Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2019:44

Functional traits and decomposition of lichens, bryophytes and vascular plants in an alpine ecosystem

Funksjonelle egenskaper og nedbrytning av lav, moser og karplanter i et alpint økosystem

Kristel van Zuijlen

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Contents

Summary

Functional traits influence how an organism responds to its environment and how this can affect ecosystem processes such as decomposition. The majority of trait-based studies have focused on vascular plants, while non-vascular primary producers such as lichens and bryophytes are underrepresented in the trait literature. This is despite their large contribution to aboveground biomass and species richness in high latitude and high elevation ecosystems, and prevalent role in ecosystem processes such as decomposition and nutrient cycling. The objective for this thesis was to study functional traits of three different primary producer groups, i.e. vascular plants, lichens and bryophytes, and identify how these groups and their traits affect decomposition in an alpine ecosystem. This was done using an elevational gradient and a lichen transplant experiment in Finse, southern Norway. Across the elevational gradient, we measured community-level functional traits of vascular plants, lichens and bryophytes (**Paper I**), decomposability of lichens and bryophytes (**Paper III**) and secondary compounds of vascular plants and lichens (**Paper IV**). In addition, we assessed the relative importance of species turnover and intraspecific variation on these responses. In the lichen transplant experiment, we studied the effects of different mat-forming lichens on microclimate and decomposition of plant litter (**Paper II**).

Temperature (and corresponding growing season length) is assumed the main environmental variable that changes across the elevational gradient, but there are other factors that also change, such as precipitation, available nutrients, and herbivory. These additional factors might also have played a role in the observed responses of vascular plants, lichens and bryophytes across elevation. We found that lichens had higher intraspecific variation than vascular plants and bryophytes for N concentration and N:P ratio, inplying a great deal of intraspecific plasticity (**Paper I**). In general, the drivers of community-level functional traits differed among traits as well as primary producer groups. Some traits, e.g. increase in N concentration indicated a shift to increasing resource acquisition with elevation, which is opposite of what we expected. In line with increasing N at higher elevation, community-level decomposability of lichens and bryophytes increased, which was mainly driven by species turnover (**Paper III**). Decomposability, both at the community-level and across the entire dataset, was explained by tissue pH, primary producer group (lichens vs bryophytes) and nutrient

concentration. Vascular plant secondary compounds decreased while lichen secondary compounds increased with elevation (**Paper IV**). Variability in lichen cortical compounds were for a large part driven by intraspecific variation. Furthermore, plant secondary compounds shifted from those associated with herbivore defence towards those protecting against light and oxidative stress as elevation increased. Mat-forming lichens reduced the mean soil temperature and the number of soil freeze-thaw cycles, and *Cladonia rangiferina/stygia* insulated better than other lichens, as a result of its high water holding capacity (**Paper II**). Decomposition of plant litter was faster under *Nephromopsis nivalis* than under *Alectoria ochroleuca*, but this was not related to microclimate or functional traits.

Our findings highlight that vascular plants, lichens and bryophytes may respond differently to the same environmental gradient, which has implications for ecosystem processes. Intraspecific variation contributed substantially to functional traits and was especially important for lichen traits and lichen secondary compounds. High intraspecific plasticity implies that lichen species might be more resilient to environmental changes than vascular plant and bryophyte species. However, high intraspecific variation may not necessarily be important for ecosystem processes such as decomposition, as species turnover was the main driver of variation in decomposability of lichens and bryophytes. Further, as mat-forming lichens can affect decomposition of other litter types, this could affect carbon and nutrient dynamics of mixed plant and lichen communities on a larger scale. Finally, future climate warming may result in a shift towards slower decomposable species, which might counterbalance the increased microbial respiration under higher temperatures.

List of papers

Paper I

Ruben E. Roos*, Kristel van Zuijlen*, Tone Birkemoe, Kari Klanderud, Simone I. Lang, Stef Bokhorst, David A. Wardle, Johan Asplund

Contrasting drivers of community-level trait variation for vascular plants, lichens, and bryophytes across an elevational gradient

* These authors contributed equally

Revised manuscript submitted to Functional Ecology

Paper II

Kristel van Zuijlen, Ruben E. Roos, Kari Klanderud, Simone I. Lang, Johan Asplund

Mat-forming lichens affect microclimate and decomposition by different mechanisms

Manuscript submitted to Fungal Ecology

Paper III

Kristel van Zuijlen, Ruben E. Roos, Kari Klanderud, Simone I. Lang, David A. Wardle, Johan Asplund

Community-level decomposability of lichens and bryophytes across an elevational gradient

Paper IV

Johan Asplund, Kristel van Zuijlen, Ruben E. Roos, Tone Birkemoe, Kari Klanderud, Simone I. Lang, David A. Wardle, Line Nybakken

Contrasting responses of plant and lichen secondary metabolites across an elevational gradient

Synopsis

1 Introduction

This thesis is about functional traits of lichens, bryophytes and vascular plants and their effects on decomposition in an alpine ecosystem. In this section, I will introduce the general study system and study organisms, the use of elevational gradients, and general concepts of decomposition and trait-based ecology.

1.1 Alpine vegetation

The alpine life zone is defined as the vegetated zone at high elevation above the treeline (Körner, 2003). Because the treeline is rarely a sharp line, it is often referred to as the treeline ecotone, and the vegetation within this ecotone is sometimes referred to as 'subalpine'. The upper limit of alpine vegetation is formed by the permanent snowline. With increasing elevation and associated decline in temperature, the alpine life zone changes from a closed lush vegetation to scarce and fragmented patches of vegetation. Near the permanent snowline these fragmented vegetation patches are referred to as nival or subnival (Körner, 2003). At high latitudes such as in Scandinavia, the alpine terrestrial vegetation consists mainly of three primary producer groups: vascular plants, lichens and bryophytes.

Vascular plants, also known as tracheophytes, are those plants that have vascular tissues for transporting water and nutrients, and include angiosperms (flowering plants), gymnosperms (non-flowering seed plants), and pteridophytes (spore-producing vascular plants, e.g. ferns). Bryophytes are a paraphyletic group of non-vascular plants, including mosses, liverworts and hornworts (Ingrouille and Eddie, 2006). In contrast, lichens are not plants, not even single organisms, but a symbiosis between a fungal partner, the mycobiont, and one or more photosynthetic partners, the photobiont (green alga or cyanobacterium; Nash III, 2008). Thus, from an evolutionary perspective, vascular plant and bryophytes are similar, while lichens are a completely different group of organisms. However, from an ecological perspective, bryophytes and lichens are similar, because both are poikilohydric, which means that they lack the ability to maintain and regulate their tissue water content. In contrast, vascular plants have developed the capacity to maintain homeostasis of their water status, referred to as homoihydry. Furthermore, one of the most important advancements in vascular plant evolution was the development of a rooting system, which lichens and bryophytes lack. Through their roots, vascular plants are anchored to the soil and are able to absorb water and nutrients

from it. Lichens and bryophytes sometimes have root-like structures called rhizines (lichens) or rhizoids (bryophytes) that anchor them to the surface, but they depend mainly on atmospheric water sources, mineral deposition and/or nitrogen fixation by associated cyanobateria. Because of their poikilohydric nature, direct water availability is crucial for lichens and bryophytes to become active. However, it also means that they are desiccation tolerant, i.e. they have the ability to tolerate and survive dry conditions. When desiccated, lichens and bryophytes become dormant, and in this state they can survive extreme conditions, such as temperatures far below freezing point (Larson, 1989; Glime, 2017b) while lichens can even survive outer space conditions (De la Torre *et al.*, 2010).

The capacity of lichens and bryophytes to tolerate extreme conditions makes them important primary producers in cold biomes. They often grow in places where vascular plants cannot grow, when conditions are too harsh for vascular plants to persist, e.g. too cold, too exposed or nutrient-poor. Lichens and bryophytes are therefore typical stress-tolerators (Nash III, 2008; Glime, 2017a). With increasing latitude and elevation, e.g. from the tropics to the arctic, and from lowlands to mountain peaks, vascular plants decrease in both species richness and abundance (likely following a humpback shape rather than a monotonic decline; Rahbek, 2005). The same is true for bryophytes and lichens, however, they decrease less strong than vascular plants, consequently leading to a relatively high contribution of lichens and bryophytes in cold biomes (Körner, 2003; Jägerbrand *et al.*, 2010).

1.2 Elevational gradients

Alpine vegetation is mainly constrained by physical components of the environment, notably low air temperature, which often leads to associated constraining factors such as extensive snow cover and a short growing season. Elevational gradients can serve as powerful 'natural experiments' for understanding long-term and large-scale community and ecosystem responses to climate (Sundqvist, Sanders and Wardle, 2013). Further, elevational gradients can act as space-for-time substitutions to study the effects of ongoing climate warming (e.g. Blois *et al.*, 2013; Guittar *et al.*, 2016), which is expected to be more pronounced in alpine and arctic regions compared to the global average (IPCC, 2013).

When using elevational gradients as natural experiments, one needs to be aware of the environmental factors that are physically bound to meters above sea level, and those that do not vary consistently with elevation (Körner, 2007). As such, general climatic trends with increasing elevation include decreasing air temperature, decreasing total atmospheric pressure and partial pressure of atmospheric gases such as O_2 and CO_2, increasing radiation under a cloudless sky, and a higher fraction of UV-B at any given total solar radiation. Another consistent geophysical change with elevation is the decrease in available land area, a major driver of biodiversity and evolution (MacArthur and Wilson, 1967). Climatic trends that, on a global scale, do not change consistently with elevation include precipitation, wind velocity and seasonality. However, in the temperate zone (40-60° latitude), precipitation tends to increase with increasing elevation. Further, the growing season decreases with elevation in humid climates at high latitudes (Körner, 2007).

A likely consequence of lower temperatures at higher elevation are changes in soil nutrient availability. A common trend is a decrease in plant-available nutrients with increasing elevation, due to slower nutrient turnover (Vitousek, Matson and Turner, 1988; Vitousek *et al.*, 1992; Sveinbjörnsson *et al.*, 1995; Huber *et al.*, 2007). Therefore, it is often hypothesized that plants change from a rapid resource acquisition strategy at low elevation towards a resource conservation strategy at higher elevation (e.g. Sundqvist, Giesler and Wardle, 2011; Read *et al.*, 2014). However, there are numerous exceptions to this trend of decreasing nutrients with elevation. For instance, nutrient cycling differs between vegetation types across the same elevational gradient (Sundqvist *et al.*, 2014), and decreasing trends in nutrients with elevation reverse near the treeline (Sveinbjörnsson *et al.*, 1995; Frangi *et al.*, 2005). Further, nitrogen (N) and phosphorus (P) might show contrasting patterns, resulting in shifts in the relative importance of N and P limitation across elevation (Unger, Leuschner and Homeier, 2010; He *et al.*, 2016). Where plant-available nutrients do decline with increasing elevation, plants might overcome this by shifting to organic nitrogen as their primary N source (Averill and Finzi, 2011), making the pattern of nutrient availability even more complicated.

1.3 Decomposition

The decay of organic matter, decomposition, is an important ecosystem process that drives carbon and nutrient cycling. It is determined by three main factors: the substrate

quality, the physico-chemical environment (climate and soil abiotic properties), and the decomposer community (soil fauna, bacteria and fungi), which all three interact with each other (Swift, Heal and Anderson, 1979). The main decomposers in initial terrestrial decomposition are fungi and bacteria, which generally account for 95% of the decomposer biomass and respiration. Fungi produce networks of hyphae that allow them to reallocate resources (e.g. nutrients) from one part of the network to another, giving them a competitive advantage over bacteria in decomposing nutrient-poor substrates (Chapin, Matson and Vitousek, 2011). In cold biomes, the contribution of soil fauna to decomposition is considered negligible, and low temperatures limit microbial respiration (Swift, Heal and Anderson, 1979).

The initial litter decomposition rate is high, when labile compounds are broken down, while it gradually declines when litter becomes more recalcitrant as it ages. This is described by an exponential decay function, meaning that a constant proportion of the litter is broken down each year (Chapin, Matson and Vitousek, 2011). Under future climate warming, decomposition is expected to increase due to higher microbial respiration. However, several studies have highlighted the importance of species-driven litter quality differences, which have a much larger effect on plant litter decomposition than climate-driven differences (Cornwell *et al.*, 2008; Djukic *et al.*, 2018). Therefore, the indirect effects of expected future climate change, i.e. vegetation shifts, will likely have a larger impact on decomposition than the direct effects such as increasing temperature (Cornelissen *et al.*, 2007).

1.4 Trait-based ecology

Functional traits are defined as characteristics of organisms that influence their responses to the environment and/or their effects on ecosystem processes (Violle *et al.*, 2007). In contrast to methods based on species identity (e.g. species richness and composition measures), methods based on functional traits more easily allow for generalizations across species, communities and ecosystems. As such, trait-based approaches have been used increasingly to answer ecological questions. In order to measure functional traits at the community level, it is important to take into account that common species generally contribute more to the ecological functioning than do rare species (mass ratio hypothesis, Grime, 1998). Therefore, the trait values of individual species are often weighted by their relative abundance to get a reliable mean of the whole

community (Garnier *et al.*, 2004). Functional traits do not only vary among species, but can also vary considerably within species. As such, community-level trait variation across environmental gradients can be driven by changes in species composition and abundance ('species turnover'), or within-species trait variation (intraspecific), or both (figure 1.1). In panel a) of figure 1.1, the community-weighted mean trait value changes through alterations in species abundance and identity across an environmental gradient (species turnover), while trait values within species are fixed. In panel b), the change in community-weighted mean trait value is driven by intraspecific trait variation only (no species turnover). In panel c), both species turnover and intraspecific variation drive changes in the community-weighted mean trait value, which together result in an even stronger response than in a) and b). In this case, species turnover and intraspecific variation act in similar direction and have a positive covariation (both drivers reduce the community-level trait value), but they can also drive the community-level trait value in opposite directions, in which case their covariation is negative (e.g. species turnover decreases the community-weighted mean, while intraspecific variation increases the community-weighted mean).

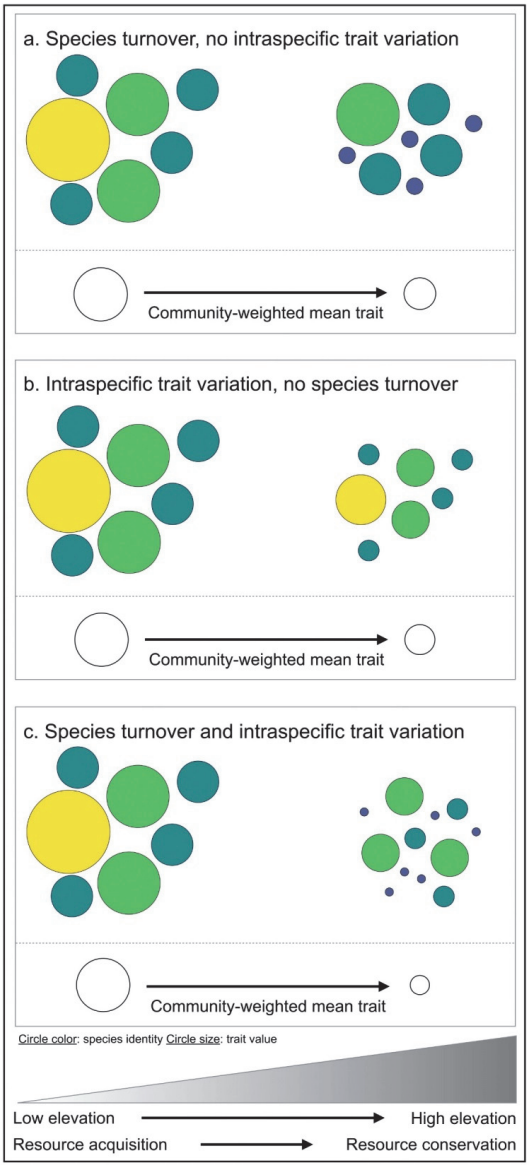

Figure 1.1. Conceptual figure of the drivers of community-level trait changes across environmental gradients such as elevation. From Paper I.

Most studies on vascular plants have shown that changes in community-weighted mean traits are

driven primarily by species turnover effects, but intraspecific variation can sometimes contribute substantially (e.g. Albert *et al.*, 2010; Siefert *et al.*, 2015; Derroire *et al.*, 2018). In contrast, a limited number of studies on lichens suggests that intraspecific variation may be more important than species turnover effects across environmental gradients (Asplund and Wardle, 2014; Coyle, 2017). Also in bryophytes, large intraspecific responses have been found in photosynthesis and nitrogen fixation (Gavazov *et al.*, 2010; Turetsky *et al.*, 2012). However, non-vascular groups such as lichens and bryophytes are underrepresented in trait-based studies (St. Martin and Mallik, 2017), and community-level trait measures of lichens and bryophytes are rare, despite the importance of these groups in many ecosystems such as in alpine environments. Thus, the relative importance of species turnover versus intraspecific variation in lichens and bryophytes still needs to be explored.

Examples of functional traits that are frequently used in trait-based studies on vascular plants are nutrient concentrations such as N and P, and leaf traits such as specific leaf area (SLA). For poikilohydric organisms such as lichens and bryophytes, water holding capacity (WHC) is an important trait that determines photosynthetic activity. Functional traits can be classified as 'response traits', which describe how organisms respond to environmental changes, and 'effect traits', which describe how organisms affect ecosystem processes and functioning (Lavorel and Garnier, 2002). Response and effect traits often overlap, for instance, SLA often responds to environmental factors such as climate and light availability, while increased SLA may in turn result in higher decomposition rates (e.g. Santiago, 2007). Trait-based studies often use 'soft' traits, which are easy to measure for a large set of species and sites (e.g. SLA) and usually good correlates of 'hard' traits, which are more accurate indicators of plant functioning (e.g. growth rate) but more difficult to measure (Hodgson *et al.*, 1999; Lavorel and Garnier, 2002). A specific group of 'harder' traits are secondary metabolites (i.e. compounds that are not involved in the primary functions growth, development and reproduction), which protect against biotic and abiotic stresses, such as defence against herbivores and light protection (Hartmann, 2007). These compounds also act as effect traits by inhibiting the activity of soil organisms and slowing down decomposition (Chomel *et al.*, 2016).

2 Objectives

The main objective for this thesis was to study functional traits of three different primary producer groups, i.e. vascular plants, lichens and bryophytes, and identify how these groups and their traits affect decomposition in an alpine ecosystem. This was mainly done at the community level, and to a lesser extent at species and within-species level. Specifically, I addressed the following questions:

1. a) How will elevation affect community-level functional traits of vascular plants, lichens and bryophytes, and b) are changes in functional traits of these different groups driven by species turnover effects or intraspecific variation? (**Paper I**, Synopsis)
2. How will different mat-forming lichens and their functional traits affect a) microclimate and b) decomposition rate, underneath lichen mats? (**Paper II**)
3. a) How does decomposability of lichens and bryophytes change across an elevational gradient and b) how are functional traits driving this? (**Paper III**)
4. How are concentration and composition of secondary compounds of vascular plants and lichens affected by elevation? (**Paper IV**)

A schematic overview of the different papers is given in figure 2.1.

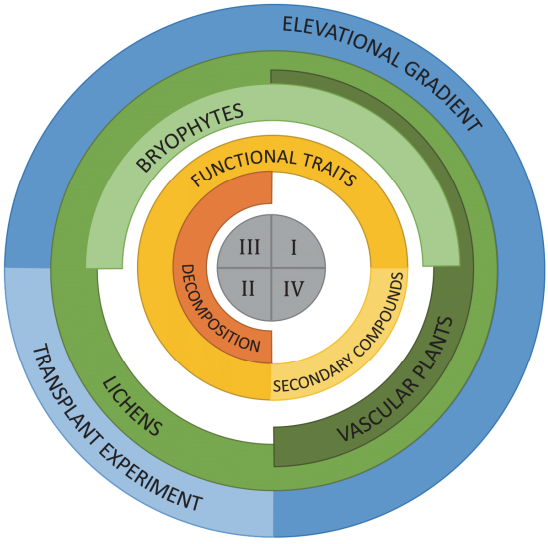

Figure 2.1. Schematic overview of the different themes, study organisms and study designs for each of the four papers (denoted with roman capitals).

3 Methods

3.1 Study site

All four papers are based on work done on carefully selected field sites nearby the Finse Alpine Research Center (60°36'N, 7°30'E), situated on the Hardangervidda (Hardanger mountain plateau) in southern Norway, in between Hardangervidda National Park in the south and Hallingskarvet National Park in the north and east. The mean annual temperature in Finse is -2.1°C (-10.1°C in January and 7.0°C in July) and mean annual precipitation is 1030 mm (Norwegian Meteorological Institute 2018, figure 3.1). The area consists of calcareous and non-calcareous bedrocks (Norwegian Geological Survey, 2019), supporting a mixture of species-rich 'calciphile' communities (found on Ca-rich substrate) such as *Dryas octopetala* heath, and less species-rich 'calcifuge' communities (found on Ca-poor substrate), such as heath dominated by ericaceous shrubs. The alpine landscape in Finse is a topographically complex terrain, with small-scale variations in relief, i.e. slope and exposure, resulting in small-scale variations in micro-climate, which in turn drive plant community structure and diversity (Opedal, Armbruster and Graae, 2015).

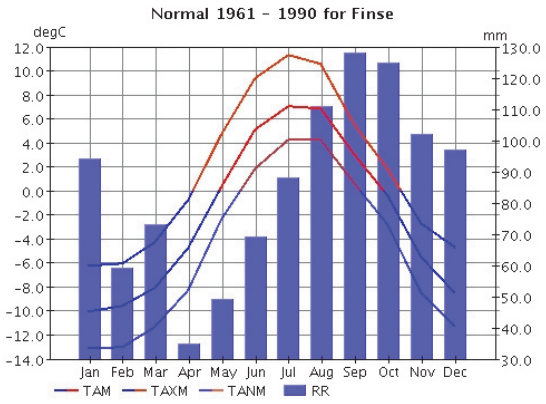

Figure 3.1. Climate data for Finse. Monthly normal temperature values: mean (TAM), minimum (TANM) and maximum (TAXM), and monthly normal precipitation (RR). Values are averaged over the normal period 1961 to 1990. Source: eklima.no

Situated in between national parks and landscape protection areas, the area is important for nature and wildlife conservation, but also recreation including skiing, hiking, cycling, fishing and hunting, as well as sheep grazing. The arctic fox (*Vulpes lagopus*), which is critically endangered in Norway, was reintroduced in Finse in 2010 (Landa *et al.*, 2017). The area north and northeast of Finse (Nordfjella) held one of the sub-populations of the last wild reindeer (*Rangifer tarandus*) in Europe. The Nordfjella population was eradicated in 2018 to prevent the spread of chronic wasting disease (CWD); Mysterud and Rolandsen, 2018), but since the field work for this thesis was

finished before the eradication, I will discuss potential effects of reindeer grazing. Reindeer depend on lichens for their diet, especially during winter, while they feed on a variety of plants and lichens during summer (Skogland, 1980; Asplund and Wardle, 2017). Other wild herbivores include the mountain hare (*Lepus timidus*), Norwegian lemming (*Lemmus lemmus*), tundra vole (*Microtus economus*), ptarmigan (*Lagopus muta*) and willow grouse (*Lagopus lagopus*). Grazing pressure of wild herbivores is assumed to be relatively low in the study area, due to a decline in rodent numbers and coherent alpine birds since the mid-nineties (Kausrud *et al.*, 2008). However, the areas away from human disturbance factors such as the railway and power lines are important for reindeer (Nellemann *et al.*, 2001; Vistnes *et al.*, 2008). Grazing pressure of the free-ranging domestic sheep is concentrated in areas closer to the railway during the summer season.

3.2 Elevational gradient

For the **Papers I, III and IV**, we established an elevational gradient in early summer 2016, ranging from approximately 1120 to 1600 m above sea level (a.s.l), consisting of five sites evenly distributed in between with a 120 m height difference between them (figure 3.2).

Site and plot selection

Other than the factors that change consistently with elevation (i.e. air temperature, atmospheric pressure, solar and UV-B radiation; Körner 2007), we tried to minimize additional environmental effects as much as possible, by selecting sites with similar physical properties that affect microclimate and nutrient status, which are both important drivers of vegetation structure. As such, we selected wind-exposed sites on non-calcareous bedrock (granite and gneiss), on south-facing slopes with an angle of 1-15 degrees (gentle to moderate steepness). Most lichens respond negatively to deep snow-cover and are therefore mostly absent from leeward sides and depressions in the landscape (Bidussi, Solhaug and Gauslaa, 2016; Niittynen and Luoto, 2018), which is why we selected ridges that support a mixed cover of lichens, vascular plants and bryophytes. Because of sun- (i.e. south-facing) and wind-exposure, all sites were snow-free in June 2016, when much of the surrounding areas were still snow-covered. The vascular plants *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* are most common at the lowest elevations, while *Carex bigelowii* and *Salix herbacea* are common on higher elevations. Abundant lichen species are *Cladonia arbuscula s. lat.* (from now on referred to as *C. arbuscula*), *C. rangiferina, Cetraria* spp. and *Nephromopsis nivalis* (note: the latter

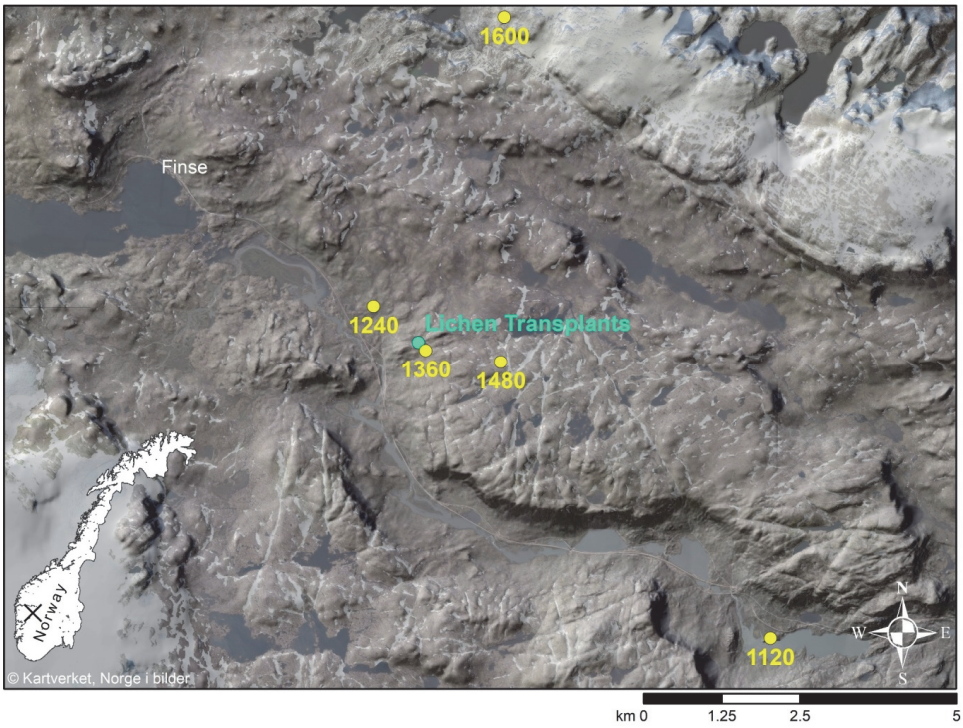

Figure 3.2. Map showing the study sites of the elevational gradient (marked in yellow; 1120, 1240, 1360, 1480 and 1600 m a.s.l.), and the lichen transplants experimental site (marked in green), near Finse in southern Norway (60°36'N, 7°30'E).

species is in the papers referred to under its former name *Flavocetraria nivalis*). The bryophyte species *Pleurozium schreberi* and *Dicranum acutifolium* are abundant at lower elevations, while *Polytrichum* spp. and *Racomitrium lanuginosum* are common at higher elevations.

