated the relative performance of the different management regimes by comparing the supply values of each service under each management regime with their corresponding values in unmanaged forests (*set aside*, SA), irrespectively of the climate scenario (see Supporting Information Table S1). In the case of harvested timber, we estimated the relative performance of the different management regimes in terms of service provision, by comparing with *no thinning*, as the later regime provided the least amount of timber (see Supporting Information Table S2) and since the value of harvested timber under *set aside* was zero.

Similarly, we compared the potential supply of each service under each climate change scenario with their corresponding values under the *baseline* scenario. For example, for bilberry under scenario RCP8.5, we divided the cumulative bilberry yield (kg ha-^{1}) under RCP8.5 by the yield (kg ha^{-1}) under the *baseline* scenario (133/141 = 0.94) (see Supporting Information Table S3). Next, we calculated the relative change as 0.94 – 1 = -0.06.

2.4. | Drivers' contribution to the future supply of ES

We tested for differences in the effects of forest management and climate scenarios on the potential supply of the ES using Generalized Linear Mixed Models (GLMMs) (Bolker et al., 2009). We fitted one model for each response variable, represented by the cumulative value of each service at the end of the 100-year simulation period. The fixed predictors were the management regimes (BAU: business as usual; EXT15: extended rotation (15 years); GTR: green tree retention; NT: no thinning; NTSR: no thinning with short rotation; CCF: continuous cover forest; SA: set aside, Table 1) and the climate scenarios (baseline climate; RCP2.6; RCP4.5; RCP8.5). We included the identity of the forest plot as a random effect to account for the spatial pseudoreplication of the data. We assumed that each response variable followed a gamma distribution and used a log-link function. We followed the protocol recommended by Zuur et al. (2009) to assess the variance contribution of both random and fixed effects; we compared a full model including the two fixed predictors with a 'null' model with no predictors (but random factor) using the AIC score (Burnham & Anderson, 2002). We used two coefficients of determination R^2 (ranging from 0 to 1): (i) the marginal $R^2_{\text{GLMM(m)}}$ to measure the variance explained by the fixed effects of the GLMMs and (ii) the conditional $R^2_{\text{GLMM(c)}}$ to measure the variance explained by both the fixed and random effects (Johnson, 2014; Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013). Following the methodology in Morán-Ordóñez et al. (2020), we quantified the relative effect of each fixed predictor on each response variable based on the estimate of the associated regression coefficient, conditional on the estimates of the random-effect variances. We fitted the GLMMs using the glmer function of the ‘lme4’ R package (Bates et al., 2015), and we calculated the R^2 estimators using the r.squaredGLMM function of the ‘MuMIn’ R package (Barton, 2019). We carried out all the statistical analyses using R software version 4.1.1 (R Core Team, 2021).

We also tested whether the relative contribution of management and climate on the potential supply of the ES differed among the biogeographical zones of Finland: hemiboreal, southern boreal, middle boreal and northern boreal (Figure 1). For this testing, we fitted GLMMs separately for different biogeographical zones, with the exception that hemiboreal zone was combined with the southern boreal zone (Figure 1).

To compare the effects of forest management and climate change on the potential supply of ES, we first calculated the mean among the GLMMs coefficient estimates associated with each management and climate variable. Then, we divided this mean for the management effects by the mean for climate effects. This quantified how many times higher or smaller (if less than one) were the effects of management versus the effects of climate change, across all services.

3 | RESULTS

3.1. | Future trajectories of key forest characteristics

Business as usual (BAU) and its four variations (extended rotation by 15 years, green tree retention, no thinning and no thinning with short rotation) favored spruce as this will be the tree species planted after clear-cut if the soil type allows. Thus, under these management regimes, spruce will become dominant by the end of the 100-year period (Figure 3 and Supporting Information Figure S2). The highest forest age was projected under set aside and continuous cover forestry (CCF). We found that CCF was the regime projected to promote the largest increased share of deciduous tree species followed by set aside. Set aside and no thinning regimes (NTSR and NT) promoted higher basal areas. The highest stem density was projected under continuous cover forestry (CCF) (over 1.5 times larger than under the other management scenarios) (Figure 3 and Supporting Information Figure S2).