The plots were selected randomly by blind throwing an object and establishing the plot where the object landed, on the condition that the object landed within the site (the ridge, i.e. within a radius of maximum 100 m), and all three primary producer groups (vascular plants, lichens and bryophytes) were present. As vascular plants and lichens are more abundant than bryophytes at the selected sites, we often had to adjust the location of the plot slightly to ensure bryophyte presence. Further, as the most exposed part of the ridge is dominated by lichens while vascular plants and bryophytes are mainly absent, we had to select the plots towards the edge of the ridge. These ridge edges are slightly less wind-exposed, but still exposed enough to support an abundant lichen

community, mixed with vascular plants and bryophytes. Lee sides were avoided since lichens were mainly absent, and therefore did not meet our criteria for plot selection. At each site, we laid out five 1 x 1 m plots, resulting in 25 plots in total (figure 3.3).

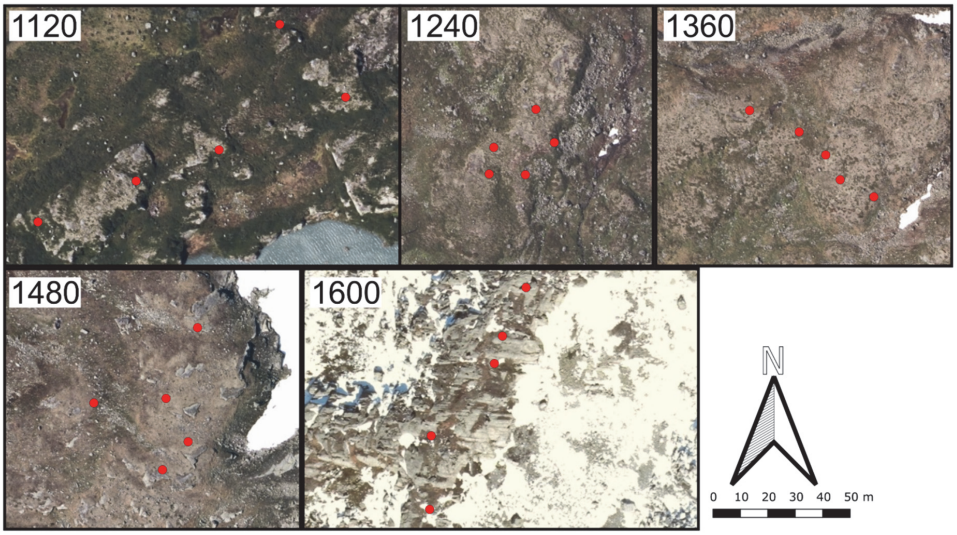

Figure 3.3. Satellite images showing the positioning of the plots (marked with red dots) within the sites (wind-exposed ridges) at different elevations (m a.s.l.).

Vegetation survey and sampling

Across the elevational gradient, we carried out a vegetation survey in July 2016 (figure 3.4). We recorded all species and estimated their cover in each plot. We identified most species in the field, except for many bryophytes (notably species within the *Dicranum* and *Polytrichum* genera and liverworts), which we identified later in the lab using a stereo- and microscope. Because of the small-stature and heterogeneous vegetation, we divided the plots into four quadrates of 50x50 cm, using a 1x1 m metal frame with wires across the middle, and each quadrate subsequently divided into 25 10x10 cm squares (figure 3.4c). Species abundance was estimated visually in each quadrate, using the squares (each representing 4% of the quadrate) to allow for accurate estimations. We calculated the whole-plot cover as the average of the four quadrates. For unknown bryophytes, we estimated cover of each 'single-species' bryophyte patch and took a sample for identification in the lab. The species abundance data were used to calculate community-weighted means for functional traits (**Paper I**), decomposability (**Paper III**), and secondary compounds (**Paper IV**).

In addition, we measured the overall vegetation height, estimated the cover of biological soil crust (biocrust), litter, and bare rock, and recorded presence/absence of animal droppings and herbivory marks in each plot. The average vegetation height decreased from 9.4 cm at the lowest site, to 8.3, 7.2, 4.2 and finally 2.1 cm at the highest site. The cover of biocrust, litter and bare rock were all highest at 1600 m a.s.l. with 4.8, 5.4 and 4.4% cover, respectively. Occasional animal droppings were recorded in 10 out of 25 plots, mainly of lemming (6 plots; 1 at 1360, 2 at 1480, and 3 at 1600), but also reindeer (2 plots at 1600), fox (2 plots at 1600), hare (1 plot at 1120), ptarmigan (1 plot at 1600), and sheep (1 plot at 1360). We recorded most dropping observations at 1600 m a.s.l. (in all 5 plots) and recordings decreased with decreasing elevation (1480:2; 1360:2; and 1120:1 plot). We did not measure the cover or amount of droppings, as they were scarce and contributed only marginally to plot cover.

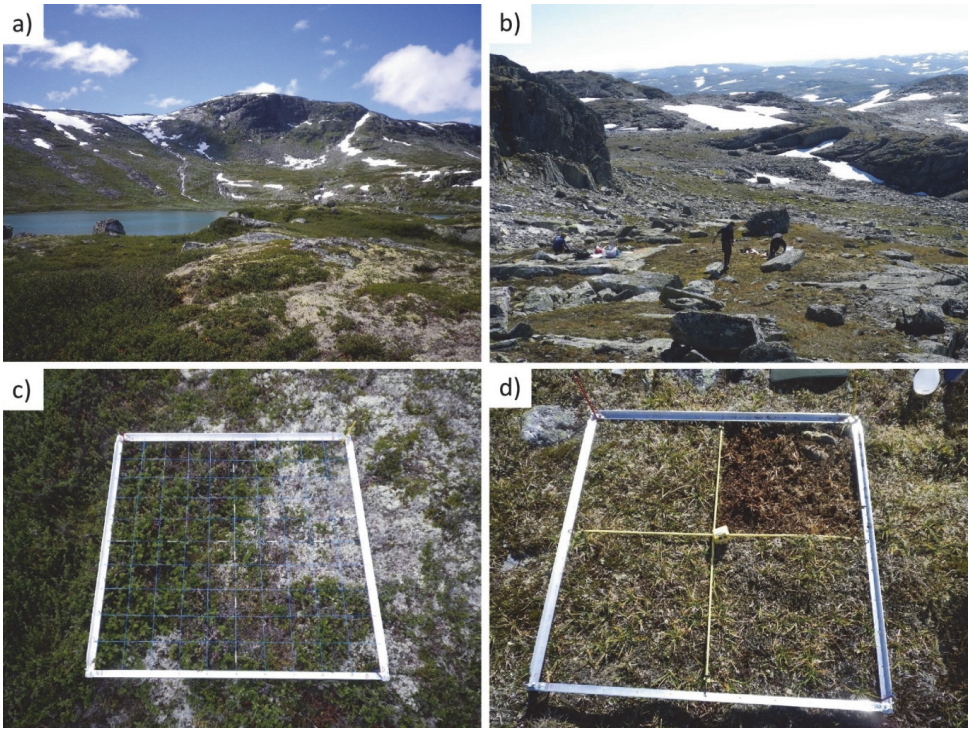

Figure 3.4. Impression of the elevational gradient used for Papers I, III and IV. View of **(a)** the lowest elevation (1120 m a.s.l.) with lush vegetation and **(b)** the highest elevation (1600 m a.s.l.) with scarce vegetation in between rock outcrops; **(c)** a plot at 1120 m during vegetation survey, divided in quadrates (white markings on blue plastic wire) and 10x10 cm squares; and **(d)** a plot at 1600 m after harvesting of aboveground biomass of one quadrate.

To gather material for lab analyses, we destructively harvested all aboveground material of one quadrate per plot in late July and August 2016 (figure 3.4d). In the field, we roughly sorted the material to species, and sampled extra material for species with little biomass from the other quadrates or the immediate surroundings of the plot. For some rare species, it was not possible to collect enough material. As a rule, we made sure to capture at least 80% of each primary producer community (vascular plants, lichens, and bryophytes) in each plot, to allow for reliable community estimates (Pakeman and Quested, 2007). Consequently, we had to exclude some of the plots for the lichen and bryophyte community because we could not capture 80% of the community per plot, due to high species richness and evenness, and overall low abundance of the given primary producer group within the given plot. We excluded liverworts from the analysis due to their minor contribution to vegetation cover, except for the common and easily recognizable liverwort *Ptilidium ciliare*. After harvesting, we kept vascular plants in sealed plastic bags, sprayed with demineralized water, and stored them at 4°C until measurements of 'fresh' traits (specific leaf area (SLA) and leaf dry matter content (LDMC)), within a few days after harvesting. Lichens and bryophytes, and vascular plant material for chemical traits, were kept in paper bags and air dried at room temperature. After the field season, the material was stored at -17°C until further lab analyses.

Environmental factors

We measured air temperature in each plot just above the vegetation (approximately 20 cm from the soil), every 20 minutes from 5 September 2016 to 22 August 2017, from which we calculated several temperature parameters (table 3.1). The mean temperature in July, i.e. the peak of the growing season, decreased on average by 0.9°C with each level of increasing elevation, and the growing season length was 54 days shorter on the highest compared to the lowest elevation. To check how environmental factors other than temperature change across the elevational gradient, we extracted precipitation data from a gridded dataset of modelled daily precipitation for Norway (Lussana *et al.*, 2018). Mean annual precipitation from 1986 to 2015 increased with elevation from 843, 944, 968, 976, to 1026 mm, with high interannual variation (figure 3.5). Further, we measured available nutrients in the soil using ion exchange resin capsules (Unibest International, USA), which we buried at 3 cm depth in each plot during the growing season. Available

nutrients for each elevation are given in table 3.2; soil N:P increased at the highest elevations, mainly caused by a decrease in available P from 1240 m a.s.l. and upwards.

Table 3.1. Temperature parameters for each elevation (m a.s.l.) from September 6, 2016 to August 21, 2017. Mean ± SE of mean annual temperature (MAT, °C), temperature at coldest day (MinT, °C), temperature at warmest day (MaxT, °C), no. of diurnal freeze-thaw cycles (FTC), mean January temperature (JanT, °C), mean July temperature (JulyT, °C), and growing degree days (GDD; number of days when average temperature exceeded 5°C). Values are averaged over the plots (n=4 or n=5) per elevation. From **Paper I**.

Elevation	n	MAT	MinT	MaxT	FTC	JanT	JulyT	GDD
1120	5	1.2 ±0.03	-18.5 ±0.27	16.1 ±0.33	138 ±1.58	-5.6 ±0.01	10.4 ±0.07	119 ±0.75
1240	4	1.4 ±0.11	-16.1 ±0.29	15.7 ±0.19	122 ±5.12	-3.8 ±0.27	9.4 ±0.08	106 ±0.91
1360	5	0.9 ±0.25	-15.0 ±1.47	15.5 ±0.35	103 ±9.83	-4.5 ±0.83	8.6 ±0.12	97 ±0.80
1480	5	-0.7 ±0.05	-17.0 ±0.30	14.2 ±0.13	90 ±9.55	-7.0 ±0.08	7.3 ±0.12	81 ±0.89
1600	4	-0.4 ±0.43	-14.1 ±3.34	14.1 ±0.07	65 ±4.85	-4.6 ±1.23	6.7 ±0.08	65 ±1.04

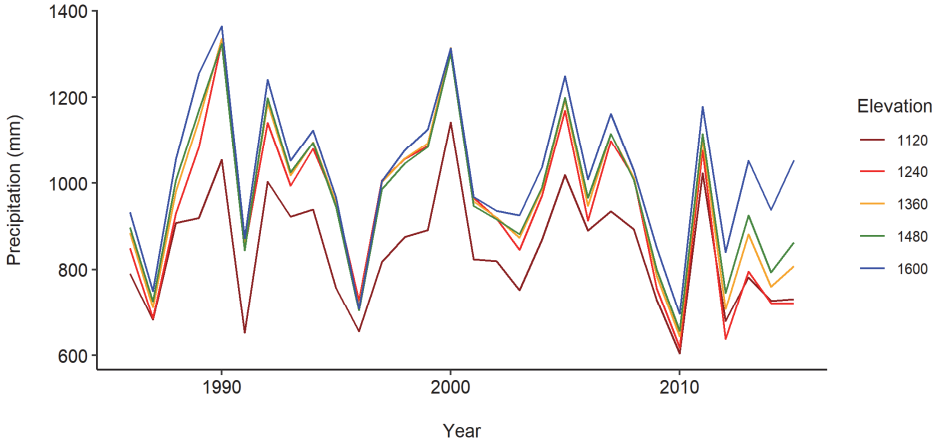

Figure 3.5. Yearly precipitation (mm) from 1986 to 2015 for each elevation (m a.s.l).

Table 3.2. Available nutrients (in ppm) and pH in the soil for each elevation (m a.s.l.) from 11-12 June to 18-19 September 2018. Mean ± SE of total available nitrogen (N), nitrate (NO_3^-), ammonium (NH_4^+), available phosphorus (P), N:P ratio, available potassium (K) and soil pH. Values are averaged over the plots (n=5 or n=3).

Elevation	n	Total N	NO_3^-	NH_4^+	P	N:P	K	pH
1120	5	1.36 ±0.11	-	1.36 ±0.11	0.70 ±0.18	2.35 ±0.56	15.1 ±2.85	3.77 ±0.10
1240	5	1.67 ±0.08	-	1.66 ±0.08	2.23 ±0.54	1.04 ±0.32	33.1 ±3.62	3.94 ±0.24
1360	5	1.63 ±0.10	0.07 ±0.04	1.57 ±0.13	0.78 ±0.17	2.45 ±0.43	40.0 ±5.30	4.28 ±0.12
1480	5	1.87 ±0.22	0.26 ±0.21	1.61 ±0.05	0.34 ±0.05	5.79 ±0.69	14.7 ±3.62	4.66 ±0.28
1600	3	1.62 ±0.23	0.06 ±0.03	1.56 ±0.21	0.18 ±0.03	9.41 ±0.79	24.3 ±10.9	4.33 ±0.04

3.3 Lichen transplant experiment

For **Paper II**, we set up a lichen transplant experiment at a wind-exposed ridge at approximately 1360 m a.s.l. (figure 3.6). The natural vegetation at the site consists mainly

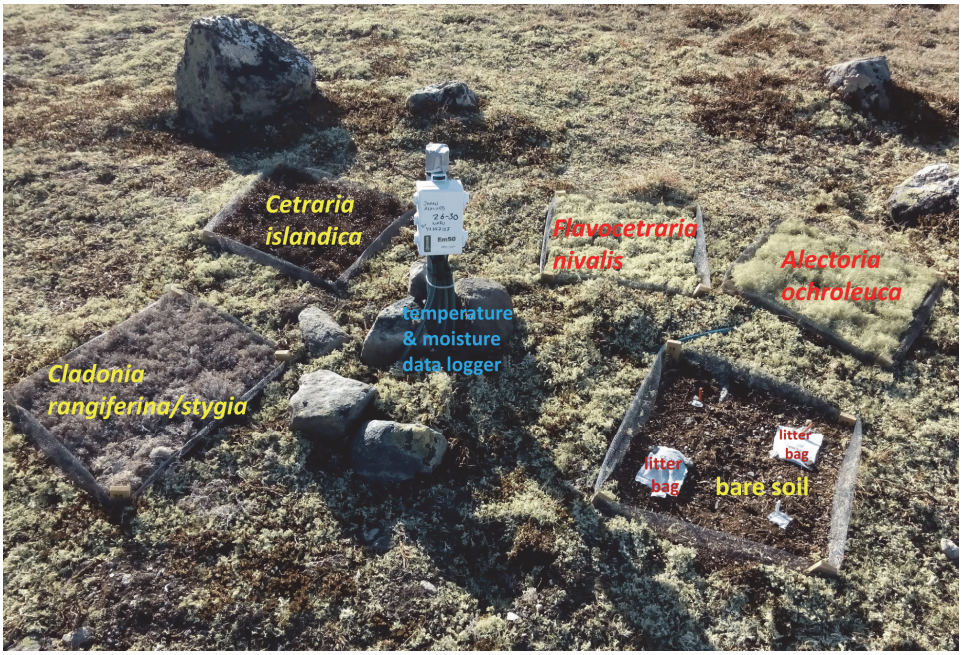

Figure 3.6. Set-up of the lichen transplant experiment, showing one block (Paper II). Each block consisted of five plots, four plots with different mat-forming lichens, and one bare soil control plot. Soil temperature and moisture sensors in each plot were connected to a data logger for each block. In each plot, two types of litter bags were placed under the lichen mats and on top of the soil surface.

of mat-forming lichens *Alectoria ochroleuca* and *Nephromopsis nivalis*. In late August 2016, we established six blocks of five 50×50 cm plots, where we removed all aboveground vegetation. To stabilize and mark the plots, we fenced them with a nylon mesh and wooden poles in the corners, matching vegetation height (ca. 10cm). We filled four plots in each block with thalli of *A. ochroleuca*, *N. nivalis*, *Cetraria islandica*, or a mixture of *Cladonia rangiferina* and *Cladonia stygia*, which we collected from the same site. We combined *C. rangiferina* and *C. stygia* because they are very similar and grow intermixed at the site. The fifth plot in each block acted as a lichen-free control (i.e. bare soil), in order to assess the impact of lichens relative to when they are absent. We placed soil moisture and temperature sensors at 3 cm soil depth, which recorded measurements every 30 minutes for 14 months. From these measurements, we calculated mean soil moisture and temperature over the snow-free season, and soil freeze-thaw cycles throughout the experimental period.

3.4 Functional traits

For **Paper I**, we selected a set of 'soft' (i.e. easy to measure) eco-physiological traits that are known to have a strong impact on carbon and nutrient cycling and are related to the 'leaf economics spectrum', which describes leaf investment strategies from rapid resource acquisition to resource conservation (Wright *et al.*, 2004). An overview of the selected traits and their associations with decomposition is presented in table 3.2. To make the trait measurements comparable between primary producer groups, we used photosynthetic tissues only. As such, we used vascular plant leaves, excluding stems and belowground parts. For lichens and bryophytes we used complete thalli and shoots, respectively, with the exception of bryophyte SLA for which we used only the leaves to enable a better comparison with SLA of vascular plants. Previous studies on bryophyte SLA have mainly considered shoot-level measurements rather than leaf-level measurements (the term Specific Leaf Area is technically incorrect) (Bond-Lamberty and Gower, 2007; Jonsson *et al.*, 2014), because of the small stature of bryophytes and the argument that bryophyte shoots within the bryophyte canopy, could act as an equivalent to vascular plant leaves (Waite and Sack, 2010). We measured leaf-level SLA for bryophytes following the protocol by Lang *et al.*, 2019. An impression of the leaf-level SLA measurements for bryophytes is given in figure 3.7. Detailed descriptions of all trait measurements are given in **Paper I**.

Table 3.2. Description of the functional traits used in **Paper I**; some of them are reused in **Paper III.** Associations and links to decomposition are based on Lavorel and Garnier, 2002; Wright *et al.*, 2004; Santiago, 2007; Lang *et al.*, 2009; Asplund and Wardle, 2017.

Trait	Explanation	Associated with	(Assumed) link to decomposition
N	**Nitrogen concentration**, mass-based (%)	Leaf economics spectrum; relative growth rate	Litter quality
P	**Phosphorus concentration**, mass-based (%)	Leaf economics spectrum	Litter quality
N:P	**N to P ratio**	N limitation versus P limitation; soil age	N-limited vs P-limited decomposition
pH	**Tissue pH**, acidity	Tissue chemistry	Litter quality; acidifying potential
SLA	**Specific leaf area** for vascular plants and bryophytes ($mm^2\ mg^{-1}$)	Leaf economics spectrum; relative growth rate; light exposure	Litter quality
STA	**Specific thallus area** for lichens ($mm^2\ mg^{-1}$)	Water relations; reactivation time and retention time	(Litter quality)
LDMC	**Leaf dry matter content** for vascular plants; homoihydric organisms ($g\ g^{-1}$)	Leaf economics spectrum; correlates negatively with SLA	Litter quality; microclimate
WHC	**Water holding capacity** for lichens and bryophytes; poikilohydric organisms ($mg\ mm^{-1}$ for lichens; $g\ g^{-1}$ for bryophytes)	Water economy; photosynthetic capacity	Microclimate

To link functional traits to decomposability, in **Paper III**, we reused the traits from **Paper I** that were directly comparable between lichens and bryophytes, i.e. N, P, N:P, pH, and WHC (for lichens recalculated to $g\ g^{-1}$). We measured the traits per species per plot, from which we calculated community-level trait means (see Data analysis). For **Paper II**, we measured functional traits of mat-forming lichens on the mat-level. We measured mat density and WHC by taking 10 cm diameter cores of the lichen mat, expressed per mat area (detailed trait measurement descriptions are given in **Paper II**). For **Paper IV**, we studied identity and concentration of secondary metabolite groups in plants and lichens using high-performance liquid chromatography (HPLC); detailed method descriptions are given in **Paper IV**.

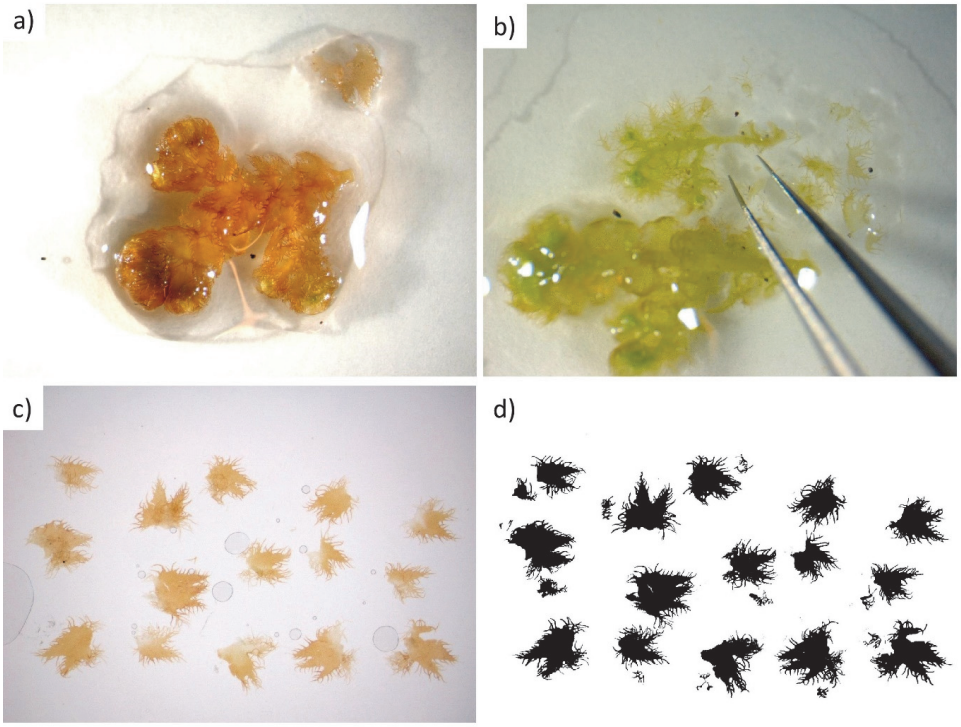

Figure 3.7. Leaf area measurements of *Ptilidium ciliare*, a) shoot tip in a droplet of water, showing the leaves folded around the stem; b) picking leaves from the stem with very fine tweezers; c) stereoscope image of a microscope slide with 15 leaves; c) the same image showing the calculated area, with folded parts of leaves measured twice.

3.5 Decomposition measures

In **Paper II**, decomposition *in situ* was quantified using litter bags of two litter types: freshly senesced leaves of 1) *Vaccinium uliginosum* and 2) *Rubus chamaemorus*, which were collected near the Finse Alpine Research Center. The litter bags were placed under the lichen mats on top of the soil surface in October 2016, and retrieved after one year. In **Paper III**, decomposability was measured following a standardized laboratory bio-assay (Wardle *et al.*, 1998; Asplund and Wardle, 2013). Lichen and bryophyte material from the elevational gradient were incubated in petri-dishes with standardized soil, for 90 days at 22°C, in darkness. Details on the methodologies are given in **Paper II** and **III**.

3.6 Data analysis

For **Papers I, III and IV**, we calculated community-weighted means of functional traits, decomposability and secondary compounds, respectively. We weighted each species'

value with its relative abundance within the community per plot, and calculated the community-weighted mean by taking the sum of the weighted trait values of all measured species per plot (Garnier *et al.*, 2004). To quantify the contributions of species turnover (changes in species composition and abundance) and intraspecific variation to total variation across elevation, we followed the method provided by Lepš et al. (2011). We calculated a 'specific' community-weighted mean using plot-specific measurements for each species, and a 'fixed' community-weighted mean using species averages (plot-independent). The latter reflects the 'mean trait approach': the same species has the same trait value, regardless of where it is found. We calculated the intraspecific variation based on the following principle: if there is a change in fixed community-weighted means across elevation, this can only be the result of species turnover, but if there is a change in the specific community-weighted mean, this can be the result of both species turnover and intraspecific variation. Hence, we can define intraspecific variation as the difference between the specific and fixed community-weighted means. We used these three components in separate one-way ANOVAs with elevation as a factor, for each trait for each primary producer group (**Paper I**), for decomposability, and functional traits, of lichens and bryophytes combined (**Paper III**), and for each secondary compound group for vascular plants and lichens separately (**Paper IV**). Further, we quantified how much variability can be accounted for by the individual components (species turnover effects and intraspecific variation) using Sum of Squares (SS) decomposition. When species turnover effects and intraspecific variation vary independently, then $SS_{specific} = SS_{fixed} + SS_{intraspecific}$; however if they are correlated, then $SS_{specific}$ will be higher (positive correlation) or lower (negative correlation). We calculated the covariation between species turnover effects and intraspecific variation, SS_{cov}, by subtracting SS_{fixed} and $SS_{intraspecific}$ from $SS_{specific}$ (Lepš *et al.*, 2011). Detailed descriptions on further data analyses are given in the separate papers.

4 Results and discussion

In this section, I will summarize and discuss the main findings of the four papers. I will also highlight some aspects that were less discussed in the individual papers, but are still relevant for the overall objectives of this thesis.

4.1 Functional trait responses to elevation

In **Paper I**, we found that responses of functional traits to elevation, i.e. the direction of change across the gradient, differed among traits and between primary producer groups. Community-level N and N:P increased or tended to increase, while P and WHC decreased or tended to decrease with increasing elevation and thus declining temperature, which was consistent across the vascular plant, lichen and bryophyte communities. The responses of other measured traits to elevation, tissue pH, SLA/STA, differed between functional groups. Vascular plant tissue pH increased with increasing elevation, while lichen and bryophyte pH did not respond to elevation. Vascular plant SLA and lichen STA increased or tended to increase, while bryophyte SLA decreased with increasing elevation. Leaf dry matter content (LDMC) in vascular plants decreased with increasing elevation. The responses of community level traits are summarized in figure 4.1.

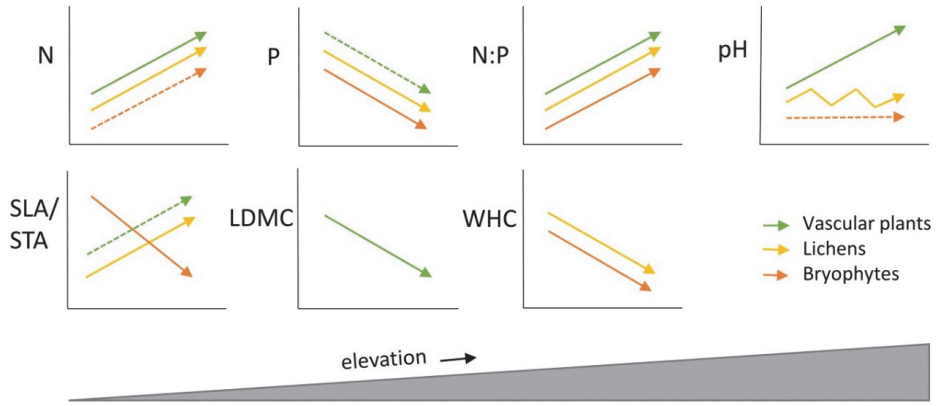

Figure 4.1. Summary of vascular plant (green), lichen (yellow) and bryophyte (orange) functional trait responses to increasing elevation: nitrogen (N) and phosphorus (P) concentration, N:P ratio, tissue pH, specific leaf area (SLA) and specific thallus area (STA), leaf dry matter content (LDMC), and water-holding capacity (WHC). Solid lines indicate significant responses to elevation ($p<0.05$), dotted lines indicate trends when increasing or decreasing ($p<0.1$), or no effect when horizontal ($p>0.1$). Note that arrows only indicate general patterns across elevation, y-axes do not represent the same scales across primary producer groups and measurements of SLA/STA and WHC differ between primary producer groups. Adjusted from Paper I, figures 4 and 6.

Some of the functional trait responses from **Paper I** point towards a shift from a resource-conservative towards a resource-acquisitive strategy with increasing elevation (e.g. increasing N and STA, decreasing LDMC). This is opposite of what we hypothesized, as theory predicts that nutrient availability decreases with elevation due to slower nutrient turnover (e.g. Vitousek, Matson and Turner, 1988; Sveinbjörnsson *et al.*, 1995). However, available nutrients in the soil across the gradient (table 3.2) do not show a clear decreasing trend with elevation (with the exception of P), indicating that our gradient is one of the numerous exceptions to the existing theory (e.g. Frangi *et al.*, 2005; Sundqvist *et al.*, 2014). Nevertheless, increasing N:P ratio with elevation in all three primary producer groups are in line with increasing available N:P in the soil, and tissue N:P and available N:P are significantly correlated for all three groups (figure 4.2).

The total available N in the soil cannot fully explain the increasing N concentration in vascular plant and lichen tissue with increasing elevation. However, increasing N concentrations with increasing elevation are not uncommon (Körner, 1989). A possible explanation is that high-elevation plants experience constraints on growth, which prevents dilution of N within the plant, and therefore leaf N concentrations do not necessarily reflect soil fertility or N supply (Körner, 2003). Less dilution of N might also result from a shift in plant-plant interactions from competition at lower elevation towards facilitation at higher elevation where abiotic stress is high (Choler, Michalet and Callaway, 2001; Callaway *et al.*, 2002). At higher elevations and more exposed sites, plants may profit from their neighbours, for instance through insulation, wind reduction or soil stabilization, which might result in a surplus of resources, such as N, that do not need to be invested in growth. Another explanation of increasing N at higher elevation

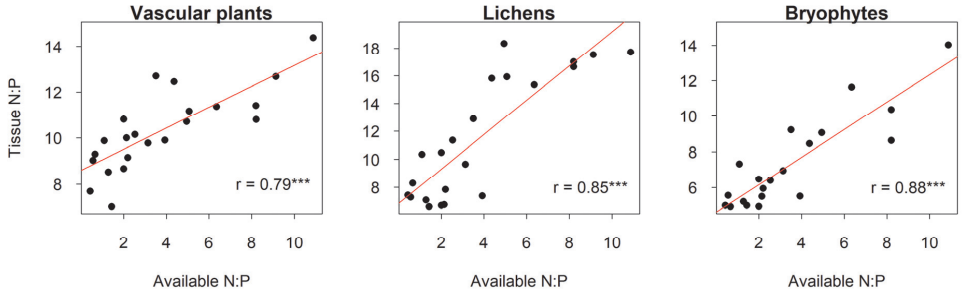

Figure 4.2. Tissue nitrogen to phosphorus ratio (N:P) in vascular plants, lichens and bryophytes explained by available N:P in the soil. Pearson's correlation coefficients (r) are given and significant correlations are denoted with *** for p<0.001.

might be an increased uptake of organic N forms such as glycine instead of inorganic nitrate and ammonium (Averill and Finzi, 2011).

At high elevation, low temperature leads to less transpiration from lichens and plants and less evaporation from soil. This effect is strengthened by the increased precipitation levels we found at higher elevation. Decreased evapotranspiration is likely the reason why water-holding capacity (WHC) decreases with elevation, because lichens and bryophytes can manage with lower WHC while remaining photosynthetically active, compared to lower elevations where evapotranspiration is higher. Alternatively, the decrease in bryophyte WHC could also be the result of a change in strategy, from high water storage towards minimizing water loss. This is indicated by high abundance of species with hyaline hair points at higher elevations (*Polytrichum spp.* and *Racomitrium spp.*). Hyaline hair points have been hypothesized to reduce speed of water loss of a tuft by forming a thick boundary layer with quieter air, and by reflecting solar radiation (Ah-Peng *et al.*, 2014). Because of the poikilohydric nature of lichens and bryophytes, WHC also depend for a large part on externally held water, e.g. in capillary spaces on the thallus surface or in between leaves (Proctor, 2000; Esseen *et al.*, 2017). However, we only measured internal WHC to allow for better comparison with vascular plants. We therefore do not know how elevation affects the total water-holding capacity (i.e. internal and external).

In lichens, specific thallus area (STA), or the inverse, specific thallus mass (STM), strongly relates to WHC (Gauslaa, 2014; Phinney, Solhaug and Gauslaa, 2018), with low STA resulting in high WHC. Across elevation, STA follows a similar increasing pattern as vascular plant SLA, which is in line with previous studies that found that lichen STM followed the same pattern as vascular plants across a soil fertility gradient (Asplund, Sandling and Wardle, 2012; Asplund and Wardle, 2014). In contrast, bryophyte SLA strongly decreased with elevation, which is the result of a shift towards species with thicker leaves at higher elevations. Thus, the bryophytes seem to follow the trend of declining SLA with increasing elevation, which we predicted for the vascular plants, although we do not know if bryophyte SLA relates to resource strategy similar to vascular plants.

4.2 Secondary compound responses to elevation

In **Paper IV**, we found that vascular plant secondary compounds decrease, while lichen secondary compounds increase with increasing elevation. The decrease in plant secondary compounds is in contrast to De Long et al. (2016), who found increasing concentrations with increasing elevations in a similar ecosystem. However, these opposing responses to elevation can be attributed to the decrease in ericaceous shrubs along our gradient, versus an increase in ericaceous shrubs at higher elevations in De Long et al. (2016). The increase in lichen secondary compounds with increasing elevation is in line with the Growth-Differentiation Balance Hypothesis, which predicts higher investments in secondary metabolism because of a surplus in carbon (C) when conditions limit C to be invested in growth (Herms and Mattson, 1992; Stamp, 2003).

Within plant secondary compounds, the ratio of flavonoids to condensed tannins increases with elevation, which means that at lower elevations, the concentration of condensed tannins (anti-herbivory) is higher than flavonoids (photo-protection), while at higher elevations, the opposite is true. This indicates a shift from invertebrate herbivore defence at low elevation (Moreira *et al.*, 2017) towards photo-protection at high elevation. Within lichen secondary compounds, medullary compounds (anti-herbivory) increase with elevation while cortical compounds (photo-protection) peak at the second-highest elevation. The general increase in usnic acid concentration with elevation is in line with previous work (Bjerke *et al.*, 2004).

4.3 Species turnover and intraspecific variation

In **Paper I**, we found that the contribution of intraspecific variation to community-level trait variation differs between primary producer groups as well as between functional traits (figure 4.3).

Species turnover is the most important contributor to community-level trait variation for most of the **vascular plant** traits across elevation, in line with previous studies (e.g. Kichenin et al. 2013; Mayor et al. 2017), although intraspecific variation is an important contributor to total variation in nutrient concentrations (in line with Siefert *et al.*, 2015). The responses of vascular plant pH, SLA and LDMC can be explained by a shift in dominance of *Betula nana* at the lowest elevation, to ericaceous shrubs at the middle elevations, and *Salix herbacea* and graminoids (mainly *Carex bigelowii*) at the highest

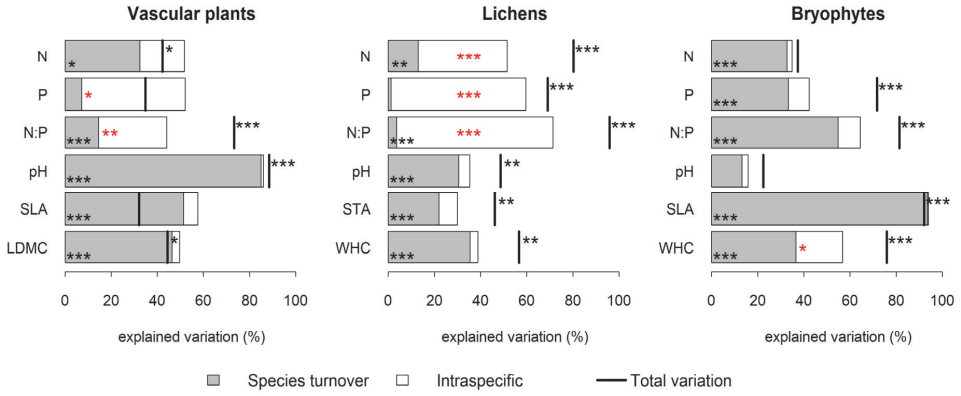

Figure 4.3. The contributions of species turnover and intraspecific variation to trait variation explained by elevation (as percentage of total variation in traits, including variation not explained by elevation) for vascular plant, lichen, and bryophyte functional traits (see table 3.2 for explanations). Grey bars indicate effects of species turnover, while white bars correspond to intraspecific variability effects. The black lines denote total variation (i.e. the sum of species turnover and intraspecific variability effects and their covariation) explained by elevation. If the black bar is above the column, covariation between species turnover and intraspecific variation is positive. In contrast, if the black bar crosses the column, the covariation is negative. The significance of the response of the different components to elevation is denoted with * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$); subscript refers to species turnover, superscript to total variation, and symbols at the baseline to intraspecific variation (in red). From Paper I.

elevations (Paper I, table S2). Graminoids have higher SLA, lower LDMC and higher pH compared to ericaceous shrubs.

The species shifts in the vascular plant community are most likely the result of declining temperature, as shrubs are more temperature-limited than graminoids and are expanding in arctic, high-latitude and alpine tundra as a result of climate change (e.g. Myers-Smith *et al.*, 2011). However, the observed species shifts might also be related to changes in soil nutrients and herbivory. In subarctic ecosystems, invertebrate herbivory usually decreases with elevation (Moreira *et al.*, 2017), while vertebrate herbivory often increases with elevation (Vistnes *et al.*, 2008; Hoset *et al.*, 2014), which is in line with the increase in dropping observations at higher elevations across our gradient. Lemmings probably have the strongest impact on vascular plants on ridges, as their diet consist for a large part of graminoids and mosses, supplemented with other seed plants (Soininen *et al.*, 2013), matching the vegetation we observed at high elevation. In contrast, reindeer will likely select for sites with lusher vegetation because of their high energy demand

during summer (Vistnes *et al.*, 2008), thus having limited effect on vascular plants on ridges such as our sites.

In **lichens**, intraspecific variation is the most important contributor to nutrient concentrations across elevation, while species turnover effects are more important in non-chemical traits. This is in line with previous studies that found high intraspecific variation in lichens (Asplund and Wardle, 2014; Coyle, 2017), and corresponds to a meta-analysis study on plants highlighting the importance of intraspecific variation in nutrient concentrations (Siefert *et al.*, 2015). Further, even when intraspecific variation is small, it greatly enhances the total variation explained by elevation in lichen traits, through positive covariation with species turnover effects.

Although the lichen community is more similar across the gradient than the vascular plant and bryophyte communities (see figure 3 in Paper I), there are still some changes in species composition, which generally involve a decrease in mat-forming *Cladonia* spp., an increase in melanic species such as *Cetraria* spp. and small-stature *Cladonia* species with increasing elevation. These changes could be the result of increased reindeer grazing, as reindeer do not prefer small *Cladonia* spp. and melanic species, which therefore increase in abundance under higher grazing pressure. The presence of the pioneer bryophyte *Polytrichum piliferum* at the highest two elevations further supports this notion (Vistnes and Nellemann, 2008). Increased reindeer herbivory with elevation are in line with literature (Vistnes *et al.*, 2008), although there seems to be more reindeer observations from the middle sites (1360 and 1480 m a.s.l.) than from the highest site (Strand *et al.*, 2011). This means that the increase in STA and the decrease in WHC with elevation could be partly driven by reindeer grazing.

Species turnover is the main contributor in all of the **bryophyte** traits, which can be explained by the strong shift in species composition across the gradient. The change in composition of the bryophytes generally involves a decrease in 'forest' species such as *Pleurozium schreberi* and *Hylocomium splendens*, towards more arctic-alpine species such as *Polytrichum hyperboreum* and *Racomitrium lanuginosum* (Paper I, table S2), although the changes in bryophyte composition are likely also related to changes in soil pH (Becker Scarpitta *et al.*, 2017). Lemmings also feed on mosses, notably *Dicranum* species, which could also have affected the observed bryophyte composition (Soininen *et al.*, 2013). The vegetation shift fully explains the decreasing SLA with increasing elevation, as

P. schreberi and *H. splendens* have one cell-layer thin leaves (thus high SLA), while *Polytrichum* species have thick leaves formed by lamellae of several cell layers (thus low SLA). Even though species turnover in the bryophytes is strong, intraspecific variation explains a substantial part of WHC, indicative of high within-species plasticity in this trait. Further, intraspecific variation enhances the total variation explained by elevation through positive covariation with species turnover effects in WHC, P and N:P, highlighting that intraspecific variation can be important even when species turnover is strong.

In **Paper IV**, we found that total secondary compounds in plants and lichens are mainly driven by species turnover effects, but intraspecific variation greatly increases the total variation explained by elevation. Lichen cortical compounds, notably usnic acid, are for a large part driven by intraspecific variation, in line with previous studies showing trends in usnic acid concentrations across climatic gradients in *Nephromopsis nivalis* (Bjerke *et al.*, 2004) and *Cladonia arbuscula* (Nybakken, Sandvik and Klanderud, 2011).

4.4 Effects of lichens on microclimate and decomposition

In **Paper II**, we found that lichen mats affect the microclimate by insulating the soil against warm and cold temperatures, but lichens do not affect soil moisture. Further, *Cladonia rangiferina/ C. stygia* insulates better than other lichens. Insulation capacity of lichen mats is stronger with higher water-holding capacity (figure 4.4a), which is partly related to mat density, while lichen colour has no effect on microclimate. This is in line with a study on bryophytes, which found that differences in heat transfer through bryophyte mats were explained by mat thickness and water content (Soudzilovskaia, van Bodegom and Cornelissen, 2013). Thus, the influence of poikilohydric organisms such as lichens and bryophytes on microclimate seems to follow basic physical processes, affected by mat structure, rather than biological processes.

Decomposition of *Vaccinium uliginosum* litter was faster under *Nephromopsis nivalis* than under *Alectoria ochroleuca* (figure 4.4b). Lichen traits or lichen effects on microclimate could not explain this difference, but soil moisture was weakly correlated with decomposition rate. The selected lichen species differ in their secondary chemistry, e.g. *N. nivalis* does not have medullary compounds. However, we found that secondary compounds hardly leach from the lichens, in line with Stark et al. (2007) who found that lichen phenolic compounds are not leached out by rainwater and are not anti-microbial in soil. We propose that lichens' secondary chemistry impact on the microbial

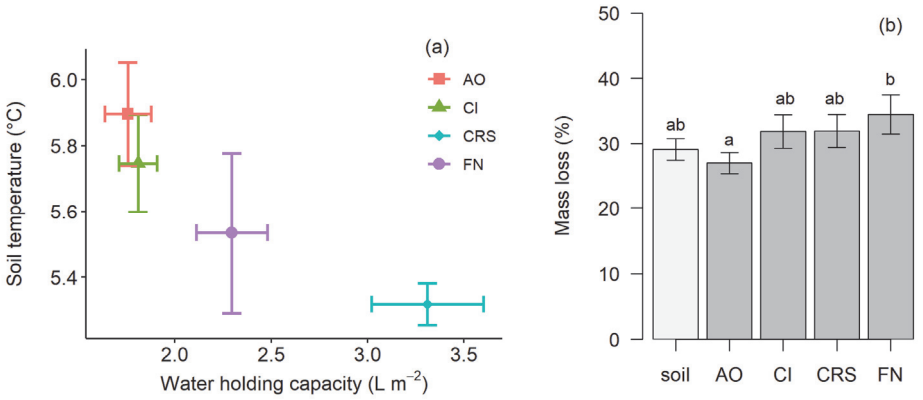

Figure 4.4. (a) Observed relationship between growing season soil temperature (°C) at 3 cm depth and lichen mat water holding capacity, given in mean ± SE per lichen species. (b) Mass loss (%) of *Vaccinium uliginosum* litter after one year of incubation under lichen mats and on bare soil. Different letters indicate significant differences between lichen mats ($p<0.05$). AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina/C. stygia*, FN = *Nephromopsis nivalis*. Adjusted from Paper II, figures 2 and 3.

communities living in the lichen thallus, as lichens host a large variety of microbes (Pankratov *et al.*, 2017). Differences in microbial communities could have resulted in the observed differences in decomposition rates underneath lichen mats.

4.5 Decomposability across elevation

In **Paper III**, we found that community-level decomposability of lichens and bryophytes increases with increasing elevation, in contrast to our expectations. Decomposability is explained by nutrient concentrations, tissue pH and the relative contribution of bryophytes versus lichens at the community level, while only tissue pH and primary producer group (lichens versus bryophytes) explain decomposability across the whole dataset (figure 4.6). The increase in decomposability with elevation can be partly explained by a parallel increase in N concentration and N:P ratio. Higher N indicates higher litter quality, which enhances decomposition, in line with previous work on lichens and bryophytes (Lang *et al.*, 2009; Asplund and Wardle, 2013), and general theory based on vascular plants (Cornwell *et al.*, 2008). Increasing N:P indicates a decrease in N-limited decomposition at higher elevations (Güsewell and Verhoeven, 2006). Irrespective of elevation, tissue pH was an important predictor of decomposability, in line with previous work (Cornelissen *et al.*, 2006; Asplund and Wardle, 2013). Primary producer group was another important predictor, with bryophytes having overall lower

decomposability than lichens, consistent with previous studies showing that bryophytes decompose very slowly (Hobbie, 1996; Lang *et al.*, 2009).

We found that species turnover drives community-level decomposability of lichens and bryophytes across elevation, while intraspecific variation contributes little to decomposability, in line with Jackson, Peltzer and Wardle (2013). This indicates that although intraspecific variation may be important in functional traits, it may not necessarily be an important driver of ecosystem processes such as decomposition. It also indicates that decomposability may be more responsive across environmental gradients where there is strong species turnover. Changes in reindeer and lemming herbivory across the gradient might have played a role in the observed shift from slow to faster decomposing species with elevation. In contrast to decomposability, intraspecific variation was important in N and P release during decomposition, implying that nutrient cycling might be more affected by intraspecific variation than carbon cycling.

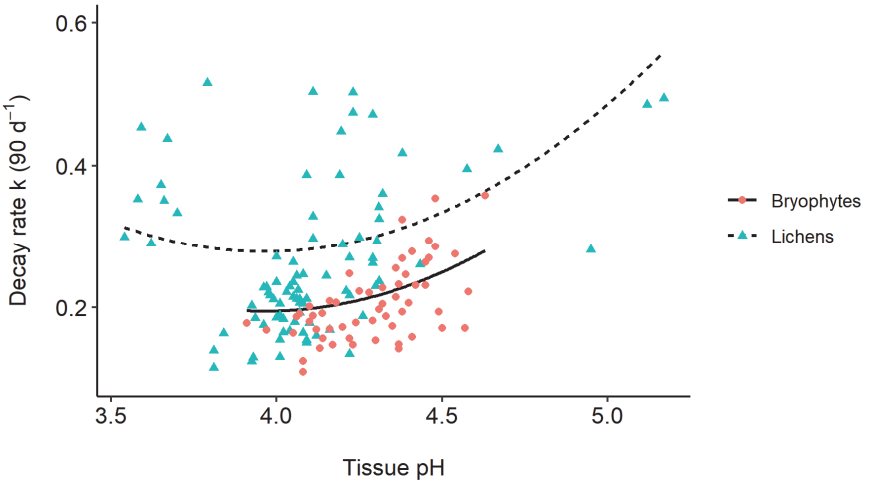

Figure 4.6. Decomposability (decay rate k) of individual lichens and bryophytes explained by tissue pH. Dots and triangles denote the actual plot-level measurements for each bryophyte and each lichen, respectively, while lines denote model predictions. From Paper III.

5 Concluding remarks and implications

Our findings from the elevational gradient highlight that our gradient does not necessarily follow the theory based on previous studies across elevation, as many trait responses indicate a shift towards resource acquisition with elevation, rather than the expected shift to resource conservation (**Paper I**). In line with these findings, we found that decomposability of lichens and bryophytes across the gradient increased with elevation, caused by a shift from slow- to faster-decomposing species (**Paper III**). Secondary compounds showed contrasting responses: they decreased in vascular plants and increased in lichens with increasing elevation (**Paper IV**). Many of the functional trait responses were at least partly driven by intraspecific variation, notably in lichens, while decomposability was almost entirely driven by species turnover effects. Finally, in the lichen transplant experiment, we found that mat-forming lichens insulated against temperature extremes and affected decomposition of plant litter (**Paper II**).

The elevational gradient is primarily a temperature gradient, but other factors also change with elevation. I presented additional data on precipitation, available nutrients in the soil, and herbivory; which indicate an increase in precipitation, variable soil nutrient status, and an increase in vertebrate herbivory with increasing elevation. In addition to temperature, these factors might have affected species composition and/or the observed responses in functional traits, secondary compounds and decomposability. However, all of these factors are hard to separate from elevation, and it is likely that they would have shown similar patterns across any elevational gradient in the same study area. Despite changes in other factors than temperature, the elevational gradient can be used as a space-for-time substitution to predict how vascular plants, lichens and bryophytes may respond to climate change.

Under future climate change, across the gradient, I expect that lichen species may be more capable than vascular plant and bryophyte species in adapting to new environmental conditions, because of high intraspecific plasticity in functional traits that respond strongly to elevation (**Paper I**), and high intraspecific plasticity in cortical secondary metabolites (**Paper IV**). Intraspecific variability can help to maintain community stability and functioning under changing conditions (Jung *et al.*, 2010; Malyshev *et al.*, 2016), implying that the lichen community may be more resilient than vascular plants and bryophytes, which lack the intraspecific variation to cope with

environmental change. This is somewhat contradictory to previous studies, as lichens (and bryophytes), have been shown to respond negatively to global change phenomena such as increased temperatures (e.g. Elmendorf *et al.*, 2012). However, this response is at least partly due to increased competition from vascular plants. Thus, lichen communities will only benefit from their intraspecific plasticity in areas where conditions are too harsh for vascular plants to establish, even under climate warming. In contrast, I expect that the vascular plant and bryophyte species across the gradient may be more vulnerable to future climate change, because they exhibit less intraspecific plasticity across elevation. The bryophyte and vascular plant communities are likely to experience species turnover when temperatures are increasing, which may be strongest for the bryophytes (Becker Scarpitta *et al.*, 2017). Further, as variation in decomposability of the lichen and bryophyte community across elevation is mainly driven by species turnover effects (**Paper III**), in line with work on vascular plants (Jackson, Peltzer and Wardle, 2013), I expect that climate change will impact mostly on decomposability of bryophytes and vascular plants. Finally, the increase in decomposability of lichens and bryophytes with elevation suggests a shift to slow-decomposing species, which might counterbalance increased microbial respiration under higher temperature.

Even though we found that lichen secondary compounds increased (**Paper IV**), cryptogam decomposability (which consisted for the largest part of lichens) did not decline, but increased with elevation (**Paper III**). Although we could not directly test the link between decomposability and secondary compounds, our findings suggest that across the gradient, secondary compounds do not affect decomposability in lichens substantially. Other functional traits could be more important than secondary compounds in driving decomposability, or qualitative differences (i.e. compound composition) could be more important than quantitative differences (Asplund and Wardle, 2013). The decrease in vascular plant secondary compounds and palatability with elevation suggests an increase in vascular plant decomposability (Cornelissen *et al.*, 2004), in line with the observed increase in lichen and bryophyte decomposability with elevation. The strong increase in tissue pH in vascular plants with elevation (**Paper I**) might enhance this pattern even further, as tissue pH is an important predictor in lichen and bryophyte decomposability and has previously been linked to vascular plant decomposition (Cornelissen *et al.*, 2006).