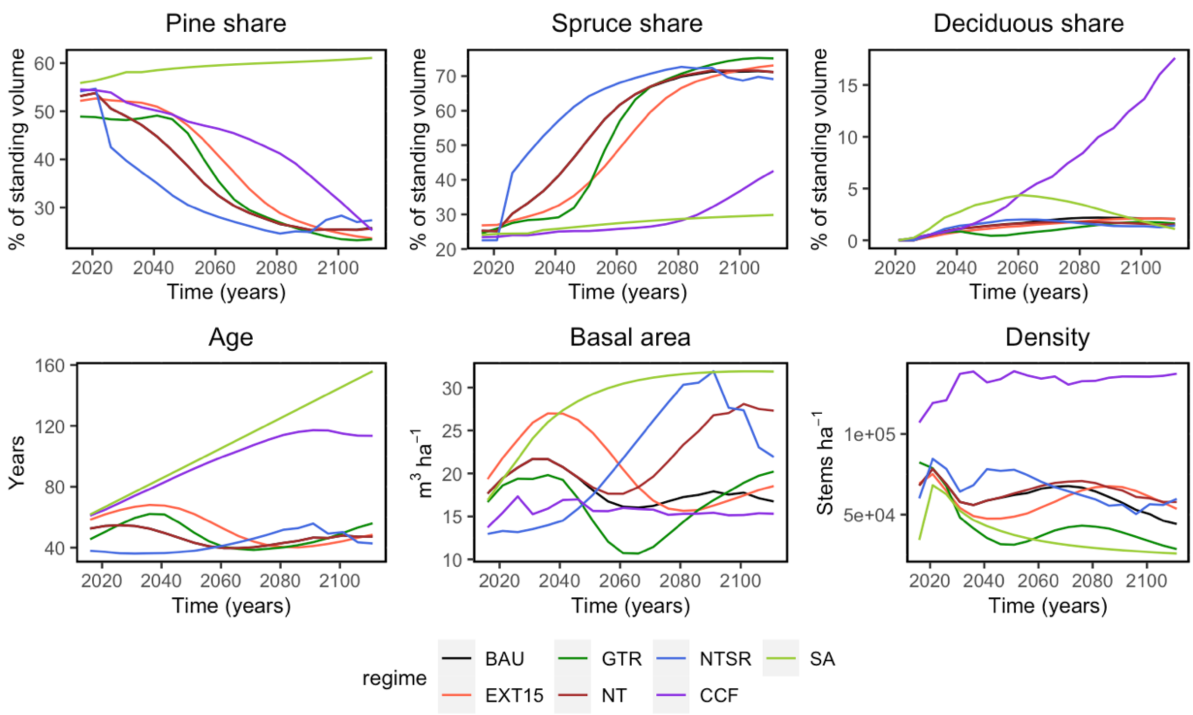

Figure 3. Temporal trajectories in selected forest characteristics - which represent changes in forest composition and structure - under the baseline climate scenario. The lines represent the mean value of each characteristic for every 5-year period. Lines colours indicates the different management regimes (legend at the bottom): BAU: business as usual; EXT15: 15 years extended rotation; GTR: green tree retention; NT: no thinning; NTSR: no thinning with short rotation; CCF: continuous cover forest and SA: set aside. Temporal trajectories under all climate change scenarios are represented in Supporting Information Figure S2.

3.2. | How will the potential supply of ES change under different management and climate scenarios?

By the end of the 100-year simulation, the potential supply for half of the assessed services (carbon storage, scenic beauty, habitat availability for key forest species and deadwood), was higher under set aside (SA) than for the rest of the management regimes (Figure 4, Supporting Information Table S2). Continuous cover forestry (CCF) provided the highest potential supply values for harvested timber and bilberry, whereas the regime no thinning with short rotation (NTSR) projected the highest values for cowberry and commercial mushrooms. We found that no thinning with short rotation (NTSR) provided the lowest values for bilberry and deadwood (Figure 4, Supporting Information Table S2).

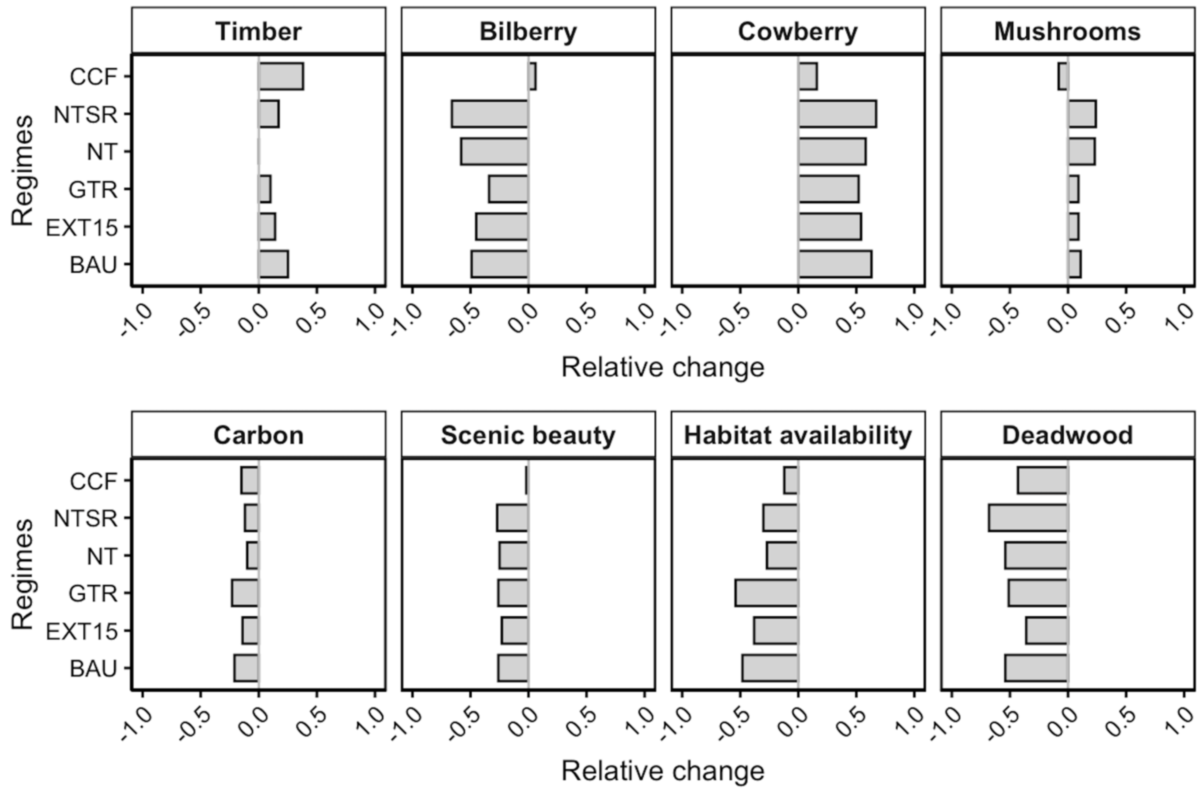

Figure 4. Relative change for each ecosystem service's supply values under different management regimes (BAU: business as usual; EXT15: 15 years extended rotation; GTR: green tree retention; NT: no thinning; NTSR: no thinning with short rotation; CCF: continuous cover forest). The bars represent relative supply values compared to the *set aside*, except for timber where the reference regime is *no thinning*, represented with a vertical grey line in each plot. For each service we calculated their cumulative supply after the 100-year period (values were summed up over all simulation years and averaged across all forest plots in the study area).

The potential supply of ES was quite stable across the different climate scenarios (Figure 5, Supporting Information Table S3). Projections suggested that the potential supply of six out of eight services (timber, mushrooms, carbon storage, scenic beauty, habitat availability for key forest species and deadwood) will increase under climate change compared to the baseline scenario. The most extreme climate change scenario (high-end; RCP8.5) projected the highest supply values for all services, except for bilberry and cowberry for which this scenario projected the lowest supply values (Figure 5, Supporting Information Table S3).