Lichen species identity can affect both soil microclimate and plant litter decomposition (**Paper II**); however, the mechanisms behind these processes differ. Differences in how lichens affect soil microclimate are driven by lichen mat morphology resulting in different water holding capacity and thus insulation capacity. Meanwhile, decomposition of plant litter seems unrelated to lichen traits and insulation capacity, likely because the differences in microclimate are too small to overrule the effects of litter quality and decomposer community (Bradford *et al.*, 2017). Further, it indicates that lichens can affect decomposition of other litter types, possibly by affecting the microbial community. This may have consequences for carbon and nutrient cycling in mixed communities of vascular plants and lichens.

The findings from my thesis highlight the importance of including lichens and bryophytes in trait-based studies, especially in ecosystems where they contribute substantially to primary production, as they might show completely different responses to the same environmental gradient. The strength of the elevational gradient is that it allows for a direct comparison between vascular plants, lichens and bryophytes, because they were sampled from the same plots across the same gradient. This holds true even when temperature is not the only environmental factor that changes across the gradient. My thesis shows that contrasting drivers of trait variation in lichens, bryophytes and vascular plants across environmental gradients, i.e. species turnover and intraspecific variability effects, can have large implications for ecosystem functioning and ecosystem processes such as decomposition.

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Paper I

Contrasting drivers of community-level trait variation for vascular plants, lichens, and bryophytes across an elevational gradient

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Abstract

1. Across environmental gradients, community-level functional traits of plants can change due to species turnover, intraspecific variation and their covariation. Studies on vascular plants suggest that species turnover is the main driver of trait variation across gradients, although intraspecific variation can also be important. However, there is limited knowledge about whether this holds for non-vascular primary producers such as lichens and bryophytes. We hypothesized that intraspecific variation is more important for non-vascular than for vascular primary producers because they lack specialized structures to maintain homeostasis, and should therefore be more responsive to extrinsic factors.
2. To assess the relative importance of species turnover versus intraspecific variation for vascular plants, lichens and bryophytes, we estimated species abundance and measured chemical (tissue nitrogen (N) and phosphorus (P) content, N:P ratio and pH)

and non-chemical (specific leaf or thallus area, dry matter content and water holding capacity) functional traits along an elevational gradient in alpine southern Norway. We calculated community-weighted mean traits and quantified the relative contribution of species turnover, intraspecific variation, and their covariation to total trait variation across the gradient.

3. We found mixed support for our hypothesis: the contribution of intraspecific variation to total trait variation for N and N:P was higher in lichens than in vascular plants and bryophytes, but in general the contribution of intraspecific variation differed among functional traits and producer groups. Nutrient variables (N, P and N:P) were significantly impacted by intraspecific variation for vascular plants and lichens but not for bryophytes. Non-chemical traits and pH were mainly driven by species turnover effects in all primary producer groups.
4. Our results highlight that while nearly all studies on primary producer trait variation across environments have focused on vascular plants, trait variation of other largely neglected but ecologically important producer groups, such as lichens and bryophytes, may show very different responses to the same environmental factors. In order to fully understand how future environmental changes impact on community and ecosystem level processes, traits of primary producers other than vascular plants – and their-within species variation – need to be considered in systems where these groups are abundant.

Keywords: alpine ecology, climate gradient, community-weighted mean, functional traits, intraspecific variation, non-vascular plants, species turnover, tundra

Introduction

Over the last decades, trait-based approaches have taken center stage in ecological research. In contrast to methods based on species identifications, trait-based approaches allow for generalizations across multiple species, communities, and entire ecosystems necessary to answer a variety of ecological questions (McGill *et al.*, 2006; Violle *et al.*, 2007; Enquist *et al.*, 2015; Levine, 2016; Funk *et al.*, 2017). Recent examples of such trait-based studies include those that attempt to understand how traits relate to community assembly (Bagousse-Pinguet *et al.*, 2014; Kumordzi *et al.*, 2015), competitive interactions (Kunstler *et al.*, 2016)

and coexistence (Adler *et al.*, 2013); how communities respond to disturbance (Mouillot *et al.*, 2013) and climate change (Bjorkman *et al.*, 2018); and how traits underpin ecosystem services (Lavorel *et al.*, 2011; Lavorel, 2013; Faucon, Houben & Lambers, 2017; Kohler *et al.*, 2017), agricultural production (Wood *et al.*, 2015), and ecosystem restoration (Zirbel *et al.*, 2017). Although the trait-based approach finds its roots within plant ecology, there is also a growing use of it beyond the plant kingdom (e.g. Moretti *et al.*, 2017).

Functional traits of common species contribute more to the ecological functioning of a community than those of rare species in the majority of cases, in line with Grime's mass ratio hypothesis (Grime, 1998). Thus, in order to capture a community by one mean trait value, this value is often weighted by the relative abundance of each species within that community to yield a 'community weighted' trait value (Garnier *et al.*, 2004). To understand how these community-weighted trait values respond to environmental change, gradients provide powerful tools (Malhi *et al.*, 2010). For example, lower temperatures with increasing elevation (Körner, 2007), and subsequent declining availability of nutrients (notably nitrogen (N) and phosphorus (P), see Huber *et al.*, 2007), lead to a shift in community-weighted trait values from those associated with rapid resource acquisition to resource conservation in vascular plants (Sundqvist, Sanders & Wardle, 2013; Read *et al.*, 2014). As such, plants at higher elevations generally have leaves with lower tissue nutrient concentrations and low specific leaf area (SLA), although there are many exceptions (Reich & Oleksyn, 2004; van de Weg *et al.*, 2009; Sundqvist, Giesler & Wardle, 2011; Read *et al.*, 2014).

An increasing number of studies over the past decade have contributed to the realization that traits can vary considerably within as well as between species (Kraft, Valencia & Ackerly, 2008; Messier, McGill & Lechowicz, 2010; Violle *et al.*, 2012; Adler *et al.*, 2013; Enquist *et al.*, 2015; Kuebbing, Maynard & Bradford, 2018). This poses questions about whether variation in community-level trait values along gradients is driven primarily by species turnover (which incorporates both the presence/absence of species in the community and the abundance structure of species that are present) or intraspecific trait variation. In most studies on vascular plants, species turnover is the main driver of community-weighted mean trait values, but intraspecific variation often plays an important role (Albert *et al.*, 2010a; Albert *et al.*, 2010b; Messier, McGill & Lechowicz, 2010; Lepš *et al.*, 2011; Kichenin *et al.*, 2013; Siefert *et al.*, 2015; Mayor *et al.*, 2017), depending on the trait considered (Derroire

et al., 2018). In contrast to vascular plants, a limited number of studies suggest that intraspecific variation in other primary producers such as lichens, may be more important than changes in species composition. For example, Asplund & Wardle (2014) showed that intraspecific variation was the main driver of changes in community-level trait values of epiphytic lichens across a strong successional gradient, and Coyle (2017) found that phenotypic plasticity allowed lichen species to persist along gradients within forest canopies. In Figure 1, we present a conceptual framework of the drivers of community-level trait changes across environmental gradients such as elevation. It shows that species turnover and intraspecific variation can each result in the same community-level trait response, and that when they occur together they can also increase each other's effects and thus result in an even stronger response. This is potentially applicable to any trait of any group of organism across any environmental gradient.

The apparent lack of trait studies on the non-vascular component of vegetation, in particular lichens and bryophytes (Deane-Coe & Stanton, 2017; Martin & Mallik, 2017), persists despite their ubiquitous presence and importance in many ecosystems around the world, and notably those at high elevations and latitudes. Lichens and bryophytes contribute to global nutrient and carbon (C) cycling, hydrology, and are involved in many trophic interactions (Turetsky, 2003; Cornelissen *et al.*, 2007; Lindo & Gonzalez, 2010; Elbert *et al.*, 2012; Turetsky *et al.*, 2012; Porada *et al.*, 2014; Asplund & Wardle, 2017). In addition, both lichens and bryophytes respond strongly to experimental climate change (Tuba, Slack & Stark, 2011; Elmendorf *et al.*, 2012; Matos *et al.*, 2017). They differ from vascular plants in their lack of specialized structures to regulate rates of water loss from their tissues (i.e. poikilohydry) and poor ability to take up nutrients from soil – although many are well adapted in absorbing N from atmospheric sources or in association with N_2-fixing cyanobacteria. As expected from organisms that reflect their immediate environment, large intraspecific variation has been found in lichen traits such as nutrient concentrations (Palmqvist *et al.*, 2002; Asplund & Wardle, 2014) and specific thallus area (STA – analogous to plant's specific leaf area, see: Snelgar & Green, 1981; Gauslaa *et al.*, 2009; Solhaug *et al*., 2009; Asplund, Sandling & Wardle, 2012). Similarly, large intraspecific responses have been found in bryophyte traits, such as photosynthetic and N_2- fixation rates (Skre & Oechel, 1981; Gavazov *et al.*, 2010; Turetsky *et al.*, 2012). Yet, the relative importance of species turnover versus intraspecific variation as

drivers of community-level traits across gradients has not directly (i.e. in the same study system) been compared among vascular and non-vascular components of vegetation.

In this study, we aim to assess the relative importance of species turnover versus intraspecific variation as drivers of community-level trait variability across an elevational gradient, separately for each of three groups of primary producers: vascular plants, lichens, and bryophytes. To do this, we sampled species for all three groups along a gradient with a range of approximately 500 m in alpine Finse, southern Norway. We test the hypothesis that community-level trait variation across the gradient is driven mainly by changes in species turnover for vascular plants, and mainly by intraspecific variation for lichens and bryophytes (Figure 1). We expect this because lichens and bryophytes reflect their immediate surroundings more than vascular plants, since they are less capable of regulating their moisture and nutrient status. The results of this study will contribute to our understanding of drivers of trait variation of previously understudied but ecologically important non-vascular primary producers, and how this compares to drivers of trait variation for vascular plants. Further, because elevational gradients can be used as space-for-time substitutions for predicting the effects of future climate warming (Sundqvist, Sanders & Wardle, 2013; Elmendorf *et al.*, 2015), our study aims to better understand the mechanisms by which community-level trait variation of vascular plants, lichens and bryophytes will respond to future increases of temperature in alpine ecosystems.

Materials and methods

Study site and plot selection

This study was performed at Finse, southern Norway (60° 33' N – 60° 38' N, 7° 34' E – 7° 42' E) in July and August 2016. The Finse meteorological station is located at 1210 m a.s.l., and has an average yearly temperature of -2.1 °C and 1030 mm yearly precipitation (1969-90, Norwegian Meteorological Institute). The average summer (June-August) temperature in 2016 was 7.3°C and total summer precipitation was 303.9 mm (Norwegian Meteorological Institute, 2016).

We selected five sites along an elevational gradient spanning 480 m, at approximately 1120, 1240, 1360, 1480 and 1600 m a.s.l., all on south-facing slopes on acidic granite and gneiss bedrock. The lowest site is situated approximately 150 m above the nearest tree line

(*Betula pubescens* ssp. *czerepanovii*). Because most lichens respond negatively to snow cover (Bidussi, Solhaug & Gauslaa, 2016; Niittynen & Luoto, 2018) and are therefore absent from depressions in the landscape where snow accumulates, we selected sites on exposed ridges that support communities with a mixed cover of vascular plants, lichens and bryophytes. The vascular plant communities are relatively species poor, with *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* as most common at the lowest elevations, and *Carex bigelowii* and *Salix herbacea* at the higher elevations. Common lichen species are *Cladonia arbuscula s. lat.*, *C. rangiferina* and *Flavocetraria nivalis*. The bryophyte species *Pleurozium schreberi* and *Dicranum acutifolium* are common at lower elevations, while *Polytrichum hyperboreum*, *P. alpinum* and *Racomitrium lanuginosum* are common at higher elevations. At each site, we selected five 1 m^2 plots within a 100 m radius by randomly throwing an object, on the condition that all three groups (i.e. vascular plants, lichens and bryophytes) were present. Within elevations, the median distance between replicate plots was ca. 43 m. Because of the high small-scale spatial heterogeneity (e.g. in topography, microclimate, soil fertility and biodiversity) in these communities, which occurs over the meter scale (Björk *et al.*, 2007; Opedal, Armbruster & Graae, 2015), this distance is sufficient to ensure adequate independence among plots and is in line with previous studies along elevational gradients in these types of environments (e.g. Veen *et al.*, 2017).

Temperature gradient

Air temperature was measured 20 cm above ground in each plot at 20-minute intervals between 5 September 2016 and 22 August 2017, using shaded Tinytag loggers (Plus 2 TGP-4017, Gemini Co., UK). For each elevation, we calculated mean annual temperature, average temperature at the coldest and the warmest day, number of diurnal freeze-thaw cycles, monthly mean temperature in January and July, and the number of growing degree days (defined as number of days with average temperature above 5°C (see Table S1). Mean July temperature decreased on average by 0.9 °C with each level (120 m) of increasing elevation (ANOVA, $F=240.7$, $p<0.001$; Figure 2), which corresponds well with the mathematical dry adiabatic lapse rate with elevation of 9.8 °C/1000 m. The growing season was 54 days shorter at the highest site compared to the lowest site in our gradient (GLM with Poisson distribution; Analysis of Deviance, Resid. Dev=0.716, $p<0.001$; Figure 2). These data show that our selected sites were placed along a distinct and strong growing season temperature gradient.

Vegetation survey and harvesting

To quantify species composition along the gradient, vascular plant, lichen, and bryophyte cover were estimated in each plot between 11 and 24 July 2016 (see Table S2 for a species list). This cover was estimated visually with a 1 x 1 m metal frame, divided with plastic wire into four quadrates of 50 x 50 cm. Each quadrate was divided into 25 10 x 10 cm squares to allow for more accurate cover estimates. We estimated the cover for each species per quadrate and subsequently calculated the whole-plot cover from the average cover across all four quadrate. Between July 28 and August 18, 2016, one quadrate per plot was destructively harvested and all aboveground material was collected and sorted to species for functional trait measurements. For some rare species, it was not possible to collect sufficient material, and we therefore restricted our analysis to the most abundant vascular plant, lichen, and bryophyte species that collectively composed at least 80% of the cover per group per plot, in line with other studies (Pakeman & Quested, 2007). For bryophytes, we were not able to attain data on 80% of the cover for one plot at 1480 m a.s.l and one at 1600 m a.s.l., and these two plots were therefore excluded from further analyses. In case insufficient material was available for a given species within the harvested quadrate, we sampled additionally from the other quadrates in the same plot or within the immediate surroundings of the plot, making sure that equal numbers of individuals were sampled from both infrequent and abundant species. After harvest, vascular plant samples were stored in moist, sealed plastic bags at 4 °C until trait measurements. Lichens and bryophytes were kept in paper bags and air dried at room temperature. Except for the common species *Ptilidium ciliare*, liverworts were excluded from bryophyte community trait analysis due to their minor contribution to vegetation cover.

Selection of functional traits

In this study, we use a selection of “soft” (i.e. easy to measure, *sensu* Hodgson *et al.*, 1999) eco-physiological traits that are known to exert a strong impact on ecosystem C and N cycling rates (Perez-Harguindeguy *et al.*, 2013) and are related to the fast-slow continuum of plant strategies (e.g. Wright *et al.*, 2004; Reich & Flores-Moreno, 2017). Specifically, we measured N and P concentrations and their ratio, specific leaf area (SLA) for vascular plants and bryophytes, specific thallus area (STA) for lichens, and leaf dry matter content (LDMC) in vascular plants. Further, we measured water holding capacity (WHC) for lichens and bryophytes. Such hydration traits are particularly relevant in poikilohydric organisms like

lichens and bryophytes, as their ability to retain moisture ultimately determines their photosynthetic activity (Gauslaa, Solhaug & Longinotti, 2017). In addition, we measured tissue pH, identified by Cornelissen *et al.* (2006) as a proxy for "hard" traits such as decomposability and acidification potential. To allow comparisons between groups, we used only leaves from vascular plants, excluding stems and belowground parts. For lichens and bryophytes we used complete thalli and shoots respectively (cleaned from decaying necromass if present), with the exception of bryophyte SLA for which we used only the leaves to enable a better comparison with SLA of vascular plants.

Specific leaf area and leaf dry matter content in vascular plants

To determine SLA and LDMC for each vascular plant species in each plot, we used 30 young but fully developed (i.e. current growing season) and undamaged leaves sampled from 15 shoots, except for small leaved species (leaf length <0.5 cm) for which we used 150 leaves. For LDMC, the partial rehydration method (Vendramini *et al.*, 2002; Vaieretti *et al.*, 2007) was used and for SLA we followed the standard protocols described in Perez-Harguindeguy *et al.* (2013) and Cornelissen *et al.* (2003). Leaves were scanned with a CanoScan LiDE220 at 400 dpi and leaf surface area was calculated in the image processing software ImageJ (version 1.51p). After scanning, leaves were dried at 60 °C for 72 hours and weighed (Sartorius ED224S, 0.1 mg readability). Measures of LDMC were determined as the oven-dry mass divided by the fresh mass (expressed in mg g^{-1}), while SLA was calculated as leaf area divided by dry mass (expressed in mm^2 mg^{-1}).

Specific thallus area and water holding capacity in lichens

To determine STA and WHC in lichens, an adaptation of the protocol described by Gauslaa & Coxson (2011) was used. For each species in each plot, 10 intact thalli of each species were selected and cleaned. The thalli were saturated by spraying with demineralized water and incubated for 30 minutes in a sealed container lined with moistened (demineralized water) tissue paper. The lichen thalli were then placed on a light table and flattened under a glass plate. Highly branched thalli were cut into several pieces to minimize overlap. Images of these thalli were taken with a Nikon D5500 in combination with a Sigma 105mm f2.8 DG macro HSM lens with a resolution of 6000 × 4000 pixels (jpeg-format). Thallus surface area was measured using the image processing software Image J (version 1.51p). After taking the images, lichens were again saturated (see above), blotted dry, and weighed (using a Sartorius ED224S scale).

Finally, thalli were dried at room temperature and stored in desiccators with silica gel 48 hours prior to weighing dry mass. We calculated STA as thallus area divided by dry mass (expressed in in mm^2 mg^{-1}), and WHC was calculated as '(wet mass – dry mass) / area' (expressed in mg mm^{-2}; water per thallus area).

Specific leaf area and water holding capacity in bryophytes

SLA of bryophytes was measured using an adapted version of the protocol of Lang *et al*. (in prep.) which provides more accurate measurements than previous bryophyte SLA-protocols that measure shoot area rather than leaf area (Bond-Lamberty & Gower, 2007). Leaves were picked carefully from the bryophytes by using extremely fine anti-magnetic tweezers (Dumont Swissmade type 5, Electron Microscopy Sciences, USA) and a dissecting microscope. For larger-leaved mosses (such as *Polytrichum* spp. and *Dicranum* spp.), we selected 20 leaves from three shoots, while for small-leaved species (such as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilidium ciliare*), we selected 45 leaves from three shoots. We selected young but fully developed leaves from the upper one-third of the shoots. For branched species, leaves were selected from both the main stem and side branches. These leaves were then prepared on microscope slides and flattened with a cover glass. Pictures were taken using a Leica DFC320 digital camera mounted on a Leica MS5 stereo microscope (Leica Microsystems GmbH, Germany), using a 0.63x objective together with a 1.0x 0.63x camera objective and a light table. Photoshop Elements 14 and ImageJ v1.51k were used to select and measure leaf area (mm^2). Since bryophyte leaves were often curled and folded under the cover glass, the area of all double parts was measured twice. To allow comparisons of bryophyte SLA with vascular plant SLA, we oven-dried the leaves at 50°C for 24 hours and weighed using a Mettler Toledo UMX2 ultra-microbalance (1 µg readability, Mettler Toledo, Switzerland). We calculated SLA as leaf area divided by dry mass (expressed in mm^2 mg^{-1}).

For each bryophyte species for each plot, WHC was measured using an adaptation of the protocols of Pypker, Unsworth & Bond (2006), Elumeeva *et al.* (2011), and Michel *et al.* (2013). For each sample, 10 living shoots were collected (i.e. the top part of the shoot with green leaves) and submersed in demineralized water for 30 minutes. Shoots were then placed on moistened filter paper in sealed petri-dishes for approximately 24 hours. Subsequently, shoots were blotted dry and water-saturated mass was weighed (Sartorius EDS224S), after which the samples were air-dried and weighed again. For each batch of samples, one sample

was oven-dried at 40°C for 6 hours and weighed to provide a conversion factor for that batch from air-dry to oven-dry mass. WHC was calculated as '(wet mass – dry mass)/dry mass' (expressed in g g^{-1}).

Nitrogen and phosphorus content and tissue pH

Vascular plant, lichen and bryophyte samples were ground to powder using a Retsch MM400 ball mill (5mL tubes, 30 Hz, 5-10 min) for analysis of N and P (in %), by using Kjehldahl analysis, from which the N:P ratio was calculated. For pH measurement, powder from each sample was suspended in demineralized water in a 1:8 ratio (Cornelissen *et al.*, 2006) using a KS 501 digital shaker (1 hour at 325 rpm; IKA-Werke GmbH & Co. KG, Germany) and subsequently centrifuged for 10 minutes at 4000 rpm (RCF = 2115 x g, Hettich Universal 16). We then measured pH with a WTW InoLab pH 720 instrument equipped with a WTW pH SenTix 81 electrode (pH 0 - 14, temp. 0 - 100 °C; Xylem Analytics, USA) after calibration to pH 4 and 7 calibration fluid.

Data analysis

Community composition across elevation

We performed a two-dimensional Non-Metric Dimensional Scaling analyses using Bray-Curtis dissimilarity coefficients to depict differences with elevation in vascular plant, lichen, and bryophyte communities using the R package vegan (Oksanen *et al.*, 2015). For these analyses, we used two dimensions (k = 2). Although adding a third dimension would decrease stress (Figure S1), stress levels at two dimensions were acceptable and below the stress > 0.2 criterion *sensu* Clarke, 1993 (vascular plants: 0.147, lichens: 0.128, bryophytes: 0.161). We therefore reported stress levels for two dimensions, bearing in mind that depiction of ordination plots in more than two dimensions creates significant difficulties in interpretation. Data was subjected to Wisconsin double standardization, but was not transformed. We used the ordiellipse function (Oksanen *et al.*, 2015) to plot the 95% confidence intervals (CI) of group scores of the five elevations onto the NMDS ordination.

Community-level trait calculations

To assess how traits vary across elevation, we calculated community-weighted mean values for all traits for each group (vascular plants, lichens and bryophytes) per plot. The community-weighted mean is the sum of the relative trait values of all species, in which the trait value of

each species is weighted by its relative abundance within the community (e.g. Garnier *et al.*, 2004; Kichenin *et al.*, 2013). To quantify the contribution of species turnover and intraspecific variation to changes in community-weighted mean traits, we calculated community-weighted means in two different ways: as so-called "specific" averages and "fixed" averages (see Lepš *et al.*, 2011). First, "specific" averages were calculated from the plot-specific trait values per species as follows:

$$Specific\ average = \sum_{i=1}^{s} p_i x_{i\_plot}$$

where p_i is the relative abundance of the i-th species based on cover in the plot, S is the number of species, and x_{i_plot} is the specific trait value of the i-th species for the specific plot in which it was sampled. Second, "fixed" averages were calculated in similar fashion but with trait values averaged over all plots within the gradient for each species. Fixed average traits are therefore plot-independent, meaning that they reflect the "mean trait approach": one species has one mean trait value regardless of the specific plot where it is found. Then, we calculated the contribution of intraspecific trait variation based on the following principle: if there are differences in "fixed" averages between plots, this can only be the result of species turnover. However, if there are differences in "specific" averages between plots, this can be the result of both species turnover and intraspecific trait variation. Hence, we can define:

$$Intraspecific\ variability\ effect = Specific\ average\ - Fixed\ average$$

For the analyses, we treated the specific average (which includes the effect of both species turnover and intraspecific variation), fixed average (effect of species turnover) and the difference between them (effect of intraspecific variation) in each group for each functional trait as response variables in parallel one-way ANOVAs, with elevation treated as a factor with five levels. Because the distributional assumptions for the regular F-test were not fulfilled, we used permutation tests instead. Iterations terminated when the estimated standard deviation fell below 0.1 of the estimated p-value, with a minimum of 50 iterations, or continued until a maximum of 5000 iterations (*sensu* Anscombe, 1953). Whenever the specific average (= total trait variation) was impacted by elevation at a significance level p = 0.05, pairwise comparisons using permutation tests were performed to check for differences between elevation levels. In addition, we quantified how much variability can be accounted for by the

individual components (species turnover effects or intraspecific variability effects) by following the Sum of Squares (SS) decomposition method described by Lepš *et al.*, 2011. When species turnover effects and intraspecific effects vary independently, then $SS_{specific} = SS_{fixed} + SS_{intraspecific}$; however if they are correlated, then $SS_{specific}$ will be higher (positive correlation) or lower (negative correlation). As such, we calculated the SS_{cov} component, which is the covariation between species turnover and intraspecific variability effects, by subtracting SS_{fixed} and $SS_{intraspecific}$ from $SS_{specific}$. The analyses were performed using the R-packages lmPerm (Wheeler, 2010) and rcompanion (Mangiafico, 2016) in R, version 3.4.0 (R Core Team, 2017).

Contribution of intraspecific variability between groups

To test whether the proportional contribution of intraspecific variation (in comparison to species turnover) to community-level trait changes across the elevational gradient differed between vascular plants, lichens and bryophytes, we calculated the absolute difference between specific averages and fixed averages for each group, divided by the specific average. We performed this analysis on chemical traits (N, P, N:P, and pH) only, because non-chemical traits (SLA, STA, WHC and LDMC) were measured differently between primary producer groups and their values cannot be compared directly. The calculated proportions were arcsine transformed to meet the assumptions for ANOVA using linear mixed effects models with elevation and primary producer group as fixed factors and plot as a random effect. Whenever ANOVA results were significant, Tukey's post-hoc tests at p=0.05 were used to test differences between means for elevations. These analyses were performed in R, version 3.4.0 (R Core Team, 2017), using the packages nlme (Pinheiro *et al.*, 2017) and emmeans (Lenth, 2018).

Results

The NMDS results show that for all three primary producer groups, the communities at the lowest three elevations (1120, 1240 and 1360 m a.s.l.) group together along the first ordination axis, and separately from the two highest elevations (1480 and 1600 m a.s.l.) (Figure 3). In the ordination space, the lichen community compositions appear more similar across elevations than do the vascular plant and the bryophyte communities (Figure 3).