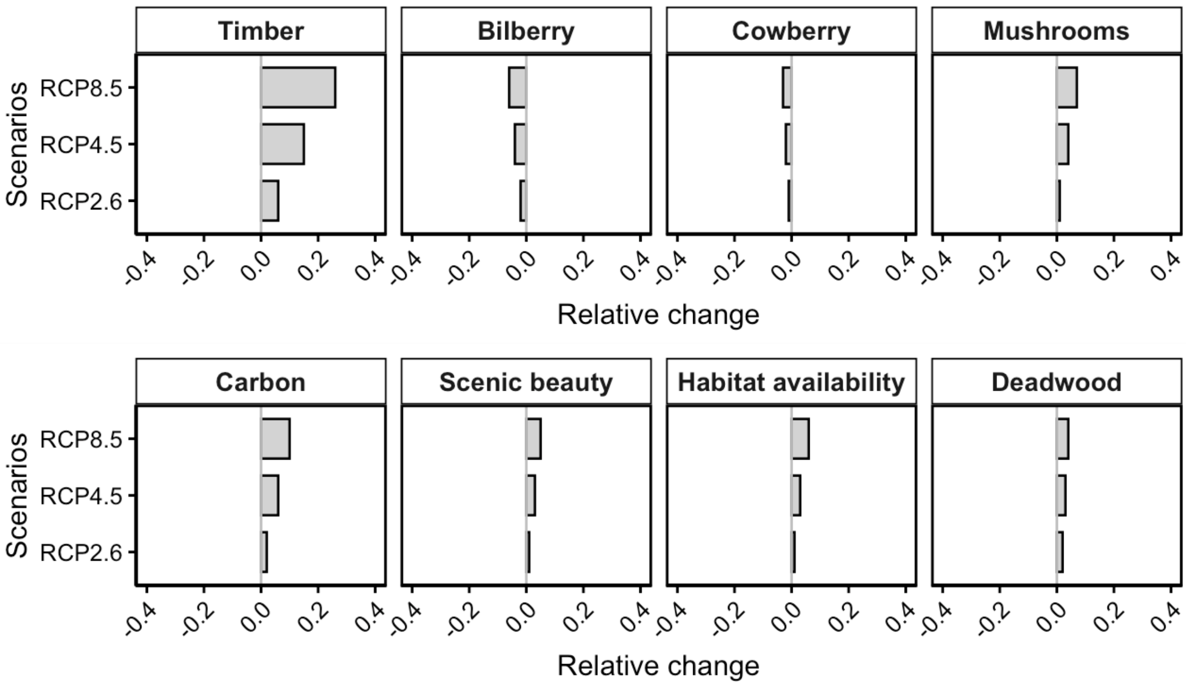

Figure 5. Relative change for each ecosystem service's supply values under different climate scenarios. The bars represent relative supply values compared to the *baseline* climate scenario, represented with a vertical grey line in each plot. For each service we calculated their cumulative supply after the 100-year period (values were summed up over all simulation years and averaged across all forest plots in the study area).

3.3. | What drives the future supply of ES?

The variation in the future potential supply explained by forest management regimes and climate change in relation to set aside and baseline climate, respectively, ranged between 18% and 47% depending on the studied ecosystem service (Supporting Information Table S4).

Forest management was the most important driver explaining the future supply of the evaluated services (quantified by standardized coefficient estimates, see Supporting Information Figure S1 and Table S5). The effect of management was on average eleven times larger than the effect of climate change across all services but differed greatly between them — ranging from 0.7 times higher for timber to 23 times higher for cowberry (Supporting Information Table S5). There was not a single management regime that maximized the provision all services evaluated. For example, green tree retention provided the lowest values for carbon storage and for the habitat availability of key vertebrate species but high values of cowberry provision (Supporting Information Figure S3).

We also tested for interactions among management regimes and climate change scenarios. We decided not to include them because the coefficient estimates for the interaction terms were much smaller than the coefficient estimates for the management or climate alone (Supporting Information Table S6), thus we found no support for interacting effects of management and climate on the future supply of boreal forest ES.

3.4. | Is the relative importance of forest management versus climate change differing between biogeographic zones?

The effects of management regimes and climate change differed among the three biogeographical zones (Table 3, see Supporting Information Table S7 for details for each ecosystem service). Overall, when comparing the mean values across all services, the positive effects of climate change were 1.6 times higher in the northern zone (mean value of 0.045) than in the southern one (mean value of 0.028) (Table 3 and Supporting Information Table S7). The patterns for management were the opposite – the negative effects of management were 3 times higher in the south (mean value of 0.235) than in the north (mean value of 0.078). Thus, in the southern zone the effect of management was 13.9 times higher than the effect of climate change, whereas in the northern zone the effect of management was 8.4 times higher than the effect of climate change (Table 3).

Table 3. Mean estimates from the generalized linear mixed effect models (GLMMs) used to assess the contribution of management and climate on the supply of eight forest ES. Here, we present for each biogeographical zone of Finland, the mean values across all management estimates, climate estimates and comparison estimates. The comparisons were made between the management and climate values for each ecosystem service (see all values in Supporting Information Table S7).

	South	**Middle**	**North**
Management	-0.235	-0.142	-0.078
Climate	0.028	0.032	0.045
Comparison	13.9	9.7	8.4

Considering individual services, we selected three of them to illustrate how the effects of management and climate shift along the south-north gradient. However, full results are presented in Supporting Information Figure S3 and Supporting Information Table S8. We chose harvested timber as it is the most important provisioning ecosystem service, carbon storage as an example of a regulating service and deadwood as an important biodiversity indicator. For harvested timber, we found that the positive effects of climate change were slightly stronger in the northern boreal zone than in the southern one (Figure 6 and Supporting Information Table S8). We also found that continuous cover forestry (CCF) had the largest contribution to timber supply compared to other management regimes with an increasing positive effect from south to north gradient. Green tree retention (GTR) had a positive effect on the supply of harvested timber in all biogeographical zones except in the northern one, where GTR had a negative effect (Figure 6 and Supporting Information Table S8).