Functional traits across elevations

Chemical traits

For the vascular plant community, foliar N increased by 24%, foliar N:P increased by 42%, and pH increased by 16% from the lowest to the highest elevation; foliar P showed a marginally non-significant decline (total trait variation values in Figure 4). Species turnover contributed most to the total variation in N and pH, whereas intraspecific variation contributed most to total variation in P and N:P across the elevational gradient (Figure 5). The covariation of species turnover and intraspecific variation was negative for N and P but positive for N:P.

All lichen chemical traits changed significantly with elevation (total trait variation values in Figure 4). Lichen N increased by 78% and N:P increased by 136% with increasing elevation while P generally decreased. Acidity (pH) varied significantly with elevation but not in a clear overall direction. Intraspecific variability effects contributed to most of the trait variation explained by elevation for N, P and N:P, though species turnover effects were also significant for N and N:P (Figure 5). In contrast, species turnover effects were the main driver of pH variation. There was a strong positive covariation of species turnover and intraspecific variation for all traits.

Bryophyte P decreased by 43% and N:P ratio increased by 120% with increasing elevation, while N showed a marginally non-significant increase and pH was unresponsive (total trait variation values in Figure 4). Species turnover was the main driver for total trait variation across the elevational gradient for the chemical traits in the bryophytes, and this effect was statistically significant for all traits except pH (Figure 5). There was no significant change of intraspecific variation across elevation, but there was a strong positive covariation between species turnover effects and intraspecific variation for P and N:P.

Non-chemical traits

Vascular plant SLA showed a marginally non-significant increase across the gradient, while LDMC decreased by 16% with increasing elevation (total trait variation values in Figure 6). Species turnover explained most of the total trait variation across the elevational gradient for both SLA and LDMC (Figure 5). Although the relative contribution of species turnover to total variation in SLA across the elevational gradient was large and significant, a strong negative covariation with intraspecific variability effects led to marginally non-significant response of

total variation. The covariation of species turnover and intraspecific variation was also negative for LDMC.

For the lichen community, STA increased by 37%, while WHC decreased by 24% with increasing elevation (total trait variation values in Figure 6). Species turnover had a significant role in determining the total response of both traits to elevation, while there was no effect of intraspecific variation (Figure 5). There was a strong positive covariation between species turnover and intraspecific variation for both traits.

For the bryophyte community, SLA decreased by 68%, and WHC decreased by 25%, from the lowest to highest elevation (total trait variation values in Figure 6). For both SLA and WHC, total variation explained by elevation was mainly driven by species turnover effects, which was significant for both traits (Figure 5). For WHC, intraspecific variation also contributed significantly to total trait variation. The covariation of species turnover and intraspecific variation was slightly negative for SLA, while for WHC it was strongly positive.

Intraspecific variability effects between groups

The contribution of intraspecific variation to the community level trait values showed a significant interaction between elevation and group identity (vascular plants, bryophytes or lichens) for N, P and N:P but not for pH; which means that the contribution of intraspecific variation changes differently across elevation for the three groups (Table 1). Furthermore, lichens overall showed greater intraspecific variation when compared to vascular plants and bryophytes for N (15% in lichens vs 7% in vascular plants and 8% in bryophytes; $p<0.001$) and N:P (36% for lichens vs 10% for vascular plants and 17% for bryophytes; $p<0.001$).

Discussion

We hypothesized that across elevation, intraspecific variation is the most important driver of community-level trait variation in lichens and bryophytes while species turnover is most important in vascular plants. In line with our hypothesis, we found that species turnover is the most important contributor to total variation across the gradient for most of the vascular plant traits that we considered (Figure 1a-b). Further and in support of our hypothesis, some of the lichen traits are mainly driven by intraspecific variation (Figure 1c-d), although others are driven by species turnover (Figure 1a-b). Against our predictions, species turnover effects

mainly drive variation for all bryophyte functional traits across the gradient (Figure 1a-b). However, even when intraspecific variation is small, we found that it greatly enhances the total variation explained by elevation for lichen traits and some bryophyte traits, through positive covariation with species turnover effects (Figure 1e-f). We now explore these findings and discuss their broader implications.

Our finding that species turnover is the main contributor to variation in most vascular plant traits across elevation is consistent with previous studies (e.g. Albert *et al.*, 2010a; Mayor *et al.*, 2017). However, we also found that intraspecific variation is the most important contributor to vascular plant P and N:P, which confirms earlier findings that the relative contributions of inter- and intraspecific variation can differ greatly among both traits and study systems (Derroire *et al.*, 2018). For lichens, we found that intraspecific variation is the main contributor to variation in nutrient concentrations across the gradient, which is consistent with the fact that lichens lack specialized organs for nutrient and water uptake and are therefore less well adapted than vascular plants in regulating their physiology across changing environmental conditions. Although intraspecific variation does not contribute to changes in lichen STA and WHC across elevation, the residual variation in these traits shows a relatively large intraspecific component (Figure S2), indicating that intraspecific changes occur independent of elevation, e.g., as a response to local variation in light exposure through shading by vascular plants (Hilmo, 2002; Gauslaa *et al.*, 2006).

Our results for the bryophytes are in direct contrast to our hypothesis, since species turnover is the main driver of total variation for all traits across the gradient, which is likely driven by the high rate of species turnover across the gradient. However, bryophyte WHC also showed significant intraspecific variation, suggesting that the overlap of bryophyte species among elevations was still large enough to enable within-species variation to be detected. Further, intraspecific variation may still be important at some spatial scales even when it is very weak at others. As such, the residual variation in bryophyte traits that cannot be explained by elevation has a large intraspecific variability component (Figure S2), suggesting that within-species variation may be important at more local spatial scales in response to factors that vary within elevation, such as light availability, snow depth (Niittynen & Luoto, 2018), and soil moisture (Tobias & Niinemets, 2010).

The relative importance of intraspecific variation across the gradient does not only differ between the three producer groups in our study, but also between traits within groups, which is in line with what has been shown in the vascular plant literature (see Siefert *et al.*, 2015). In our study, tissue nutrient concentrations of vascular plants and lichens show more intraspecific variation across the gradient than the other, non-chemical traits. Although we found similar responses for nutrient concentrations within bryophyte species that are present at more than one elevation, this effect is unimportant in influencing the community-weighted means across the gradient because of very high species turnover. Meanwhile, variation across the gradient in tissue pH is driven almost exclusively by species turnover for all three groups. This is in line with the results from Cornelissen *et al.* (2011) for vascular plants, which show that tissue pH is highly species-specific and therefore unlikely to be strongly responsive to environmental factors such as substrate pH at the within-species level. Similarly, SLA in bryophytes seems also species-specific; within-species variation could be unresponsive to changes across the gradient because bryophyte leaves are often consistently one cell-layer thick, meaning that leaf thickness cannot be varied by changing the numbers of cell layers, leading to leaf thickness being relatively inflexible.

While theory predicts that as elevation increases and environmental conditions become harsher, plant traits should shift from those associated with rapid resource acquisition towards resource conservation, some field studies reveal contrasting patterns (e.g. Sundqvist, Sanders & Wardle, 2013; Read *et al.*, 2014; Mayor *et al*., 2017). In our study we found that some traits change towards being more resource conservative with increasing elevation, as shown by a decrease in P and WHC for lichens and bryophytes, a decrease in SLA for bryophytes, and an increase in N:P in all groups, in accordance with previous work (Koerselman & Meuleman, 1996; Güsewell, 2004). However, other traits show opposing responses. For instance, vascular plant and lichen tissue N, vascular plant SLA, and lichen STA increase while vascular plant LDMC decreases with elevation, indicating a shift towards a more nutrient acquisitive strategy. However, for vascular plant SLA and N, the strong negative covariation between species turnover and intraspecific effects indicates that within some individual plant species, values of these traits may decrease with elevation (see also Kichenin et al., 2013; Anderegg *et al.*, 2018). A likely mechanism for more acquisitive community-level traits at higher elevations is a shift in the dominant functional types. For example, for vascular

plants, as elevation increases, shrubs are replaced by species with lower stature or tussock-like growth forms (such as graminoids) which characteristically have more acquisitive leaf traits (Freschet *et al.*, 2010).

The mechanisms behind the responses of STA and SLA to elevation for lichens and bryophytes are likely to be different to those for vascular plants, because their poikilohydric nature means that their traits are likely to be less related to resource strategy. We found that lichen STA increases with elevation in a similar manner to vascular plant SLA, but suggest that this is driven by a different mechanism. As such, lichen STA is strongly linked to WHC and is therefore mainly associated with water economy (e.g. Gauslaa, 2014; Phinney, Solhaug & Gauslaa, 2018), meaning that decreasing water loss by evapotranspiration with increasing elevation due to lower temperatures would cause a shift towards a lichen community with a higher STA and thus lower WHC. This is likely to also be the mechanism underpinning the decreasing WHC in bryophytes with elevation, and is in line with findings from (Henriques *et al.*, 2017), who showed that bryophyte leaf traits associated with protection against water loss decreased with elevation. In contrast to lichens and vascular plants, SLA in the bryophyte community decreased strongly with increasing elevation, and this was driven by a shift from species with one cell-layer thin leaves (such as *Pleurozium schreberi*) towards those with thicker leaves containing lamellae (such as *Polytrichum spp*). Since bryophyte SLA was measured at the leaf-level while WHC was measured on shoots, our measurements for bryophyte SLA and WHC are likely to be at least partly decoupled. However, we still lack a complete understanding of the mechanisms behind the strong response of bryophyte SLA to elevation.

Conclusions

Our findings highlight that the contribution of intraspecific versus species turnover to community-level shifts in plant traits differs greatly among primary producer groups. Across our gradient, lichens exhibited a great deal of intraspecific plasticity in traits that respond strongly to elevation, notably N concentration and N:P ratio. This suggests that under future climate warming, lichen species may be more capable than vascular plant and bryophyte species in adapting to new environmental conditions, at least if these parallel the environmental changes along our elevational study gradient. Because intraspecific variability can help maintain community stability and functioning under changing environmental

conditions (Jung *et al.*, 2010; Malyshev *et al.*, 2016), the lichen communities would be more likely to resist environmental change than the bryophyte and vascular plant communities which lack the intraspecific plasticity needed to cope with environmental change. This line of thought is contrasted by studies showing that lichen (and bryophyte) communities respond negatively in terms of diversity and abundance to global change phenomena such as increased temperatures and changes in precipitation and snow cover (Elmendorf *et al.*, 2012; Jägerbrand *et al.*, 2012; Lang *et al.*, 2012; Bidussi, Solhaug & Gauslaa, 2016; Alatalo *et al.*, 2017). In most of these studies, the decline of non-vascular vegetation observed under climate warming is likely due to increased competition from vascular plants. Thus, lichen communities would only benefit from their intraspecific plasticity in areas where conditions are too harsh for vascular plants to establish, even under climate warming, such as higher elevations and exposed ridges.

While nearly all studies on primary producer trait variation across environments have focused on vascular plants, our study shows that trait variation of other largely neglected producer groups such as lichens and bryophytes may show very different responses to the same environmental factors. Non-vascular groups such as lichens and bryophytes are severely underrepresented in the trait literature (but some trait databases now exist, e.g. Rambold *et al.*, 2014; Henriques, Ah-Peng & Gabriel, 2017; Bernhardt-Römermann, Poschlod & Hentschel, 2018), even though lichens and bryophytes are important components of many ecosystems, notably at high elevation and latitude. In order to fully understand and predict how future environmental changes will translate into shifts in community structure and ecological functioning, traits of primary producers other than vascular plants need to be considered in systems where these groups are important components of the overall community of primary producers. Further, our study highlights the importance of including intraspecific variation in functional trait studies, as we showed that some traits were almost completely driven by intraspecific variation, while for other traits, intraspecific variation greatly enhanced or mediated the community-level response to elevation.

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Data sharing statement

Data associated with this manuscript are deposited in the NMBU Open Research Data (http://dataverse.no/) at (DOI will be given upon acceptance of the manuscript). Species occurrences are registered in the GBIF database, for vascular plants (https://doi.org/10.15468/fsoskq), lichens (https://doi.org/10.15468/asarqe), and for bryophytes (https://doi.org/10.15468/g28uix).

Author statement

KvZ and RR contributed equally to this work. JA designed the study in consultation with DW, KK, SB, SL, and TB. Field and lab work was conducted by KvZ and RR with support of JA, KK, SL, and TB. Writing and data analysis was led by KvZ and RR. All authors contributed to revisions and discussions, and approved the final version.

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Tables and figures

Table 1. Results of ANOVA combined with mixed effects models testing the effect of elevation, group (vascular plants, lichens and bryophytes), and their interaction on intraspecific variation (proportion of total trait value) for chemical traits. The response variable, i.e., intraspecific variation (proportion of total trait value), was arcsine-transformed before analysis. Significant p-values (at α=0.05) are in bold.

		Nitrogen		**Phosphorus**		**N:P**		**pH**	
	df	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Elevation	4	2.24	0.102	0.81	0.537	2.71	0.059	0.89	0.489
Group	2	**9.51**	**<0.001**	2.05	0.143	**42.53**	**<0.001**	0.14	0.867
Elevation x Group	8	**3.09**	**0.009**	**3.53**	**0.004**	**7.63**	**<0.001**	1.96	0.080

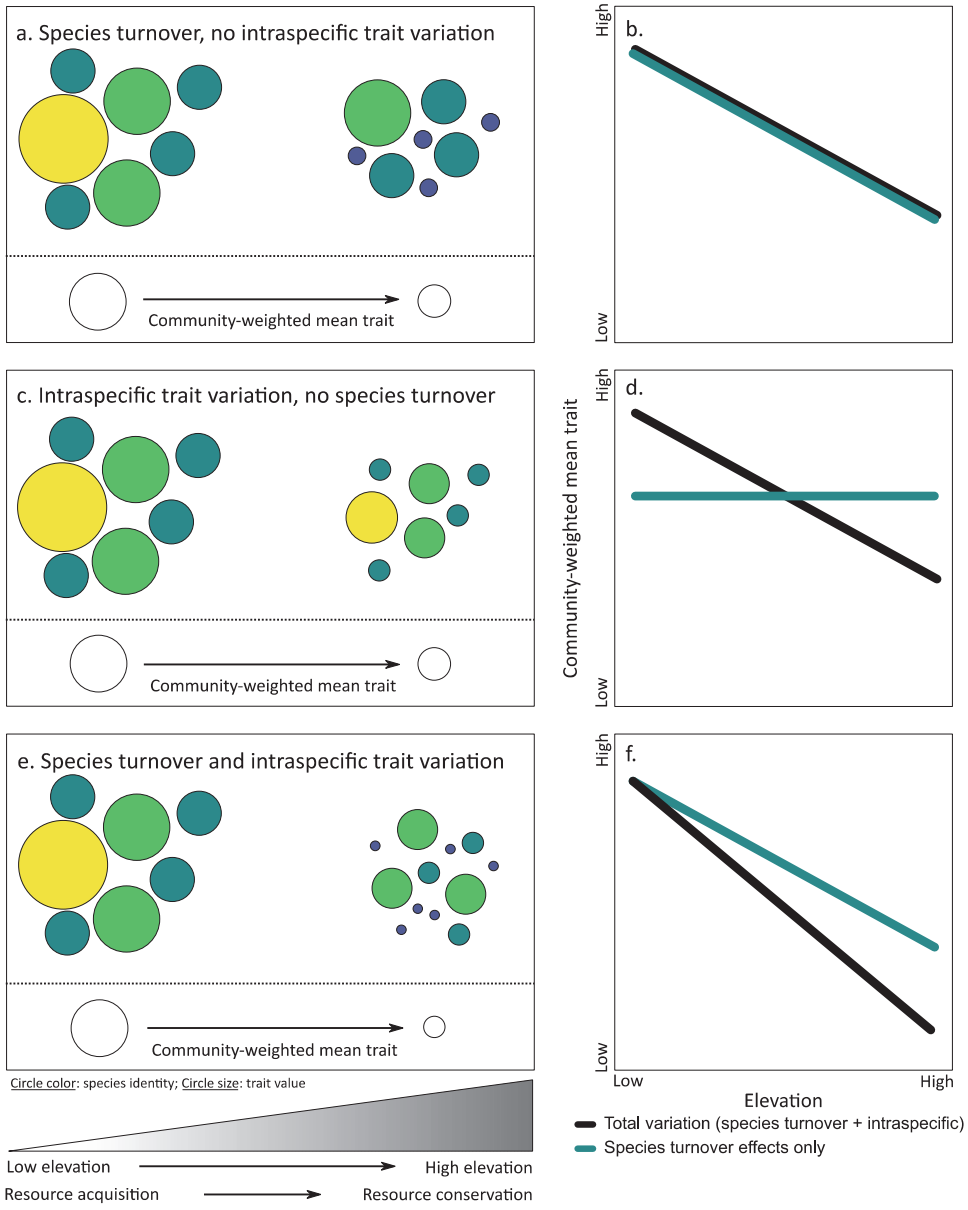

Figure 1. A conceptual figure of the drivers of community-level trait changes across environmental gradients such as elevation. As elevation increases, primary producer traits will change from those associated with resource acquisition towards those associated with resource conservation. The panels to the left illustrate communities, where symbol colour indicates species identity and symbol size depicts the trait value (e.g. tissue nitrogen content). The size of open circles indicate the community-weighted mean trait value as calculated from the sum of each species' trait value multiplied by its relative abundance. The right hand panels show the change in community-weighted mean, depicted in x-y plots, that corresponds to the examples in the left hand panels. In (a) and (b), the community-

weighted mean trait value changes through alterations in species abundance and identity (i.e. species turnover), while trait values within species are fixed (no intraspecific trait variation). In contrast, in (c) and (d), the change in community-weighted mean trait value is driven only by intraspecific trait variation (no species turnover). In (e) and (f), both species turnover and intraspecific trait variation drive changes in the community-weighted mean trait value, which together result in an even stronger response. Note that in this case, species turnover and intraspecific variation act in a similar direction and have a positive covariation (both mechanisms reduce the community-level trait value), but they can also act in opposing directions, in which case their covariation is negative. In this study, we test our hypothesis that, although both species turnover and intraspecific trait variation will likely contribute simultaneously across an elevational gradient, species turnover will be the dominant driver of changes in community-weighted traits for vascular plants, while intraspecific trait variation will be the dominant driver for lichens and bryophytes.

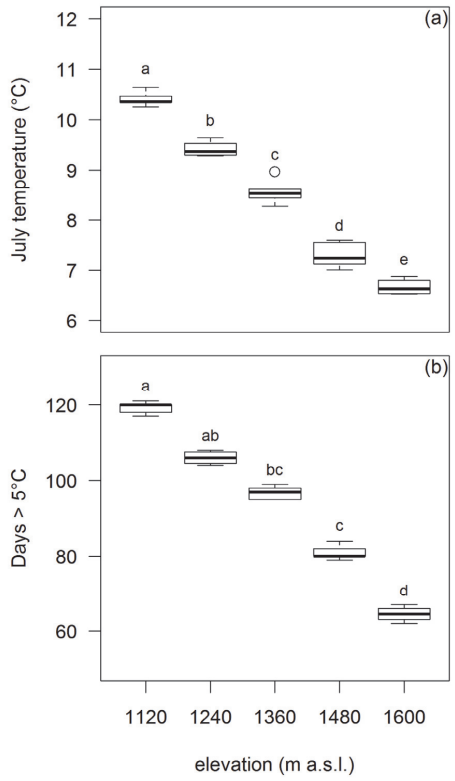

Figure 2. Box-and-whisker plot of mean July temperature (a) and number of days when average temperature exceeded 5 °C (b) for each elevation. Significant differences between elevation levels are denoted with different letters (at α=0.05, Tukey post-hoc tests).

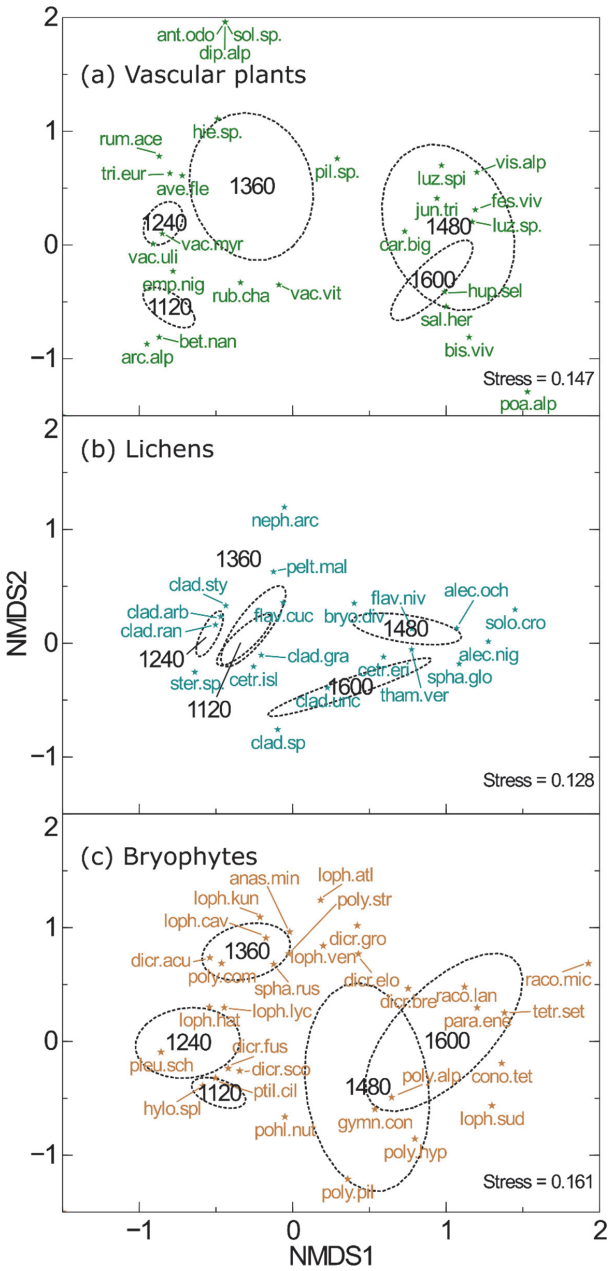

Figure 3. Results of Non-Metric Multidimensional Scaling (NMDS) analysis showing differences with elevation for (a) vascular plant, (b) lichen, and (c) bryophyte community composition. The elevation label (in m a.s.l.) denotes the positions of the centroid for community composition for each elevation; dashed ellipses denote 95% confidence intervals around these positions. Species abbreviations place species in ordination space, but were moved in some cases to increase readability (indicated with an arrow); abbreviations correspond to species names in Table S2.

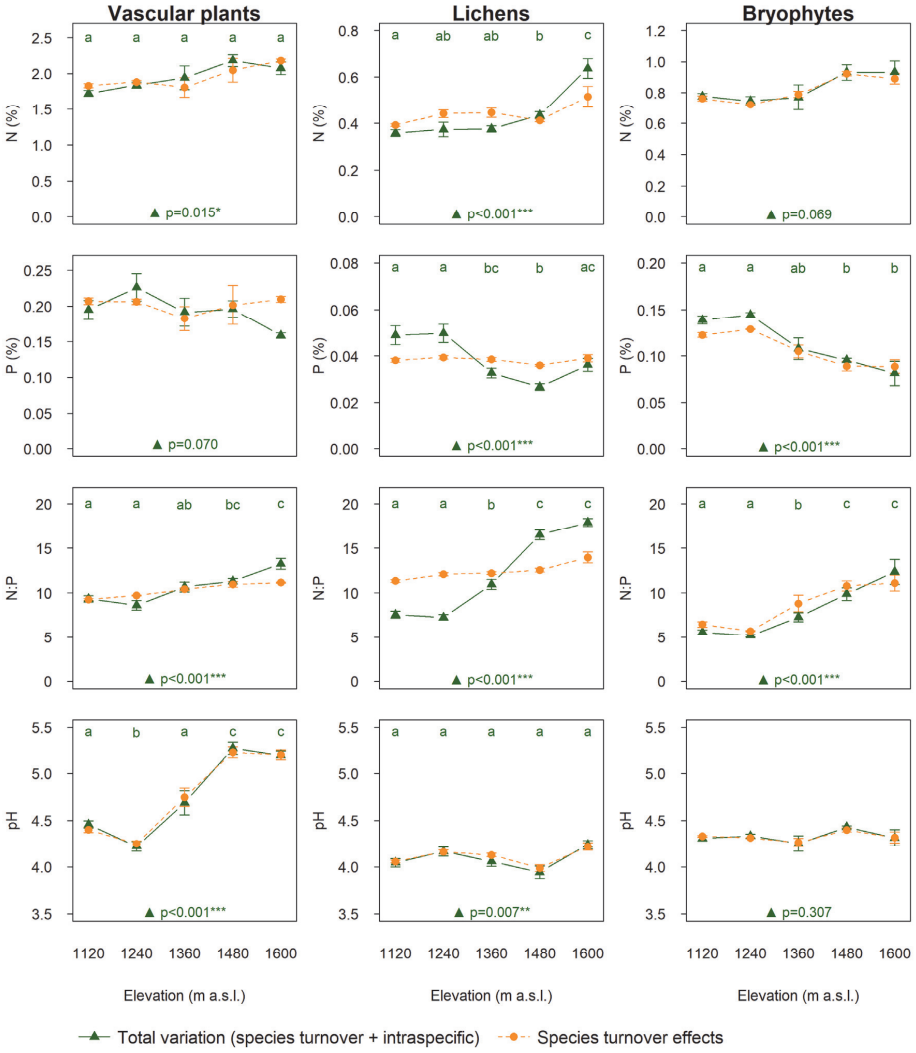

Figure 4. Community-weighted means (± SE) of nitrogen concentration (% N), phosphorus concentration (% P), N:P ratio and pH for vascular plants (left column), lichens (middle column) and bryophytes (right column) across elevation. The green lines with triangles denote the total variation (specific average values), and orange dotted lines with circles denote species turnover effects only (fixed average values). Therefore, the larger the difference between green and orange lines, the larger the contribution of intraspecific variation. In the bottom of each panel, the P-values from the permutational ANOVAs are presented for the response of total trait variation to elevation, and denoted with * (<0.05), **(<0.01), or *** (<0.001). Significant differences between elevation levels are denoted with different letters (at α=0.05, permutational pairwise comparisons). Note that the scales for N and P are different for the three groups.