For carbon storage, the positive effect of climate change remained quite similar across all biogeographical zones. It is interesting to note though, that when comparing with a set aside reference scenario, all management regimes had a negative effect on carbon storage in all biogeographical zones except for the northern one where they had a positive effect on the future storing of carbon (Figure 6 and Supporting Information Table S8).

For the future potential supply of deadwood volume, we found that the positive effects of climate change on this ecosystem service were slightly larger in the northern boreal zone than in the southern one (Figure 6 and Supporting Information Table S8). Nevertheless, this positive contribution of climate change was still dwarfed by the negative effects of management on deadwood, even though the management effects gradually improved northwards. Specifically, no thinning with short rotation (NTSR) had the most negative effects on deadwood availability, followed by no thinning (NT) and business as usual (BAU) regimes, this negative effect was particularly strong in the south (Figure 6 and Supporting Information Table S8).

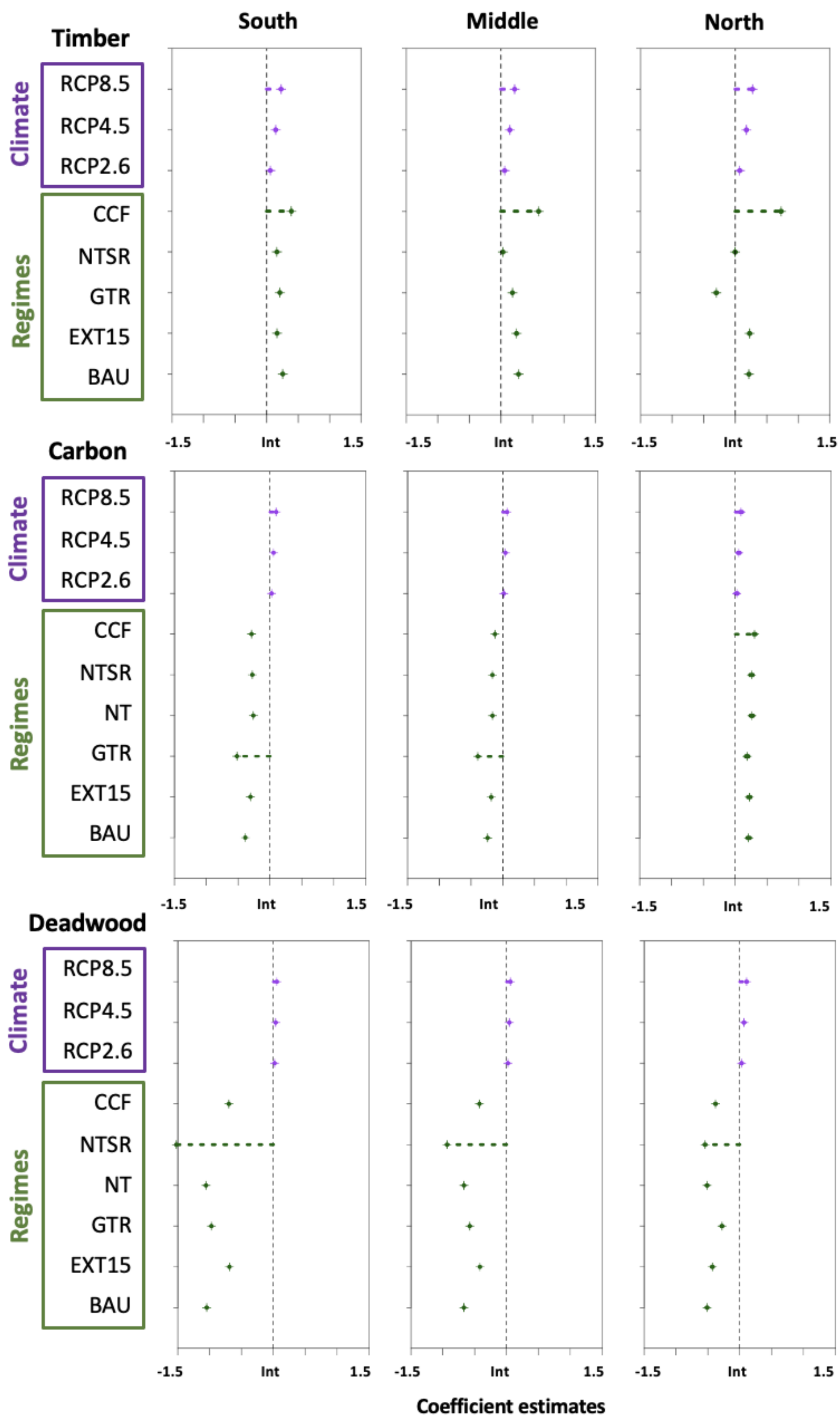

Figure 6. Relative effect of each management regime and climate scenario on the cumulative projected supply values by simulation year 100 of three ES in the biogeographical zones of Finland. The effect is relative to a reference (Int = intercept; dashed black vertical line), which is *set aside* (except *no thinning* for timber) and *baseline* climate. The vertical and horizontal lines show the mean and standard error, respectively of the coefficient estimate of the GLMMs and the dashed horizontal lines show the largest deviance from the intercept.