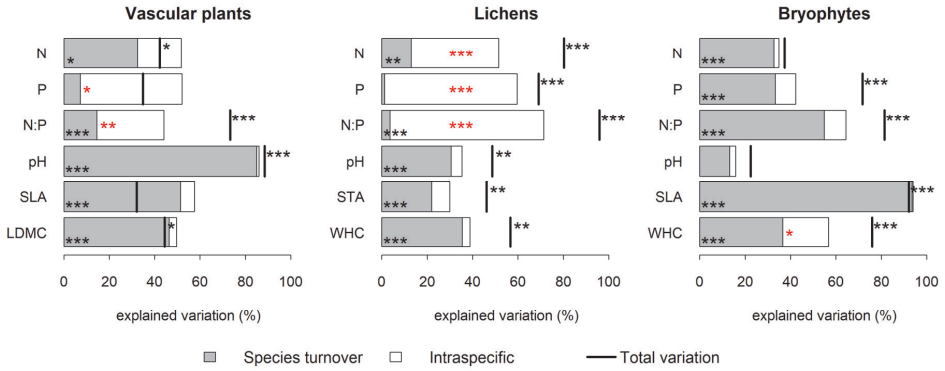

Figure 5. The contributions of species turnover and intraspecific variation to trait variation explained by elevation (as percentage of total variation in traits, including variation not explained by elevation) for vascular plant, lichen, and bryophyte functional traits. The measured traits include nitrogen concentration (N), phosphorus concentration (P), N:P ratio, pH, specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC), and water holding capacity (WHC). Grey bars indicate effects of species turnover, while white bars show intraspecific variability effects. The black lines denote total variation (i.e. the sum of species turnover and intraspecific variability effects and their covariation) explained by elevation. If the total variation is greater than the sum of species turnover and intraspecific variability effects (black bar above the columns), covariation is positive. In contrast, if total variation is smaller than the sum of its components the covariation is negative (black bar crossing the column). For example, intraspecific variability effects explain most of the variation for lichen tissue N and the covariation between intraspecific and species turnover effects is strongly positive. The significance of the response of the different components to elevation is denoted with * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$); subscript refers to species turnover, superscript to total variation, and symbols at the baseline to intraspecific variation (in red).

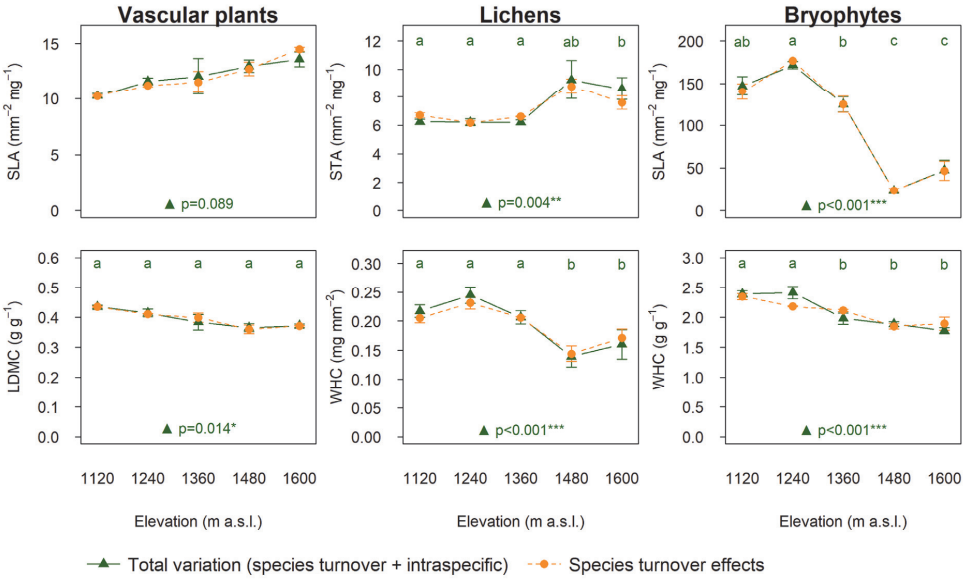

Figure 6. Community-weighted means (± SE) of specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC), and water-holding capacity (WHC) for vascular plants, lichens and bryophytes across elevation. Green lines with triangles denote the total variation (specific average values); orange dotted lines with circles denote species turnover effects only (fixed average values). The green lines with triangles denote the total variation (specific average values), and orange dotted lines with circles denote species turnover effects only (fixed average values). Therefore, the larger the difference between green and orange lines, the larger the contribution of intraspecific variation. In the bottom of each panel, the P-values from the permutational ANOVAs are presented for the response of total trait variation to elevation, and denoted with * (<0.05), **(<0.01), or *** (<0.001). Significant differences between elevation levels are denoted with different letters (at α=0.05, permutational pairwise comparisons). Note that the scales and units may differ among the three groups.

Supplementary information

Table S1. Temperature parameters for each elevation (m a.s.l.) from September 6, 2016 to August 21, 2017. Mean ± SE of mean annual temperature (MAT, °C), temperature at coldest day (MinT, °C), temperature at warmest day (MaxT, °C), no. of diurnal freeze-thaw cycles (FT), mean January temperature (JanT, °C), mean July temperature (JulyT, °C), and growing degree days (GDD; number of days when average temperature exceeded 5 °C). Values are averaged over the plots (n=4 or n=5) per elevation.

Elevation	n	MAT	MinT	MaxT	FTC	JanT	JulyT	GDD
1120	5	1.2 ±0.03	-18.5 ±0.27	16.1 ±0.33	138 ±1.58	-5.6 ±0.01	10.4 ±0.07	119 ±0.75
1240	4	1.4 ±0.11	-16.1 ±0.29	15.7 ±0.19	122 ±5.12	-3.8 ±0.27	9.4 ±0.08	106 ±0.91
1360	5	0.9 ±0.25	-15.0 ±1.47	15.5 ±0.35	103 ±9.83	-4.5 ±0.83	8.6 ±0.12	97 ±0.80
1480	5	-0.7 ±0.05	-17.0 ±0.30	14.2 ±0.13	90 ±9.55	-7.0 ±0.08	7.3 ±0.12	81 ±0.89
1600	4	-0.4 ±0.43	-14.1 ±3.34	14.1 ±0.07	65 ±4.85	-4.6 ±1.23	6.7 ±0.08	65 ±1.04

Table S2. Abbreviations, full species names and relative cover (mean ±SE) in percentages of vascular plant (VASC), lichen (LICH) and bryophyte (BRYO) species found in 1x1 m plots along an elevational gradient ranging from 1120 to 1600 m a.s.l. on acidic bedrock in Finse, Norway, in 2016. The relative cover is calculated from the original field estimates, divided by the total cover per primary producer group for each plot, and aggregated for each elevation.

Group	Abbreviation	Full species name	Relative cover (in %) per elevation (m a.s.l.)				
			1120	1240	1360	1480	1600
VASC	ant.odo	*Anthoxanthum odoratum*	-	-	1.4±1.4	-	-
VASC	arc.alp	*Arctostaphylos alpina*	1.2±0.6	-	-	-	-
VASC	ave.fle	*Avenella flexuosa*	-	1.0±0.5	1.5±0.7	-	-
VASC	bet.nan	*Betula nana*	45.2±6.8	-	-	-	-
VASC	bis.viv	*Bistorta vivipara*	-	-	3.0±1.8	8.8±7.9	-
VASC	car.big	*Carex bigelowii*	-	4.0±1.6	23.8±8.4	25.5±8.0	35.7±10.7
VASC	dip.alp	*Diphasiastrum alpinum*	-	-	2.3±2.3	-	-
VASC	emp.nig	*Empetrum nigrum*	34.4±3.3	31.8±3.5	39.6±16.1	6.0±3.7	-
VASC	fes.viv	*Festuca vivipara*	-	-	0.8±0.6	14±5.6	3.0±1.3
VASC	hie.sp.	*Hieracium sp.*	-	-	1.5±1.0	-	-
VASC	hup.sel	*Huperzia selago*	-	-	-	-	0.4±0.3
VASC	jun.tri	*Juncus trifidus*	0.1±0.1	-	3.0±3.0	12.4±7.6	3.8±1.6
VASC	luz.sp.	*Luzula sp.*	-	-	-	6.0±3.9	5.2±3.0
VASC	luz.spi	*Luzula spicata*	-	-	-	2.3±2.0	-
VASC	pil.sp.	*Pilosella*	-	-	0.5±0.5	-	-
VASC	poa.alp	*Poa alpina*	-	-	-	0.1±0.1	-
VASC	rub.cha	*Rubus chamaemorus*	-	-	0.8±0.8	-	-
VASC	rum.ace	*Rumex acetosa*	-	0.1±0.1	0.2±0.2	-	-
VASC	sal.her	*Salix herbacea*	-	-	3.0±0.6	17.5±8.0	43.8±9.0
VASC	sol.sp.	*Solidago sp.*	-	-	0.2±0.2	-	-
VASC	tri.eur	*Trientalis europaea*	-	0.3±0.3	0.7±0.4	-	-
VASC	vac.myr	*Vaccinium myrtillus*	1.2±1.1	4.1±0.6	2.4±0.5	-	-

Table S2 continued

Group	Abbreviation	Full species name	Relative cover (in %) per elevation (m a.s.l.)				
			1120	1240	1360	1480	1600
VASC	vac.uli	*Vaccinium uliginosum*	12.8±6.1	54.4±3.5	11.7±7.2	-	-
VASC	vac.vit	*Vaccinium vitis-idaea*	5.1±1.2	4.4±2.4	3.7±0.9	5.9±4.9	8.1±2.9
VASC	vis.alp	*Viscaria alpina*	-	-	-	1.5±0.5	-
LICH	alec.nig	*Alectoria nigricans*	-	-	-	1.0±0.3	1.2±0.9
LICH	alec.och	*Alectoria ochroleuca*	0.1±0.1	-	-	2.8±1.2	1.6±0.9
LICH	bryo.div	*Bryocaulon divergens*	-	0.1±0.1	-	0.4±0.2	0.2±0.2
LICH	cetr.eri	*Cetraria ericetorum*	1.9±0.9	0.2±0.1	1.7±0.4	13.4±4.3	23.6±8.4
LICH	cetr.isl	*Cetraria islandica*	5.0±2.4	3.4±2.3	8.6±5.1	8.3±3.5	4.6±0.8
LICH	clad.arb	*Cladonia arbuscula s. lat.*	43.2±10.3	65.3±4.3	65.6±4.8	18.8±12.8	6.5±2.3
LICH	clad.gra	*Cladonia gracilis*	1.6±0.2	1.1±0.1	1.0±0.1	1.2±0.2	3.8±0.4
LICH	clad.ran	*Cladonia rangiferina*	29.7±9.6	12.6±1.7	5.0±1.7	2.4±2.0	2.0±2.0
LICH	clad.sp.	*Cladonia spp.*	0.8±0.5	0.6±0.1	1.3±0.2	0.2±0.2	19.7±8.5
LICH	clad.sty	*Cladonia stygia*	7.2±1.3	6.4±2.8	9.2±2.6	1.4±0.7	1.6±0.8
LICH	clad.unc	*Cladonia uncialis*	0.8±0.5	0.2±0.1	1.5±0.2	2.3±0.6	11.3±7.7
LICH	flav.cuc	*Flavocetraria cucculata*	2.1±1.2	1.1±0.7	1.5±1.0	2.0±0.8	2.0±0.8
LICH	flav.niv	*Flavocetraria nivalis*	6.4±2.2	0.2±0.1	0.4±0.1	40.7±10.2	10.4±3.8
LICH	neph.arc	*Nephroma arcticum*	-	-	0.1±0.1	-	-
LICH	pelt.mal	*Peltigera malacea*	-	-	1.2±0.8	0.1±0.1	-
LICH	solo.cro	*Solorina crocea*	-	-	-	1.8±1.0	-
LICH	spha.glo	*Sphaerophorus globosus*	-	-	-	1.1±0.3	2.3±1.1
LICH	ster.sp.	*Stereocaulon spp.*	1.1±1.1	8.7±2.9	2.5±1.9	0.9±0.2	6.4±3.8
LICH	tham.ver	*Thamnolia vermicularis*	0.1±0.1	-	0.2±0.1	1.3±0.1	2.8±1.1
BRYO	anas.min	*Anastrophyllum minitum*	-	-	0.5±0.3	-	0.1±0.1
BRYO	cono.tet	*Conostomum tetragonum*	-	-	-	0.3±0.3	0.4±0.4
BRYO	dicr.acu	*Dicranum acutifolium*	1.0±0.6	0.3±0.3	31.4±16.5	5.5±2.7	1.8±1.1

Table S2 continued

Group	Abbreviation	Full species name	Relative cover (in %) per elevation (m a.s.l.)				
			1120	1240	1360	1480	1600
BRYO	dicr.bre	*Dicranum brevifolium*	-	-	0.4±0.4	-	1.8±1.2
BRYO	dicr.elo	*Dicranum elongatum*	-	-	1.1±1.1	2.7±2.7	1.9±1.6
BRYO	dicr.fus	*Dicranum fuscescens*	8.7±3.1	2.0±0.8	1.0±1.0	-	1.4±1.0
BRYO	dicr.gro	*Dicranum groenlandicum*	-	-	0.4±0.4	-	0.1±0.1
BRYO	dicr.sco	*Dicranum scoparium*	4.4±2.1	1.3±0.5	0.1±0.1	-	7.2±6.9
BRYO	gymn.con	*Gymnomitrion concinnatum*	-	-	-	0.4±0.4	-
BRYO	hylo.spl	*Hylocomium splendens*	14.0±8.6	0.2±0.2	2.5±0.9	1.3±1.3	-
BRYO	loph.atl	*Lophozia atlantica*	-	-	0.4±0.4	1.8±1.8	-
BRYO	loph.cav	*Lophozia cavifolia*	-	-	0.7±0.3	-	-
BRYO	loph.hat	*Lophozia hatcherii*	0.8±0.8	0.4±0.4	0.9±0.4	-	-
BRYO	loph.kun	*Lophozia kunzeana*	-	-	1.0±0.4	0.4±0.4	-
BRYO	loph.lyc	*Lophozia lycopodioides*	-	0.4±0.2	0.3±0.3	0.4±0.4	-
BRYO	loph.sud	*Lophozia sudetica*	-	-	-	0.2±0.2	-
BRYO	loph.ven	*Lophozia ventricosa*	-	-	0.4±0.4	3.1±2.6	-
BRYO	para.ene	*Paraleucobryum enerve*	-	-	-	1.0±0.5	4.7±1.5
BRYO	pleu.sch	*Pleurozium schreberi*	34.3±15.5	90.0±2.4	37.4±11.3	-	-
BRYO	pohl.nut	*Pohlia nutans*	1.9±0.4	0.8±0.4	0.4±0.2	3.7±1.9	1.1±0.7
BRYO	poly.alp	*Polytrichum alpinum*	-	-	0.5±0.5	25.0±14.2	5.6±3.7
BRYO	poly.com	*Polytrichum commune*	-	1.5±0.7	3.3±1.9	2.7±2.7	-
BRYO	poly.hyp	*Polytrichum hyperboreum*	-	-	-	34.7±19.5	40.5±17.1
BRYO	poly.pil	*Polytrichum piliferum*	-	-	-	11.2±7.9	-
BRYO	poly.str	*Polytrichum strictum*	-	0.4±0.4	9.5±5.2	1.8±1.8	3.4±1.9
BRYO	ptil.cil	*Ptilidium ciliare*	34.6±9.3	2.9±1.0	6.7±1.6	3.5±3.0	1.9±0.8
BRYO	raco.lan	*Racomitrium lanuginosum*	0.2±0.2	-	-	0.4±0.4	18.2±9.7
BRYO	raco.mic	*Racomitrium microcarpon*	-	-	-	-	5.0±5.0

Table S2 continued

Group	Abbreviation	Full species name	Relative cover (in %) per elevation (m a.s.l.)				
			1120	1240	1360	1480	1600
BRYO	spha.rus	*Sphagnum russowii*	-	-	1.3±1.3	-	-
BRYO	tetr.set	*Tetralophozia setifromis*	-	-	-	-	4.8±4.2

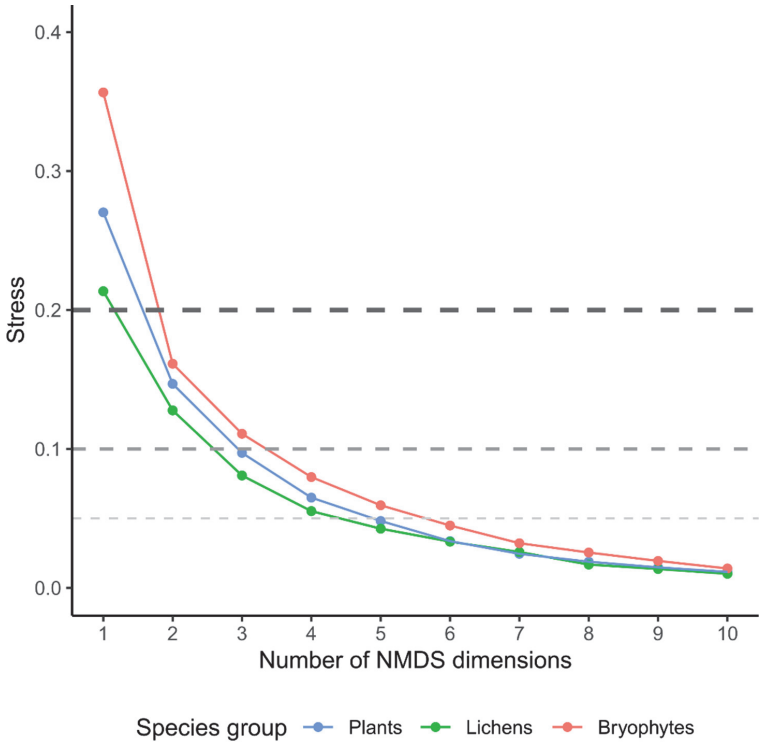

Figure S1. Stress or scree plot of stress versus dimension for Non-Metric Multidimentional Scaling (NMDS) analyses used to illustrate differences in community composition with elevation for vascular plants, lichens, and bryophytes. Increasing the number of dimensions lowers stress, indicating a better goodness-of-fit, but decreases interpretability of the results. Dashed lines indicate the guidelines for acceptable stress values *sensu* Clarke, 1993: <0.05 = excellent, <0.10 = good, <0.20 = usable, >0.20 = not acceptable. At two dimensions, stress levels are acceptable for all three primary producer groups. Adding a third or fourth dimension would improve stress levels, but simultaneously reduce interpretability of the results.

References

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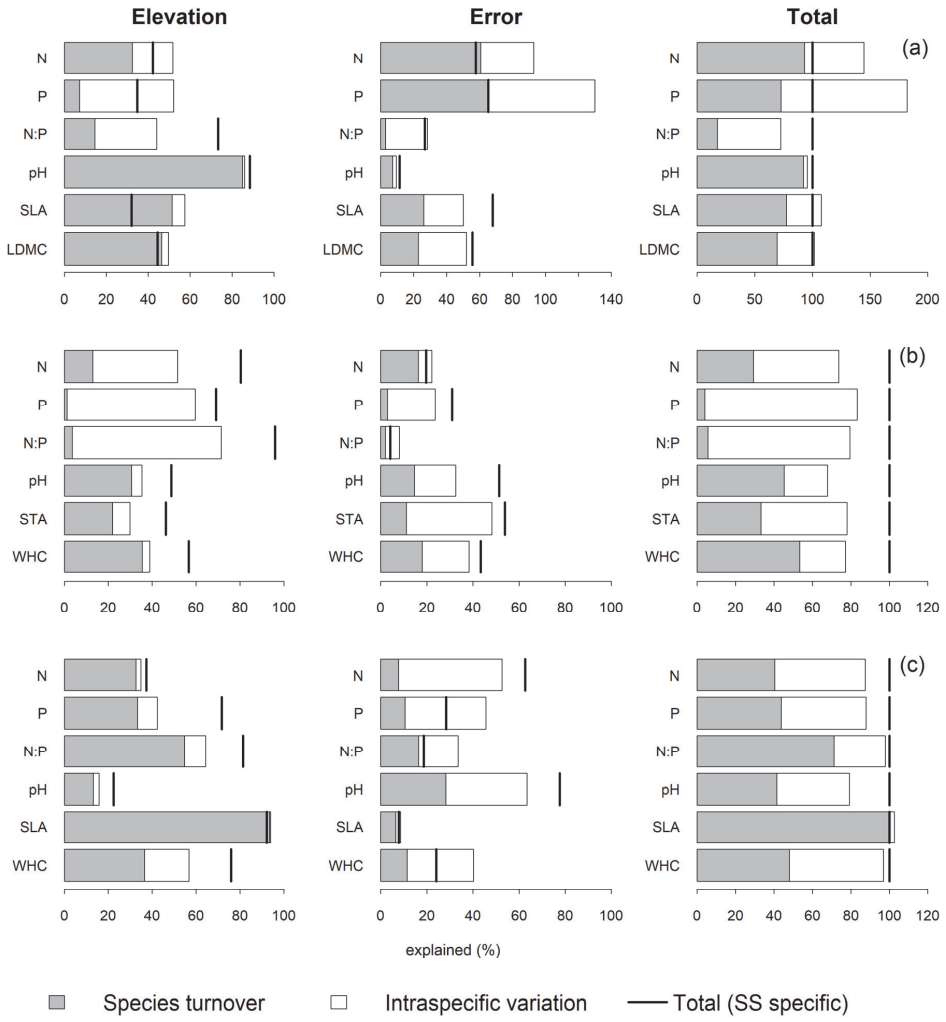

Figure S2. Decomposition of trait variability into: variation explained by elevation, error (residuals) and total (elevation + error) for vascular plant, lichen and bryophyte functional traits: nitrogen concentration (N), phosphorous concentration (P), N:P ratio, pH, specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC), and water holding capacity (WHC). Grey parts of columns correspond to the contribution of species turnover effects, white parts correspond to the contribution of intraspecific variability effects and black bars denote total variation (sum of species turnover, intraspecific variation and their covariation). If total variation is greater than the sum of species turnover and intraspecific variability effects the covariation is positive, while if it is less than the sum of these components the covariation is negative. The values are percentages of total variation of the specific averages.

Paper II

Mat-forming lichens affect microclimate and decomposition by different mechanisms

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Abstract

We studied the effects of different mat-forming lichens on microclimate and decomposition in an alpine ecosystem. We used four lichens with contrasting colour and water-holding capacity. We recorded soil temperature and moisture, and decomposition rate of two types of plant litter under the different lichen mats and in bare soil. While soil temperature and freeze-thaw cycles were reduced under all lichen mats compared to bare soil, *Cladonia rangiferina/stygia* insulated stronger than other lichens. Decomposition of *Vaccinium uliginosum* litter was faster under *Flavocetraria nivalis* than under *Alectoria ochroleuca*, but this was not related to microclimate. We conclude that insulation by lichen mats is stronger with higher water-holding capacity, while colour does not affect microclimate. Second, we suggest that microbial communities associated with lichen thalli have a larger effect on decomposition than soil conditions. Thus, lichen mats affect microclimate and decomposition through different mechanisms.

Keywords: *Alectoria ochroleuca*, alpine ecology, *Cetraria islandica*, *Cladonia*, *Flavocetraria nivalis*, functional traits, plant-soil interactions, soil moisture and temperature, transplant experiment, tundra

Introduction

Mat-forming lichens dominate the vegetation in many high latitude and high elevation environments (Matveyeva and Chernov, 2000). In alpine ecosystems, lichens are most abundant at wind-swept ridges, where conditions are generally too harsh for most vascular plants and bryophytes to persist (e.g. Dahl 1956; Smith 1990). Alpine ecosystems are mainly temperature-limited as low temperatures inhibit growth and reduce the growing season length. Effects of vegetation on microclimate, e.g. soil temperature, can thus have a big impact on ecosystem processes. For example, bryophytes and cushion plants are known to insulate the soil (Körner, 2003; Soudzilovskaia et al., 2013), thereby protecting against extreme temperatures and creating a suitable habitat for seedling establishment (Carlsson and Callaghan, 1991; Cavieres et al., 2007), or insulating permafrost soils against high temperatures (Guglielmin et al., 2008; Turetsky et al., 2012). However, the impact of mat-forming lichens on microclimate and corresponding ecosystem processes is less known.

Many lichens on ridges have a yellow or pale colour, which is the result of the secondary metabolite usnic acid (Ingólfsdóttir, 2002). As a result, areas dominated by these lichens impact the shortwave albedo of land surface, possibly resulting in a cooling effect to the atmosphere compared to other, darker-coloured lichens and vegetation types (Bernier et al., 2011). On a smaller scale, lichen colour and reflectance could potentially alter microclimatic conditions inside and underneath lichen mats. In accordance, in an alpine ecosystem, two lichen species with similar growth form but contrasting colour were shown to heat up to various extents: the bright-coloured *Alectoria ochroleuca* showed 20°C higher thallus surface temperatures than maximum air temperature, while the dark-coloured *Bryocaulon divergens* was almost 40°C warmer (Gauslaa, 1984). In another study, *Thamnolia vermicularis* painted black experienced higher thallus temperatures than unpainted white thalli, and this difference increased with increasing air temperature, while it decreased with increasing wind speed (Kershaw, 1975).

Besides temperature, moisture is another important factor driving conditions inside and underneath lichen mats. Lichens are poikilohydric, which means that they cannot regulate their water content actively and are dependent on water availability in their environment. However, structural differences in thalli allow for different water storage strategies. As such, thin and finely dissected lichens take up humidity quickly but also dry out

more rapidly, while lichens with thicker thalli need more time to hydrate but also remain hydrated longer (Gauslaa, 2014; Phinney et al., 2018). Furthermore, clumping and mat-formation increase the time required for drying, thus lichen mats remain moist longer than single thalli (Larson and Kershaw, 1976). Thallus moisture in turn also affects thallus temperature as wet thalli experience much lower-than-ambient thallus temperatures due to evaporative cooling (Kershaw, 1975). This shows that lichen traits such as colour, water holding capacity and mat density (morphology) together determine temperature and moisture conditions within lichens. However, it remains unclear how different lichen traits affect the microclimate underneath lichen mats.

Soil moisture and temperature are important drivers in soil ecosystem processes such as decomposition. Decomposition affects carbon and nutrient dynamics and is mainly driven by litter quality, (micro)climate, and the decomposer community (Gavazov, 2010; Swift et al., 1979). All of these drivers are directly or indirectly affected by vegetation. Litter quality is directly determined by the surrounding vegetation as the source of litter. Further, vegetation and decomposer community (soil biota) are closely interlinked, as shown by the 'home-field advantage'; litter often decomposes faster when placed under the same vegetation from which it originated than when placed under a different type of vegetation (Ayres et al., 2009; Gholz et al., 2000). In cold biomes, microbial activity is generally temperature-limited, and therefore, decomposition rates are hypothesized to increase under global warming. However, higher temperatures will result in increased decomposition only if soil moisture is sufficient (Aerts, 2006; Gavazov, 2010), while increased precipitation in already moist areas can decrease decomposition rates (Althuizen et al., 2018). In this light, it is important to study the effects of ground covering vegetation as a potential regulator of climate on local soil conditions and decomposition.