4 | Discussion

Here, we combine 100-year simulations (2016-2116) with GLMMs to test the relative importance of management and climate as drivers of the potential future supply of a broad set of ecosystem services in boreal forests. On one hand, we found that management greatly influences the future trajectories of boreal forest development and thus, the future supply of these services. On the other hand, climate change will potentially increase services provision by boreal forest, although the direct impacts of climate change will be smaller than the effects of management. It is well-known that forest structure and composition are the most important variables determining forest ES (e.g., Felipe-Lucia et al., 2018; Mina et al., 2017; Roces-Díaz et al., 2021) and that forest structure is strongly determined by management as the latter drives forest functioning (e.g., Cruz-Alonso et al., 2019). We also found that the relative importance of management and climate on the future supply of ES differed substantially across the biogeographical zones in Finland. Altogether, our results support the notion that intensive management reduces the deadwood volume and, thus, is a key threat to biodiversity (especially in southern Finland). Even if climate warming is projected to increase forest growth and the availability of fresh deadwood (e.g., Mazziotta et al., 2015), these increases would not compensate for the negative effects of intensive forest management on biodiversity.

4.1. | The potential supply of ES mostly increases under set aside and climate change scenarios

By the end of the 100-year simulation, the projected future supply of carbon storage, scenic beauty, habitat availability of key vertebrate species and deadwood was highest under the set aside management scenario. Forest age is on average higher in set aside forests (Figure 3), and this correlates well with tree biomass and carbon accumulation (Xu et al., 2012), thus, explaining higher values of carbon storage under this management regime which is line with results from previous studies (Triviño et al., 2015). The scenic beauty index increases with the basal area and age of trees, with increasing share of pines and deciduous trees, and with decreasing density in the number of stems (Pukkala et al., 1995). We found that set aside promoted the forest stand characteristics increasing this index (i.e., basal area, age and share of pine and deciduous trees) while reducing stem density which decreases this index (Figure 3).

Setting aside forests is especially important for biodiversity conservation in boreal forests (e.g., Triviño et al., 2017), here evaluated through the habitat availability for key forest species and deadwood volume. Forest characteristics that have a major positive influence on biodiversity such the share of deciduous trees (i.e., birch), the number of large living trees, as well as the share of old-growth forest area and the amount of deadwood (e.g., Eggers et al., 2020; Mönkkönen et al., 2022) are promoted by this management regime (see Figure 3). A larger share of deciduous trees is particularly important for two woodpecker species, the long-tailed tit and the flying squirrel (Mönkkönen et al., 2014) which are four of the key indicator vertebrate species used our habitat availability index.

Our simulations suggest that climate change will increase the future supply of six out of eight of the ES assessed, and that the positive or negative impact increases with the severity of the climate change scenario considered. Climate change is likely to increase forest growth and productivity in boreal forests (e.g., D'Orangeville et al., 2018; Kellomäki et al., 2018) where low temperatures and supply of nutrients and short growing season currently limit vegetation growth (Hyvönen et al., 2007). This increase in forest growth and productivity will especially allow a rise in harvested timber, in line with previous studies (e.g., Gutsch et al., 2018; Holmberg et al., 2019). Heinonen et al. (2018) also found that timber supply increased under climate change, except at the end of the century under the most severe scenario (RCP8.5) because very high temperatures and low soil water availability can limit forest growth. In addition, this increase in forest growth due to climate change might decrease yields of bilberry and cowberry as it is likely that forests will become too dense, leading to a decrease in wild berries production because of a reduction in sunlight reaching the understory vegetation (Mazziotta et al., 2022; Peura et al., 2016).

4.2. | Future supply of ES is driven by management rather than by climate change

Forest management had a stronger effect on the future supply of all evaluated ES than climate change (eleven times higher on average). These results are in line with previous studies, which found that the future supply of ES will be more strongly determined by management than by climate in Mediterranean (Morán-Ordóñez et al., 2020), temperate (Gutsch et al., 2018; Thrippleton et al., 2021) and mountainous forests (Mina et al., 2017). In contrast, studies in forests of the Austrian Alps found that the direct effects of climate change had a stronger influence on the future supply of several regulating services (climate, water and erosion regulation) than management (Albrich et al., 2018; Seidl et al., 2019). It is important to note that these results depend on the specific management regimes considered and that the studies from the Austrian Alps did not include large-scale clear cutting which is a common forestry practice in Finland (and as such, it was simulated here in all management scenarios except for continuous cover forestry and set aside).

The business as usual (BAU) management regime does not maximize the provision of any of the ES, not even harvested timber, as also supported by previous studies (e.g., Eyvindson et al., 2018; Peura et al., 2018). Moreover, our results suggest that there are trade-offs among ES, especially between timber production and non-wood services such as carbon storage, bilberry and biodiversity (also reported by Pohjanmies et al., 2017). Thus, there is no single management regime that maximize all forest ES simultaneously, requiring a diversification of management regimes to promote high levels of multiple ES. This has also been reported in similar forecasting approaches (e.g., Eyvindson et al., 2018; Morán-Ordóñez et al., 2020). Forest management needs to find solutions that account for these trade-offs, e.g., forest areas with different management priorities to enhance overall forest multifunctionality at the landscape scale (Blattert et al., 2018; Himes et al., 2022). This might be achieved through careful forest management planning that might pave the way for increasing timber harvest while minimizing the negative impacts on biodiversity and other ES (Eyvindson et al., 2018).

4.3. | The relative importance of forest management versus climate change differs across biogeographic zones

We found that the effects of management regimes and climate change on the future supply of ES differed between the biogeographical zones in Finland. The effects of climate change were 1.6 times higher in the northern zone than in the southern one. A study, using a gap-type forest ecosystem model, has also found that forest growth increases significantly more in northern Finland than in southern Finland because larger temperature increases are projected for that region, regardless of the climate change scenario assessed (Kellomäki et al., 2018). Despite the projected increased productivity, the expectation is that in southern Finland the conditions will become suboptimal for Norway spruce (*Picea abies*) under the most extreme scenario (RCP8.5) (Kellomäki et al., 2018). Furthermore, Norway spruce is more susceptible to spruce bark beetle outbreaks that might increase in frequency with the warmer and drier conditions projected under climate change scenarios (Venäläinen et al., 2020). Our results show that by the end of the 100-year period, spruce is projected to become the dominant tree species across all management scenarios except set aside. Thus, a relevant climate change adaptation strategy will be replacing coniferous monocultures with mixed-species forests (with a higher share of deciduous trees) as mixed stands are less susceptible to pathogens and pests while having a higher potential to store carbon (Huuskonen et al., 2021). This strategy might be beneficial across the entire study area but especially in southern Finland where conditions for spruce are expected to be suboptimal under extreme climate change conditions

(Kellomäki et al, 2018). We found that continuous cover forestry was the regime which most promoted the increased share of deciduous tree species followed by set aside.

4.4. | Study limitations and future directions

In this study, we used the SIMO forest growth simulator as a basis for our ecosystem service provision estimates. We acknowledge that applying a different modelling approach (e.g., a process-based or hybrid one instead of an empirical model) might have led to different results (Pretzsch et al., 2015). However, our results and main conclusions using an empirical model are in line with previous studies, which used different types of process models. These studies also found that the future supply of ES will be more strongly determined by management than by climate in Mediterranean (Morán-Ordóñez et al., 2020), temperate (Gutsch et al., 2018) and mountainous forests (Mina et al., 2017).

The results from this study indicate the direction and magnitude of the effects of climate on the chosen indicators but may be an under- or overestimation of the total effects. For example, the modelling of climate change effects on the formation and decomposition of deadwood are approximations because of the lack of data on climate change effects on some ecosystem processes, such as in the decomposition decay functions (Mäkinen et al., 2006). We note that the models used to translate forest characteristics and environmental factors into the potential supply of ES are mostly based on forest structural parameters, with climate only indirectly influencing the supply through changes in forest growth. For example, temperature sum is a predictor of cowberry and mushroom yields but not bilberry yields in the models we have used (Appendix S2), while it has been shown that bilberry cover is strongly explained by climate (Gamfeldt et al., 2013). This might hamper our ability to identify tipping points in ecosystem service levels directly linked to extreme natural disturbances (e.g., decrease in ecosystem service levels associated to prolonged droughts and forest die-offs).