In this study, we investigate the effects of different mat-forming lichen species and their traits on microclimate (soil temperature and moisture) and decomposition rate of plant litter in an alpine ecosystem. To do this, we set up a lichen transplant experiment on a wind-exposed alpine lichen heath in Finse, southern Norway. We measured microclimate parameters and decomposition rates of plant litter after one year of incubation underneath lichen mats of varying colour and morphology, and in bare soil. The transplants consisted of four lichen species or species combinations from the same site, i.e. *Alectoria ochroleuca*,

Cetraria islandica, a mixture of *Cladonia rangiferina* and *C. stygia*, and *Flavocetraria nivalis*. We hypothesized that 1) different mat-forming lichens have different effects on soil temperature and moisture depending on lichen mat traits, 2) these effects in turn affect decomposition rates below lichen mats, and more specifically that 3) higher soil temperature and soil moisture increase decomposition rate of plant litter under the lichen mat.

Materials and methods

Field site and experimental set-up

We set up the field experiment close to Finse, Southern Norway, at a wind-exposed ridge at approximately 1360 m a.s.l. on metadacite bedrock (60°45'N, 7°35'E). Mat-forming lichens, such as *Alectoria ochroleuca* and *Flavocetraria nivalis* dominate the site. In late August 2016, we established six blocks of five 50 × 50 cm plots and removed all aboveground vegetation. The plots were fenced with a nylon mesh (mesh size: 2.5 × 2.5 mm) and wooden poles in each corner, matching vegetation height (maximum of 10 cm high), to mark the plots and for stabilization of the transplants. We filled four plots in each block with thalli of *A. ochroleuca*, *F. nivalis*, *Cetraria islandica*, or a mixture of *Cladonia rangiferina* and *Cladonia stygia*, collected from the immediate surroundings of the blocks. We chose to combine *C. rangiferina* and *C. stygia* because these species grew intermixed, and they are similar in terms of growth form, colour and secondary compounds (Ahti and Stenroos, 2013). The fifth plot in each block acted as a lichen-free control (i.e. bare soil), in order to assess the impact of lichens on microclimate and decomposition relative to when lichens are absent. Soil moisture and temperature sensors (ECH_2O 5TM) were placed at 3 cm soil depth and connected to Em50 data loggers (Decagon Devices Inc., WA, USA), which recorded measurements every 30 minutes for 14 months. In addition, four iButton temperature sensors (Maxim Integrated, CA, USA) per plot (waterproofed in small plastic wraps) were placed underneath the lichen mats and on bare soil on the soil surface, which recorded temperature every 4 hours. To prevent the iButtons in the bare soil plots from blowing away, they were fixed to the soil surface with small plastic sticks.

Litter bags

For measurements of decomposition rates, we collected senesced leaves of *Vaccinium uliginosum*, an ericaceous dwarf shrub, and *Rubus chamaemorus*, a forb, close to the Finse

Alpine Research Center at 1220 m a.s.l., in October 2016. We chose these species because they were abundant and we expected them to have different decomposition rates due to their different growth forms (e.g. Quested et al. 2003). Senesced leaves were picked from the plants to make sure that only litter from the last growing season was included and that nutrients from the litter were not partly leached already. Each litter type was dried in a drying cabinet at 30°C until air-dry, cleaned of other plant material and mixed. Litter bags were made of a 1×1 mm mesh nylon fabric, of which the edges were sealed using a Hand Impulse Sealer. For each litter type, 30 bags were prepared including approximately 1 g of litter. The exact weight of the litter of each bag was recorded using a 0.1 mg readability scale (Sartorius ED224S) and corrected with an air-dry to oven-dry ratio calculated from spare litter for each litter type, dried at 60°C for 24 hours. In addition, some spare litter was kept to determine pre-incubation nitrogen (N) and phosphorus (P) concentrations using Kjeldahl analysis. Two litter bags (one of each litter type) were placed underneath each of the lichen transplant plots on 14 October 2016. In the bare soil plots, litter bags were placed on top of the soil and fixed to the ground with small plastic sticks. Incubation lasted for one year and the litter bags were retrieved on 20 October 2017, air-dried and weighed. Small fractions of each litter bag were combined in 4 to 5 samples for each litter type, which were oven-dried at 60 °C for 24 hours and reweighed. From this, the oven to air-dry ratio was calculated and used to correct the air-dry weights of the litter bags as retrieved from the field. Mass loss was calculated as the percentage weight loss between pre- and post-incubation weights, and relative decomposition rate was calculated following Olson (1963) as the absolute value of log (post-incubation weight/pre-incubation weight). After weighing, the samples were ground using a Retsch MM400 ball mill and analysed for N and P concentration (in %) following Kjeldahl analysis. Release of N and P after one year of decomposition was calculated as the difference between concentrations before and after incubation, expressed in percentage of initial concentration.

To account for the effect of spatial differences in soil fertility on decomposition rate, we determined plant-available nutrient concentrations in the soil using ion exchange resin capsules (Unibest International, USA). Three capsules per plot were buried at 3 cm depth on 7 June 2018 and retrieved on 18 September 2018. Capsules were cleaned and analysed for

available nutrients in ppm. Plant-available nitrogen (N), phosphorous (P) and potassium (K) in the soil were averaged per plot before data analysis.

Lichen mat traits

We selected three lichen traits, which we expect to affect the microclimate, i.e. water holding capacity (WHC), mat density and colour. To measure WHC and mat density, we collected 10 cm diameter cores of the lichen mats in August 2017. Lichens were air-dried and weighed (dry weight), hydrated and weighed again (wet weight). We hydrated the lichen cores by spraying them with demineralized water and incubating them for 30 minutes in a sealed container lined with moistened filter paper. Lichens were subsequently blotted dry to remove external water before weighing wet weight. For each sample, we calculated the water content by subtracting dry weight from wet weight, and converting to litres (L) by assuming a water density of 1 g mL^{-1}. Water holding capacity (WHC) was calculated as water content per area of the core, expressed in L m^{-2} (Gauslaa, 2014). Lichen mat density was calculated as dry weight per area of the core, expressed in g m^{-2}. Lichen colour was characterized as follows: *Alectoria ochroleuca* and *Flavocetraria nivalis* were classified as bright-coloured, *Cladonia rangiferina/stygia* as intermediate and *Cetraria islandica* as dark-coloured (similar to reflectance in Concostrina-Zubiri et al., 2014).

To check if lichens' secondary chemistry affected decomposition rate of plant litter below lichen transplants, we analysed carbon-based secondary compounds on five lichen samples per species collected at a nearby site with similar lichen heath vegetation. These were analysed from triple acetone extractions of ground material and from water extracts of intact thalli for 1 hour, in order to determine potential leakage of compounds. Both extracts were analysed on HPLC following Nybakken et al. (2007). Methods are further explained in Suppl. 1.

Microclimate calculations

Soil moisture (volumetric water content (VWC), in m^3 m^{-3}) data were checked and cleaned from insensible soil moisture values (i.e. VWC < 0 and VWC > 1) as well as soil moisture values measured when the soil was frozen (i.e. concurrent temperature ≤ 0°C). Several sensors were excluded from the soil temperature calculations because of too many missing values or because they were pulled out of the soil, resulting in n = 4 for *A. ochroleuca* and bare soil, and

n = 3 for *C. islandica*, *C. rangiferina*/*stygia* and *F. nivalis*. The effect of lichen mats on microclimate can only be investigated during the growing season, since snow cover is a more important driver of microclimate than vegetation during winter time. Therefore, we defined the growing season as the snow-free season directly after snow melt in spring and before snowfall in autumn, which was estimated visually from the soil moisture data using the peak in soil moisture during snow melt and the drop in soil moisture at first snow fall and/or when temperature dropped below 0 °C. The snow-free season for all plots was estimated as 23 May 2017 to, and including, 5 October 2017. We calculated mean temperature and moisture for this period, as well as daily minimum, maximum and amplitude. Soil freeze-thaw cycles are known to influence microbial activity (e.g. Schimel & Clein 1996; Henry 2007), and could thus affect decomposition rates. Therefore, we additionally calculated diurnal freeze-thaw cycles as the number of days when temperature went above and below 0 °C. Freeze-thaw cycles were calculated over the complete experimental period, i.e. incubation of litter bags in the field (15 October 2016 to 19 October 2017). Mean soil surface temperature was calculated for July 2017.

Data analysis

To test the effect of different lichen mats on the microclimate, decomposition and soil nutrients, we ran separate one-way ANOVAs with lichen as a fixed factor, block as a random effect, and microclimate variables (mean soil moisture and soil temperature), relative decomposition rate and N and P release per litter type, and plant-available nutrients (N, P, and K) as response variables. Soil moisture (VWC) data were arcsine transformed and soil nutrient data were log-transformed before analyses. Number of diurnal freeze-thaw cycles was analysed similarly but using generalized mixed effects models with Poisson distribution and an additional random effect of observation number to account for overdispersion (Elston et al., 2001). If significant differences were found at $p < 0.05$, post-hoc tests were performed using Tukey HSD, to test which lichen mats differed from each other.

Correlations between lichen mat traits, microclimate variables, decomposition variables and plant-available nutrients were carried out using Spearman's rank correlation, or Pearson's product-moment correlation if both variables had a normal distribution. To assess which variables explain decomposition rate of both litter types, we used linear mixed effects models to carry out an ANCOVA with microclimate variables (soil moisture and temperature),

lichen traits (WHC and colour) and plant-available nutrients (N) as fixed factors (correlated variables were excluded), and litter type nested within lichen treatments nested within block as random effects. Correlated variables were excluded and backwards model selection was done by removing interactions and main effects stepwise, starting with interactions with the highest p-value, keeping only significant p-values.

One block got destroyed by free-ranging sheep during the summer of 2017, therefore we used the remaining five blocks for data analysis. All analyses were performed in the statistical software R version 3.5.1 (R Core Team, 2018), using packages nlme (Pinheiro et al., 2015), lme4 (Bates et al., 2015) and multcomp (Hothorn et al., 2008).

Results

Lichen effects on microclimate

Mean soil temperature of the growing season was lower under lichen mats than under bare soil, and lower under *Cladonia rangiferina*/*stygia* compared to *Alectoria ochroleuca* (Table 1; Figure 1). Mean soil moisture during the snow-free season varied highly between plots but did not differ significantly between lichen mats (Table 1; Figure 1). Number of diurnal soil freeze-thaw cycles were significantly reduced under lichen mats compared to bare soil, and *C. rangiferina*/*stygia* reduced freeze-thaw cycles more than other lichen species (Table 1; Figure 1). There was a strong positive correlation between freeze-thaw cycles and mean temperature of the growing season (Table 2). Mean July temperature at the soil surface was lower under lichens than on bare soil, and lower under *C. rangiferina*/*stygia* and *Flavocetraria nivalis* mats compared to *A. ochroleuca* and *Cetraria islandica* ($F_{4,15} = 35.4$, $p < 0.001$). Soil surface temperature was highly correlated with soil temperature at 3 cm depth (Spearman's rho = 0.83, $p < 0.001$), therefore we excluded surface temperature from further analyses. Soil temperature under lichen mats was negatively correlated with lichen water holding capacity (Table 2; Figure 2a), as well as lichen mat density (Table 2; Figure 2b), while no differences in microclimate were observed between different lichen colour levels.

Lichen effects on decomposition

Litter decomposition of *Vaccinium uliginosum* was in general faster than that of *Rubus chamaemorus* (Figure 3). For *V. uliginosum* litter, the relative decomposition rate under *F. nivalis* mat was higher (i.e. higher mass loss) than under *A. ochroleuca* (Table 3; Figure 3).

Net N release of both litter types did not differ between lichen treatments (Table 3; Figure 3). Net P release in *V. uliginosum* litter was lower under *C. islandica* compared to *A. ochroleuca* and bare soil, and lower under *C. rangiferina/stygia* and *F. nivalis* compared to bare soil, while it did not differ in *R. chamaemorus* litter (Table 3; Figure 3). Decomposition rate of *V. uliginosum* litter was weakly positively correlated with soil moisture, and negatively correlated with litter P release (Table 2). Net P release was also negatively correlated with soil moisture (Table 2). Plant-available N in the soil did not differ between lichen treatments, while available P was higher in bare soil plots than in lichen plots, and available K was lower under *A. ochroleuca* and *C. rangiferina/stygia* compared to bare soil plots (Table 1; Figure S1). Available N correlated with litter N release, while available P correlated with both soil temperature and freeze-thaw cycles (Table 2). Available N, P and K were all positively correlated with each other (Table 2). None of the lichen traits, microclimate variables and plant-available nutrients could explain decomposition rate of both litter types when all data were combined in one model. Model selection using backward stepwise elimination resulted in a final insignificant model containing only soil moisture ($F_{1,7} = 1.58$, $p = 0.24$).

Carbon-based secondary compounds varied both quantitatively and qualitatively among the four lichen species (Table S1). The total concentrations of CBSCs were highest in *A. ochroleuca* followed by *C. islandica, C. rangiferina/stygia* and *F. nivalis* (Table S1). We found the medullary compounds diffractaic acid in *A. ochroleuca* and fumarprotocetraric acid in *C. islandica* and *C. rangiferina/stygia*, while *F. nivalis* had no medullary compounds. Both *F. nivalis* and *A. ochroleuca* had usnic acid, and *C. rangiferina/stygia* had atranorin in the cortical layer. We found only traces of carbon-based secondary compounds in the water extracts (Table S1).

Discussion

Cladonia rangiferina/*stygia* reduced soil temperature and number of freeze-thaw cycles more than other lichens, which seems to be related to its water-holding capacity. This is in line with our first hypothesis that different mat-forming lichens have different effects on soil temperature and moisture depending on their traits. Our second hypothesis that microclimate effects of lichens in turn affect decomposition rates of plant litter below lichen mats was not supported by our data; while we found differences in decomposition rates

under *Alectoria ochroleuca* and *Flavocetraria nivalis* mats, these were not related to the effects of lichen mats on microclimate. Thirdly, we hypothesized that higher soil temperature and higher soil moisture increase decomposition rates under lichen mats, which was only partly supported; none of the measured variables could explain decomposition rate, although we found a weak positive correlation between soil moisture and decomposition rate of *Vaccinium uliginosum* litter.

The impact of lichen mats on microclimate conditions can be summarized as thermal insulation against temperature extremes and fluctuations. Our data suggest that this is mainly the result of the water holding capacity of lichen mats, which is, from a biophysical viewpoint, due to the high specific heat capacity and thermal conductivity of water. This corresponds well with findings from Soudzilovskaia et al., (2013) on bryophytes, which showed that differences in heat transfer through bryophyte mats were fully explained by mat thickness and water content, conform to physical rules. They concluded that biological processes did not affect heat transfer through mats, which can be explained by the fact that bryophytes, as well as lichens, are poikilohydric, meaning that they lack active metabolic or physiological control of their water relations and instead reflect environmental conditions in a more direct manner. However, lichens can regulate evaporative loss by variability in thallus shape and degree of clumping or mat-formation (Larson and Kershaw, 1976). Further, more recent studies have shown that water holding capacity differs greatly between lichen species, and relates to specific thallus mass (STM), which drives rehydration and reactivation kinetics (Gauslaa, 2014; Phinney et al., 2018). As such, lichens with high thallus thickness and thus high STM, have high water holding capacity. In our study, *C. rangiferina/stygia* has round, hollow podetia and forms bush-like mats, and thus has higher thallus thickness compared to the other lichen species which have thin hair-like thalli or broad and flat lobes. Further, *C. rangiferina/stygia* had the highest mat density in our study. Thus, the thallus shape and mat structure of *C. rangiferina/stygia* enables it to have higher water holding capacity and thus higher insulation capacity compared to the other lichens we studied.

Interestingly, lichen colour did not have any effect on soil temperature. Although colour can have large effects on thallus (surface) temperature (Gauslaa, 1984; Kershaw, 1975) and on a larger scale albedo (Bernier et al., 2011), it did not affect microclimate conditions underneath lichen mats in our study. The insulating effect, driven by lichen water holding

capacity, likely overrules any effects of colour on soil temperature. A part of this explanation could be that dark-coloured, low-reflective lichens need to have an open canopy structure to allow light to penetrate to lower parts of the mat (Gauslaa, 1984). The relatively low mat density and open canopy structure of *C. islandica* in our study could have played a role in diminishing the potential heating effect due to a larger effect of wind, which reduces the boundary layer thickness and thereby the influence of absorbance on temperature. Furthermore, low mat density means low water holding capacity and thus lower insulation capacity, which still seems to be the main driver of soil temperatures underneath lichen mats.

Although we show that lichen mats insulate the soil and that different species have different insulation capacities depending on their traits, this did not impact decomposition rates underneath the lichen mats. We did find that the decomposition rate of *Vaccinium uliginosum* litter was higher under *F. nivalis* compared to *A. ochroleuca*, but these results cannot be explained by microclimate, as *A. ochroleuca* and *F. nivalis* did not differ in their effect on any of the measured climate variables. We did not find differences in decomposition of *Rubus chamaemorus* between the treatments. The generally low decomposition rate could be due to the atypical place of this species' litter to decompose. Although both litter types were collected from a different site than the experimental site, *V. uliginosum* also grows nearby the experimental site in less lichen-dominated areas, possibly benefiting from a home-field advantage effect (Gholz et al., 2000), while *R. chamaemorus* typically grows in moister areas. Soil moisture was weakly positively correlated with decomposition rate of *V. uliginosum* litter, which is in line with previous findings that moisture availability is an important driver in decomposition (e.g. Althuizen et al. 2018; Gavazov 2010; Aerts 2006). However, it did not explain decomposition rate in the linear mixed model when lichen treatment was taken into account, likely because plots varied highly in soil moisture, independently of lichen treatment.

Lichens are known for their secondary compounds, which protect against herbivores and solar radiation, and may result in slower decomposition of lichen litter (Asplund and Wardle, 2016, 2013). It is often assumed that these compounds have antibiotic properties, which affect soil microorganisms and therefore could inhibit decomposition. *Alectoria ochroleuca,* under which plant litter had the lowest decomposition rate, indeed contained a three times higher concentration of total secondary compounds than *F. nivalis,* under which

plant litter decomposed faster. However, the water extracts from all species had very low concentrations of secondary compounds, indicating that they hardly leach from the lichen thalli. In line with this, Stark et al. (2007) could not detect any lichen secondary compounds in the soil below *Cladonia stellaris* due low water solubility of these compounds, and thus argued that compounds from this species are not antimicrobial in soil. For this reason, we do not expect that secondary compounds played a direct role in the decomposition of plant litter underneath the lichen mats. However, the difference in secondary compound composition could potentially impact on the microbial communities living in the lichen thallus. Lichen thalli can be seen as a complex ecosystems hosting a large variety of microbes such as bacteria, yeasts, and protozoa (Pankratov et al., 2017). Differences in microbial communities could in turn have resulted in the observed differences in decomposition rates under the studied lichens. This is in line with a recent study showing that microbial biomass strongly regulates litter decomposition and seems to be of greater importance than previously thought (Bradford et al., 2017).

To conclude, our data suggest that lichen species identity can affect both soil microclimate and plant litter decomposition, however, the mechanisms behind these processes differ. Differences in how lichens affect soil microclimate are driven by lichen mat morphology resulting in different water holding capacity and thus insulation capacity. Meanwhile, decomposition of plant litter seems unrelated to lichen traits and insulation capacity. We propose that the differences in decomposition under lichen mats is the result of different microbial communities associated with lichen thalli. Our findings highlight the importance of lichen cover on microclimate and ecosystem processes in alpine environments, as lichens can cover large areas in alpine ecosystems, and they are among the first to decline in response to climate change, e.g. increased temperatures, increased competition with vascular plants, and changes in snow cover (Alatalo et al., 2017; Bidussi et al., 2016; Lang et al., 2012). Further, our study shows that although many different microbes associated with the lichen symbiosis have been identified (Pankratov et al., 2017), more knowledge is needed on how these microbial communities affect ecosystem processes such as decomposition.

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Author contributions

JA designed the study in consultation with KvZ, RR, KK and SL. KvZ, RR and JA conducted field and lab work. KvZ analysed the data and led the writing in collaboration with RR, KK, SL and JA.

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Tables and figures

Table 1. Results of linear mixed effects models to test for the effect of lichen mat (treatment) on microclimate and plant-available nutrient variables at 3 cm soil depth. Mean soil temperature (°C) and moisture (VWC, $m^3\ m^{-3}$) were averaged over the snow-free season; number of diurnal freeze-thaw cycles were calculated over the litter bag incubation period. Plant available nutrients (total nitrogen (N), phosphorous (P) and potassium (K) were measured over summer 2018. Block was included as a random effect in all analyses. Soil moisture (VWC) values were arcsine transformed; plant-available N, P and K were log-transformed.

Response variable	***df***	***test statistic***	***p***
Soil temperature	4, 8	F = 25.39	**< 0.001**
Soil moisture	4, 8	F = 0.88	0.517
Freeze-thaw cycles	4	X^2 = 42.76	**< 0.001**
N	4, 16	F = 2.17	0.119
P	4, 16	F = 4.19	**0.017**
K	4, 16	F = 3.28	**0.038**

Table 2. Correlation coefficients of continuous lichen traits (water holding capacity (WHC) and mat density), soil climate variables (soil temperature (Temp), soil moisture, and freeze-thaw cycles (FTC) at 3 cm depth); decomposition rate (Decomp), nitrogen (N) release, and phosphorous (P) release of *Vaccinium uliginosum* litter, and plant-available nutrients (N, P, and potassium (K)). Correlation coefficients are calculated from Spearman's rank correlation, or Pearson's product-moment correlation if both variables showed a normal distribution (indicated with [1]). Significant correlations are in bold and indicated with * at p<0.05, ** at p<0.01, or *** at p<0.001.

	WHC	Density[1]	Temp	Moisture[1]	FTC	Decomp[1]	N release[1]	P release	Soil N	Soil P
Density[1]	**0.78*** **									
Temp	**-0.67***	**-0.65***								
Moisture[1]	0.36	0.43[1]	-0.31							
FTC	**-0.58***	-0.53	**0.89*** **	-0.15						
Decomp[1]	0.23	0.12[1]	-0.15	**0.50[1]***	-0.01					
N release[1]	0.10	0.11[1]	-0.16	0.28[1]	-0.19	0.33[1]				
P release	-0.09	0.03	0.27	**-0.51***	0.03	**-0.68*** **	0.21			
Soil N	0.17	0.14	0.00	0.36	0.02	0.36	**0.49***	-0.07		
Soil P	-0.05	-0.19	**0.55***	0.25	**0.58***	0.18	0.13	-0.11	**0.64****	
Soil K	0.06	-0.04	0.26	0.11	0.28	0.21	0.14	-0.08	**0.61****	**0.74*** **

Table 3. Results of linear mixed effects models to test for the effect of lichen mat (treatment) on decomposition rate and release of nitrogen (N) and phosphorous (P) of *Vaccinium uliginosum* and *Rubus chamaemorus* litter after one year of incubation. Block was included as a random effect in all analyses. Values of N and P release were arcsine transformed.

	Vaccinium uliginosum			*Rubus chamaemorus*		
Response variable	***df***	***F***	***p***	***df***	***F***	***p***
Decomposition rate	4, 15	3.49	**0.033**	4, 12	2.44	0.104
N release	4, 15	0.89	0.496	4, 11	1.49	0.272
P release	4, 15	6.35	**0.003**	4, 11	1.10	0.402

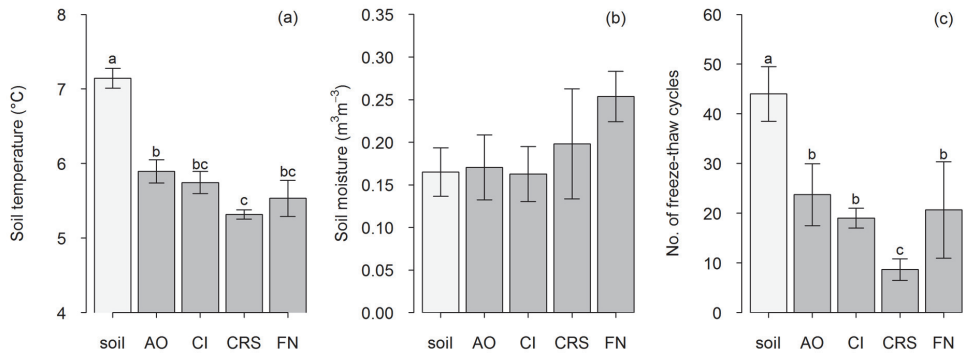

Figure 1. Mean ± SE of climate variables at 3 cm soil depth under different lichen mats and bare soil: (a) temperature (°C) and (b) moisture (VWC, m^3 m^{-3}), calculated over the snow-free season, and (c) number of diurnal freeze-thaw cycles calculated over the experimental period. Different letters indicate significant differences between lichen mats at $\alpha = 0.05$. AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina* and *C. stygia*, FN = *Flavocetraria nivalis*.

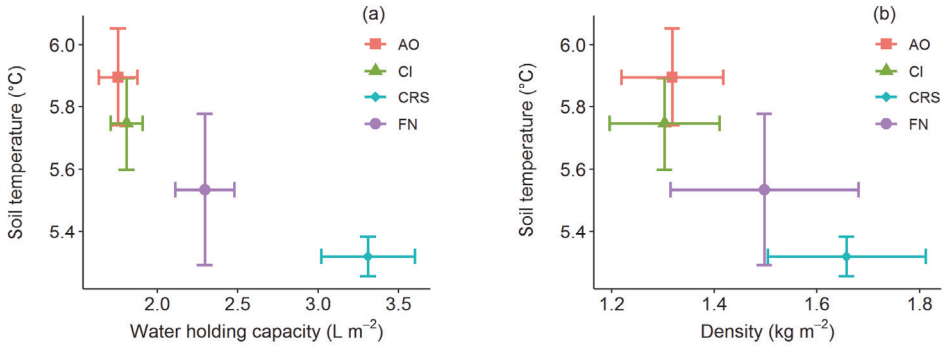

Figure 2. Proposed relationships between growing season soil temperature (°C) at 3 cm depth and (a) lichen mat water holding capacity (L m^{-2}), and (b) lichen mat density (kg m^{-2}), given in mean ± SE per lichen species. AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina* and *C. stygia*, FN = *Flavocetraria nivalis*.