We acknowledge that the positive effects of climate change may have been overestimated in our study as our simulations did not include natural disturbances, such as windthrows, insect outbreaks, droughts and wildfires, which are expected to increase in intensity and frequency under climate change scenarios (Reyer et al., 2017; Seidl et al., 2017). For example, wind damage risk is projected to increase in southern Finland, because of a longer unfrozen soil period which weakens the anchorage of trees during the windiest season (i.e., from autumn to early spring) (Venäläinen et al., 2020). Prolonged drought stress will increase the predisposition of spruce to bark beetle infestations

(Netherer et al., 2019); this potential impact may be of particular concern given that our simulations predict a dominance of this species under all management scenarios except set aside. Moreover, natural disturbances, such as windthrows, may substantially change the forest characteristics, e.g., increase deadwood volume (Kuuluvainen, 2002) and reduce harvested timber because of damaged trees (Peltola et al., 2010). Even if extreme events (e.g., severe storms) can reduce the supply of some services (e.g., timber) locally, recent studies have suggested that their effects on larger scales are generally smaller than climate and management effects (Hahn et al., 2021; Seidl et al., 2019).

Therefore, the explicit implementation of potential disturbances linked to climate change in the simulation of future provision of ES by boreal forest remains a challenge for future studies. A couple of recent studies have gone into that direction and assessed wind damage risk under different management regimes (Hahn et al., 2021; Potterf et al., 2022). Next steps could include assessing the effects of several natural disturbances simultaneously (i.e., windthrows and prolonged droughts) on a wide range of forest ES. These are challenges to overcome in future modelling of boreal systems for which experiences from other systems such as the Mediterranean (e.g., regarding prolonged droughts) (García-Valdés et al., 2021) might be useful.

5 | CONCLUSIONS

Our results suggest that forest management will have a stronger effect than climate change on the potential future supply of boreal forest ecosystem services (ES). Climate change will have an overall positive effect on the ES provision (in six out of eight of the ES evaluated), but the magnitude and direction of this effect will vary with the severity of the climate change scenario and across biogeographical zones. The climate change effect will be larger under the more extreme RCP8.5 scenario and in northern Finland and the effect of management on ES provision will also change across biogeographical zones. Thus, in the current context of climate change, careful forest management planning to maximize the future supply of ES should be context dependent and account for the biogeographic diversity of boreal forests. On one hand, a transition towards mixed-species forests (i.e., increased share of deciduous trees in coniferous forest stands) will be an important climate adaptation strategy to implement in forests of southern Finland, where conditions for spruce are expected to be suboptimal under extreme climate change conditions (Kellomäki et al, 2018). Mixed-species forests are less susceptible to the potential negative effects of climate change (e.g., drought stress, increased risk of insect outbreaks and pathogens) and potentially maximize the supply of some ES (e.g., carbon storage and scenic beauty) and the maintenance of biodiversity (Huuskonen et al., 2021). This could be promoted by increasing the share of continuous cover forestry and set aside forest stands. On the other hand, forests of northern Finland, with slower growth, could have a greater contribution for carbon sinks, for example by extending the rotation length and restoring low-productivity mires.

In addition, no single management scenario maximized the provision of all services evaluated, as each service provision depends on different forest structural attributes and, in turn, structural attributes differed among management scenarios. Provision of carbon, scenic beauty, habitat availability and deadwood were maximized under the set aside scenario, but timber, berries and mushroom provision were maximized when other management regimes were considered (i.e., continuous forest cover forestry and management without thinning but with short rotation). These results highlight the need to implement diversified forest management planning strategies across boreal forests in Finland – now dominated by actions that promote monospecific stands – as well as to increase the share of close to nature management regimes that are still poorly represented in Finnish forest landscapes (i.e., continuous cover forestry, no thinning and setting aside).

Our results provide valuable input for developing new guidelines for adapting boreal forest to global change via forest management and promote its resilience and ES supply, a key goal of the recently approved new EU forest strategy (European Commission, 2021). Our results suggest that climate change mitigation measures are particularly suited for the northern Finland, whereas in southern Finland it is better to focus on increasing forest protection (i.e., increasing the amount of forest within protected-areas and establishing voluntary forest protection by landowners) and closer-to-nature management strategies. These guidelines should account for regional differences in the boreal biome and the variation of the effects of climate change and management on different forest ES and across biogeographic zones.

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Data availability statement

We used the Finnish Multi-Source National Forest Inventory (MS-NFI) as input data for the open-source forest simulator SIMO (SIMulation and Optimization for forest management planning; https://www.simo-project.org). SIMO is released under the open-source GPL 2.0 license. We used SIMO 1.0.0, which was then modified by JYU BERG team (https://www.jyu.fi/berg). The MS-NFI data is openly available from the National Resources Institute Finland (Luke) (http://kartta.luke.fi/index-en.html). The SIMO outputs used for the generalized linear mixed models have been archived and are available in a Dryad public repository (https://datadryad.org) (https://doi.org/10.5061/dryad.4j0zpc8g4).

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