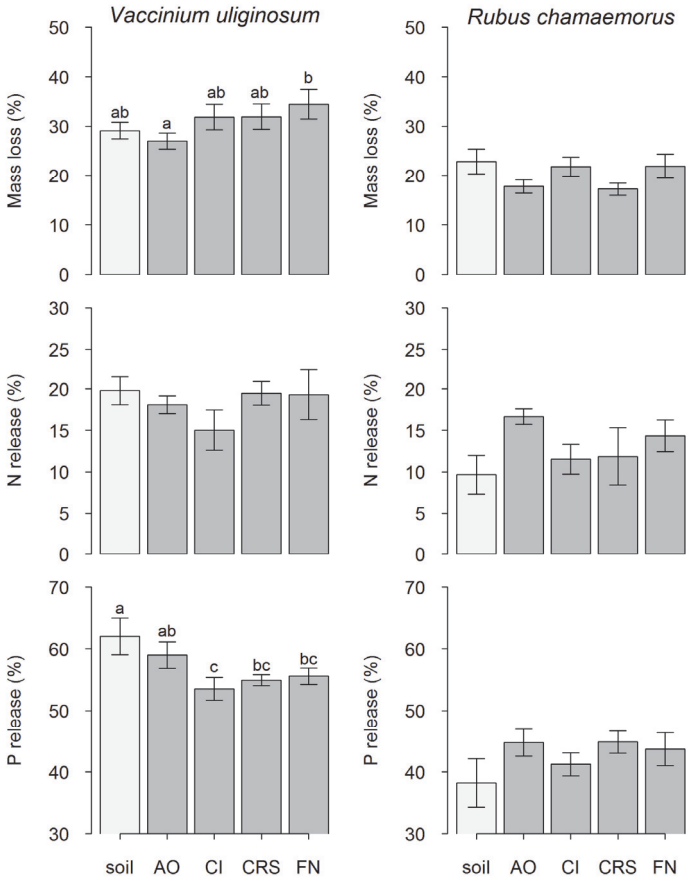

Figure 3. Mass loss (%), N release and P release (% of initial concentration) of *Vaccinium uliginosum* litter and *Rubus chamaemorus* litter after one year of incubation under lichen mats of *Alectoria ochroleuca* (AO), *Cetraria islandica* (CI), *Cladonia rangiferina* and *C. stygia* (CRS), *Flavocetraria nivalis* (FN), and on bare soil. Different letters indicate significant differences between lichen mats at $\alpha = 0.05$.

Supplementary information

Supplement 1 Material and methods

For analysis of carbon based secondary compounds (CBSCs) we extracted approximately 15 mg of lichen powder in 2 ml acetone for 3 × 30 min. The combined supernatants were evaporated and re-dissolved in 1000 µl methanol. In order to determine potential leakage of CBSCs we extracted five intact thalli (292 ± 17 mg) per species in 10 ml of deionized water for 1 hour in room temperature on a shaker. Water extracts were then filtered through a 0.45 µm PTFE membrane, evaporated and re-dissolved in 1000 µl methanol. The extracted compounds were then quantified by HPLC (Agilent Series 1200, Agilent Technologies, Waldbronn, Germany) with an ODS Hypersil column, 50 × 4.6 mm using 0.25% orthophosphoric acid and 1.5% tetrahydrofuran in Millipore water (A) and 100% methanol (B) as mobile phases at 2 ml min-1, following the gradient described in Nybakken et al., (2007). When analysing LSMs we used UV-detection at 245 nm, while PSMs were run with detection at 220, 270, 320 and 360 nm. Compound identification was based on retention times, online UV spectra and co-chromatography of commercial standards.

Table S1. Mean (± SE) concentration of carbon based secondary compounds (mg g^{-1}) in five thalli each of *Alectoria ochroleuca, Cetraria islandica, Cladonia rangiferina/stygia* and *Flavocetraria nivalis*. The total concentration is calculated for the lichen medulla and the lichen cortex, separately. The numbers in italic are from water extracts of intact thalli and all other values are from ground material extracted in acetone.

	Alectoria	***Cetraria***	***Cladonia***	***Flavocetraria***
Diffractaic acid	51.8 ± 3.4	–	–	–
Fumarprotocetraric acid	–	51.4 ± 6.5	22.3 ± 2.3	–
Lichestertinic acid	–	0.6 ± 0.1	–	–
Protolichestertinic acid	–	2.4 ± 0.6	–	–
Unknown compound	–	2.4 ± 0.6	–	–
Total medullary compounds	**51.8 ± 3.4**	**56.8 ± 7.4**	**22.3 ± 2.3**	**–**
Water extracts (medullary)	*0.0099 ± 0.002*	*0.0072 ± 0.0014*	*0.0093 ± 0.0015*	–
Atranorin	–	–	8.7 ± 1.2	–
Usnic acid	22.7 ± 5.0	–	–	23.8 ± 4.2
Total cortical compounds	**22.7 ± 5.0**	**–**	**8.7 ± 1.2**	**23.8 ± 4.2**
Water extracts (cortical)	*0.0021 ± 0.0006*	–	–	–

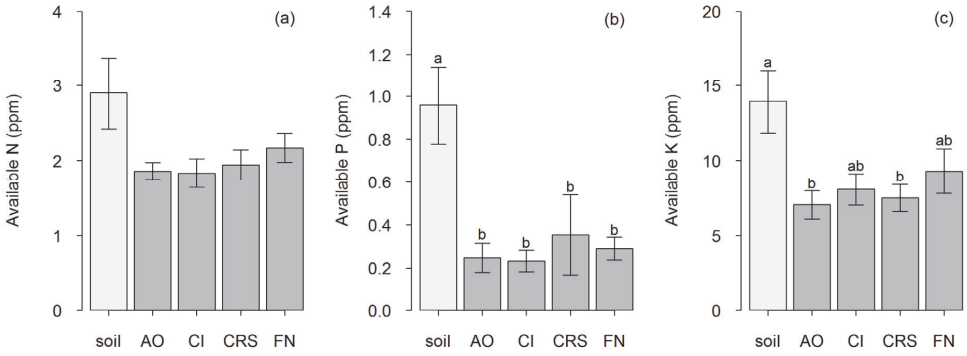

Figure S1. Mean ± SE of plant-available nutrients at 3 cm depth under different lichen mats and bare soil: (a) nitrogen (N, ppm), (b) phosphorous (P, ppm), and (c) potassium (K, ppm) accumulated over summer (7 June to 18 September 2018). Different letters indicate significant differences between lichen mats at α = 0.05. AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina* and *C. stygia*, FN = *Flavocetraria nivalis*.

Paper III

Community-level decomposability of lichens and bryophytes across an elevational gradient

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Abstract

Lichens and bryophytes are abundant primary producers in high latitude and high elevation ecosystems and play an important role in ecosystem processes such as decomposition and nutrient cycling. Despite their importance, little is known about the decomposability of lichens and bryophytes either across or within species, or at the whole community level, or how this decomposability is affected by their functional traits. Here, we studied decomposability of lichens and bryophytes across an elevational gradient in alpine Norway. In contrast to our expectations, we found that community-level decomposability increased with elevation. Nutrient release differed from decomposability; P release decreased with elevation while nitrogen release did not change. Decomposability was explained by nutrient concentrations, tissue pH and primary producer group (lichens versus bryophytes) at both the individual species and community levels. Species turnover was the main driver of decomposability across elevation at the community level, despite some of the traits explaining decomposability showing high intraspecific variability. Our study highlights the importance of among-species variation in lichen and bryophyte decomposability. Further, the higher decomposability that we found for higher elevations suggests that global warming might result in a shift towards slower decomposable species.

Keywords: alpine ecology, climate gradient, cryptogams, decomposition, elevation, functional traits, plant-soil interactions, tundra

Introduction

Decomposition, the decay of organic matter, is an important ecosystem process that drives carbon and nutrient cycling (Chapin et al. 2011). The decomposition of plant litter is determined by three main factors: litter quality (and thus the functional traits of the plant), the physico-chemical environment (e.g. climate and soil abiotic properties) and the decomposer community, which all three interact with each other (Swift et al. 1979). Traditionally, climate (temperature and moisture) has been regarded as the predominant factor controlling decomposition rates, with litter quality being of subordinate importance, and with the decomposer community exerting a regulatory role at local scales (Swift et al. 1979; Lavelle et al. 1993; Aerts 1997). However, more recent studies have shown that species-driven litter quality differences have a much larger effect than climate-driven variation on local-scale variation in plant litter decomposition both within biomes (Cornwell et al. 2008) and across biomes (Djukic et al. 2018). Therefore, the indirect effects of expected future climate change as manifested through vegetation shifts, will likely have a larger impact on decomposition than will the direct effects such as increasing temperature and altered precipitation (Cornelissen et al. 2007; DeMarco et al. 2014).

Decomposability of plant litter is determined in a large part by the functional traits of the species that form the source of the litter. For example, leaf decomposition rates have been linked to life form, specific leaf area (SLA), and other traits related to litter quality (Cornelissen 1996; Cornelissen and Thompson 1997). Traits associated with leaf economics, i.e. plant strategies from slow to fast returns on investments of nutrients and dry mass (Wright et al. 2004), have been linked to decomposition at leaf-level (Santiago 2007), whole-plant level (Freschet et al. 2012), within- and across biomes (Cornwell et al. 2008; Makkonen et al. 2012), and at the community level (Quested et al. 2007). Generally, these studies show that litter quality and decomposability increase with nutrient concentrations, SLA, and correlated traits, while they decrease with secondary compounds and structure-related traits. Further, they highlight the importance of among species variation in decomposability (e.g. Aerts, 2006; Cornwell et al., 2008; Hobbie, 1996). However, an increasing number of studies

have contributed to the understanding that traits can vary substantially within species (Albert et al. 2010; Messier et al. 2010; Violle et al. 2012), which poses the question how intraspecific variation contributes to litter decomposability. Although several studies have considered within-species variation in decomposability (Sariyildiz and Anderson 2003; Wardle et al. 2009; Sundqvist et al. 2011b), only one study to date has considered intraspecific variability at the community level (Jackson et al. 2013).

The vast majority of decomposition studies has been on vascular plants, and decomposability of other primary producers such as lichens and bryophytes have been less well studied. Further, lichens and bryophytes are underrepresented in trait-based studies on ecosystem functioning (St. Martin and Mallik 2017), despite their major contribution to aboveground biomass and species richness at higher latitudes (Matveyeva and Chernov 2000) and their impacts on biogeochemistry and ecosystem processes (Asplund & Wardle 2016; Cornelissen et al. 2007). Lang et al. (2009) explored the decomposability of several subarctic bryophytes, lichens and vascular plant species, and found high variation both across these three groups and among species within each group, which were related to the initial chemical composition of the species. Further, Asplund & Wardle (2013) found that variation in decomposability among lichen species was strongly related to N and phosphorous (P) concentrations, as well as tissue pH and secondary compounds within the lichen cortex. Further, Campbell et al. (2010) found decomposition rates of epiphytic lichens to be related to N concentration and growth form, and Hagemann & Moroni (2015) found decomposition of lichens and bryophytes in a boreal forest to be mainly controlled by interactions between litter type and litter carbon, N and hemicellulose content. However, to our knowledge, no studies have considered decomposability in relation to functional traits of lichens and bryophytes at the whole community level.

Elevational gradients act as powerful natural experiments for testing the effects of variation of climatic factors, notably temperature (Körner, 2007; Sundqvist et al. 2013), and can therefore be used for providing insights about the ecological impacts of future climate change. For vascular plants, recent studies have shown that declining temperature with increasing elevation often causes a shift in vascular plant functional traits from those associated with rapid resource acquisition to those linked to resource conservation (Sundqvist et al. 2013; Read et al. 2014; Mayor et al. 2017). This in turn often leads to a decrease in plant

litter quality characteristics such as reduced nutrient concentrations and greater levels of secondary compounds with increasing elevation (Sundqvist et al. 2011; De Long et al. 2016), although these types of changes in functional traits with elevation do not always drive decomposition per se (Sundqvist et al. 2013). So far, only one study has looked at how functional traits of non-vascular primary producers are impacted by elevation (Roos et al. 2019), but it remains unclear how this affects decomposability.

In this study, we investigated how the decomposability of non-vascular vegetation (i.e. lichens and bryophytes) at the individual and whole community levels change along an alpine elevational gradient in southern Norway. We also explored the contributions of species turnover and intraspecific variability to variation in community-level measures of decomposability across the gradient, and the role of lichen and bryophyte functional traits in driving this variability. Specifically, we tested the following three hypotheses: (i) decomposability of lichens and bryophytes decreases with increasing elevation, (ii) species turnover effects are more important in driving decomposability across elevation than is intraspecific variation, and (iii) variation in the decomposability of lichens and bryophytes can be explained by variation in their functional traits, both at the individual and whole community levels. By addressing these hypotheses in combination, we aim to improve our understanding of what drives lichen and bryophyte decomposability across elevation, which will help to inform how lichen and bryophyte communities drive ecosystem processes under future climate change.

Methods

Field site and experimental set-up

The field sites are located near Finse, in southern central Norway. Finse is situated at 1220 m a.s.l. north of the Hardangervidda mountain plateau, approximately 250 m above the treeline. It has an average yearly temperature of 2.1 °C and 1030 mm yearly precipitation. The average temperature from 1 June to 31 August 2016 was 7.3 °C and precipitation was 303.9 mm (Norwegian Meteorological Institute 2019). The elevational gradient used in this study was established in the summer of 2016, to study functional traits of vascular plants, lichens and bryophytes (Roos et al. 2019). Here, one site was selected at each of five elevations, i.e., 1120, 1240, 1360, 1480 and 1600 m a.s.l., spanning approximately 500 m in elevation. All sites were

on acidic granite-gneiss bedrock on wind-exposed ridges on south-facing slopes, and were dominated by lichen-heath vegetation. The growing season was 54 days shorter at the highest compared to the lowest elevation and air temperature in July decreased on average by 0.9 °C with each level (120 m) of increasing elevation (Roos et al. 2019). At each elevation, five 1 m^2 plots were randomly selected within a 100 m radius, consisting of a mixed vegetation of vascular plants, lichens and bryophytes. The median distance between plots within elevations was ca. 43 m, which is sufficient to ensure adequate independence among plots, given the high spatial heterogeneity in tundra communities (Björk et al. 2007; Opedal et al. 2015) and is in line with previous studies along elevational gradients in similar environments (Sundqvist et al. 2011b; Veen et al. 2017).

For each plot, all lichen and bryophyte species present were recorded, and their cover was visually estimated in July 2016 (see Roos et al. 2019 for further details). From these data, we calculated the relative cover of each lichen and bryophyte species to the total cover of lichens and bryophytes (cryptogams) per plot. One quadrat of 50 x 50 cm within each plot was destructively harvested in August 2016, and extra material was collected from outside each plot to gather enough biomass for each of the most abundant lichen and bryophyte species for performing decomposability analysis. For each plot, the selected species of lichens and bryophytes composed at least 80% of the total cover of cryptogams in that plot, which is in line with what is recommended for studies that involve determining community-level measures of plant traits and processes (Garnier et al. 2004; Pakeman and Quested 2007). We chose to combine the bryophyte and lichen communities into one cryptogam community because of limited material available for decomposability analysis, and because of the low cover of bryophytes in some of the plots. All collected material was air-dried and stored at -18 °C.

We used fresh (i.e. living) lichen and bryophyte material for decomposability analysis, because unlike vascular plants, ground-covering lichens and bryophytes do not produce senesced litter that falls off, but instead start decomposing at the bottom layer while still being photosynthetically active at the top layer. Therefore, most previous studies on lichen and bryophyte decomposition have used living material (Asplund et al. 2013; Asplund and Wardle 2013; Hagemann and Moroni 2015), although some studies have used only the senesced parts of bryophyte shoots (Lang et al. 2009; Jonsson et al. 2014).

Decomposability bioassay

To determine decomposability of lichens and bryophytes we used a standardized laboratory bio-assay as described by Wardle et al. (1998) and Asplund & Wardle (2013). For each cryptogam tissue, a petri-dish of 9 cm diameter was two-thirds filled with standardized peat soil (530 % water content at dry mass basis), freshly collected from a spruce forest in Ås, Norway (59°40'N, 10°46'E), which was homogenized (e.g. mixed and sieved) before use. A disc of nylon mesh with 1 mm holes was placed on top of the soil, above which was placed 1 g (± 0.1) of cryptogam material (air-dry). The exact weights were recorded at 0.0001 g readability, and corrected with an air-dry to oven-dry ratio calculated from spare material for each species that was dried at 60°C for 48 hours. We closed and sealed the petri-dishes with isolation tape to minimise water loss and incubated them for 90 days at 22°C, in darkness to prevent regrowth of bryophytes and lichens. After incubation, the remaining litter was cleaned from soil particles, air-dried and weighed. Weights were corrected with the air-dry to oven-dry ratio calculated for each species (60°C for 48 hours). Decomposability was expressed by decay rate k, which was calculated as log(post-incubation weight/pre-incubation weight) (Olson 1963). After weighing, samples were ground to powder using a ball mill, and nitrogen (N) and phosphorous (P) concentrations were determined following Kjeldahl digestion. Pre-incubation N and P concentrations were available from Roos et al. (2019), and paired with post-incubation N and P values from the same species and plot. For each species and each plot, N and P release during decomposition was calculated as the difference between the absolute nutrient content (concentration x biomass) before incubation and after incubation, divided by the initial content, expressed as a percentage.

Data analysis

To determine how community level decomposability changes across elevation, we calculated abundance-weighted means for the cryptogam (lichens and bryophytes) community at the whole plot level. For each plot, we weighted each species' decomposability by its relative cover. The community-weighted mean was then calculated by taking the sum of the abundance-weighted decomposability of all measured lichen and bryophyte species per plot (Garnier et al. 2004). This was calculated in two ways: 'specific' averages used plot-specific decomposability per species (or taxon-level when we were unable to sort material down to species-level), while 'fixed' averages used a fixed decomposability per species, averaged over

all plots across the gradient. Within-species (intraspecific) variation in decomposability was then calculated as the difference between 'specific' averages (total variation) and 'fixed' averages (variation caused by community changes, i.e. species turnover effects), following Lepš et al. (2011). The three components (specific, fixed and intraspecific) of community-level decomposability were used as response variables in parallel one-way ANOVAs, with elevation specified as a factor with five levels. Because the distributional assumptions for the regular F-test were not fulfilled, we used permutation tests instead. Iterations terminated when the estimated standard deviation fell below 0.1 of the estimated p-value, with a minimum of 50 iterations, or continued until a maximum of 5000 iterations (Anscombe 1953). Whenever the specific mean of decomposability (total variation) was affected by elevation at significance level $\alpha = 0.05$, pairwise comparisons were performed using permutation tests (Benjamini-Hochberg correction) to check for differences between elevation levels. In addition, we quantified how much variability can be accounted for by the individual components by breaking down the Sum of Squares (SS) across the three ANOVA models as follows: $SS_{specific} = SS_{fixed} + SS_{intraspecific} + SS_{cov}$, where SS_{cov} is the covariation between species turnover effects (fixed) and intraspecific variability effects (intraspecific) (Lepš et al. 2011). We used the same calculations for community-level N and P release and functional traits.

To assess the relationship between decomposability and functional traits at the community level, we carried out multiple linear regression using mixed effects models, with community-weighted mean decay rate k as the response variable, community-weighted mean functional traits as fixed factors, and elevation as a random effect. We expected primary producer group (lichen or bryophyte) to have an effect on the outcome of the multiple regression, so we included the ratio of bryophyte cover to total cryptogam (bryophyte + lichen) cover determined for each plot as an additional fixed effect. Functional traits measured for each species per plot were taken from the study of Roos et al. (2019), and we chose only traits that were measured in the same way for both lichens and bryophytes. As such, the traits that we selected were N and P concentration, N:P ratio, tissue pH and water holding capacity (WHC), which have been found to be related to decomposition (Cornelissen et al., 2006; Cornwell et al., 2008; Lang et al., 2009; Makkonen et al., 2012). All traits were measured at the thallus- or shoot-level; WHC (in $g\,g^{-1}$) was measured as (water-saturated weight – dry-weight)/dry-weight on intact shoots and thalli, while N and P

(% of mass) and tissue pH were measured on ground material. For further details on trait measurements, see Roos et al. (2019). For the multiple regression analysis, we removed N:P ratio before model selection because it was collinear with P (Spearman's rho=-0.74, $p<0.001$), and followed a stepwise model selection using Akaike information criterion (AIC). The conditional coefficient of determination (R^2) was calculated to provide a measure of the variance explained by the entire model, including fixed and random effects (Nakagawa and Schielzeth 2013).

To assess the relationship between decomposability and traits across the entire data set (with each species in each plot as a separate data point), we carried out an ANCOVA using mixed effects models. We included decay rate per sample as the response variable, primary producer group (lichen, bryophyte) as a categorical fixed effect, functional traits (N, P, N:P, tissue pH and WHC) as continuous fixed effects, and plot nested in elevation as random effects. To provide for the heterogeneous variance of the observations, we specified a fixed variance structure, which allows for larger residual spread if decay rate increases. Phosphorous was collinear with N:P ratio (Spearman's rho=-0.74, $p<0.001$) and WHC (Spearman's rho=0.72, $p<0.001$) and was therefore excluded before analysis. We followed a stepwise model selection using Akaike information criterion (AIC), and calculated the conditional coefficient of determination (R^2), in the same way as for the multiple linear regression of community-level decay rate.

Finally, we assessed intraspecific decomposability by analysing the effect of elevation on decay rate of individual species whenever we had decomposability measures of at least three out of five plots per elevation, using separate one-way ANOVAs for each species. If effects of elevation were significant at $\alpha=0.05$, post-hoc tests were performed using Tukey's HSD to explore differences between means. The analyses were performed using the R-packages cati (Taudiere and Violle 2015), lmPerm (Wheeler and Torchiano 2016), rcompanion (Mangiafico 2019), nlme (Pinheiro et al. 2018), MASS (Venables and Ripley 2002) and MuMIn (Barton 2018) in R, version 3.5.2 (R Core Team 2018).

Results

Community level decomposability

Decomposability of lichens and bryophytes at the whole community level increased with increasing elevation (total variation; permutational anova, iterations=5000, p=0.026), with higher decomposability at the higher two elevations compared to the lower three elevations, although differences between elevational means were not identified by Tukey's posthoc test at α=0.05 (Figure 1). The variation in decomposability across elevation was mostly driven by species composition, while intraspecific variability effects were very small (Figure 1). Nitrogen release at the community level remained constant across elevation (total variation; permutational anova, iterations=211, p=0.886; Figure 2a). Species turnover effects and intraspecific variation both changed with elevation, but in opposite directions, resulting in a strong negative covariation and the total variation being poorly explained by elevation (Figure 2a). Community-level P release decreased with increasing elevation (total variation; permutational anova, iterations=5000, p<0.001; Figure 2b). The variation in P release was mostly driven by species composition effects, but intraspecific variation greatly improved the total variation explained by elevation due to a positive covariation with species turnover effects (Figure 2b).

Community-weighted functional traits N and N:P increased while P decreased with increasing elevation, with these changes being explained to a large extent by intraspecific variability effects (Figure S1). Community-weighted tissue pH varied across elevation and WHC tended to decrease with increasing elevation, and these changes were mainly driven by species turnover effects (Figure S1). Multiple regression of community-weighted mean decomposability against community-weighted functional traits resulted in a final model that included N, P, tissue pH, the square of tissue pH, relative bryophyte cover, and the interaction of tissue pH and relative bryophyte cover as predictors (Table 1). Model predictions showed that low values of relative bryophyte cover resulted in a decrease in decomposability with increasing tissue pH, but with the reverse occurring when the relative bryophyte cover is high (Figure 3). In general, increasing N and P enhanced decomposability, while tissue pH and bryophyte cover decreased decomposability (Figure S2).

Individual level decomposability

Decomposability at the individual level (i.e., where each species in each plot represented a separate data point) was best explained by a model that included primary producer group (bryophytes versus lichens), tissue pH, and the square of tissue pH as predictors (Table 2). Lichens overall had a higher decomposability than bryophytes (Figure 4). Model predictions showed that both primary producer groups had the lowest decomposability at approximately pH = 4, while above this value, decomposability increased with increasing tissue pH (Figure 4). At the within-taxon level, decomposability of *Cladonia rangiferina/stygia* decreased while that of *Polytrichum* spp. increased with increasing elevation. The decomposability of no other species responded to elevation at p=0.05, but decomposability of *Cladonia arbuscula* and *Cetraria* spp. showed a marginally non-significant response ($p<0.1$) (Figure 5).

Discussion

Contradictory to our first hypothesis, we found that decomposability at the community level overall increased with increasing elevation. In line with our second hypothesis, species turnover was the main driver of decomposability across elevation, while intraspecific variation was mostly unimportant. Community-level P release decreased with increasing elevation, while N release did not change with elevation. Further, we found that variation in functional traits explained decomposability, both at community and at individual level, in line with our third hypothesis. At the community level, a combination of functional traits and the relative cover of bryophytes explained decomposability; while at the individual level, only primary producer group and tissue pH explained decomposability.

The increase in litter decomposability with elevation at the community level was driven by a combination of functional traits, of which N and N:P also increased with elevation (Figure S2). This is in line with previous studies in which decomposition rates of lichens and bryophytes were positively related to tissue nutrient concentrations (Lang et al. 2009; Asplund and Wardle 2013). However, the increase in N and decomposability is unexpected, since theory predicts that with increasing elevation and associated declining temperature, there will be a shift from a nutrient acquisitive towards a nutrient conservative strategy (Sundqvist et al. 2013; Read et al. 2014; Mayor et al. 2017). Previous studies in various ecosystems have found a decline in decomposability with increasing elevation, or no clear

unidirectional effects of elevation (Salinas et al. 2010; Sundqvist et al. 2011b; Fujii et al. 2017). On the other hand, increases in N concentration at higher elevations have been shown as well (Körner 1989; Morecroft et al. 1992), which could be the result of a surplus in N due to retarded growth caused by the harsher environment at higher elevations (Körner 2003). The increasing N:P ratios we found across the gradient indicate a shift from mainly N-limited decomposition towards more P-limited decomposition (Güsewell and Verhoeven 2006). As such, the amount of P released during decomposition also decreased with elevation, in line with findings from a study on vascular plants in subarctic tundra (Sundqvist et al. 2011b). This could be the result of the decrease in initial P concentration with elevation, as lichens with high initial nutrient concentrations have been found to rapidly lose the same nutrients, while low initial concentrations result in slow release (Campbell et al. 2010). In contrast, N release was not related to initial N concentration, and was poorly explained by elevation due to the opposite responses of species turnover effects and intraspecific variation.

Irrespective of elevation, decomposability was related to both the relative proportion of primary producer groups (i.e. bryophytes vs lichens) and tissue pH, both at the community level and at the individual level. The importance of growth forms in driving decomposability is well recognized (Quested et al. 2003; Dorrepaal et al. 2005), and bryophytes have been shown to decompose particularly slowly (Hobbie 1996; Cornwell et al. 2008; Lang et al. 2009; Hagemann and Moroni 2015), meaning that higher proportions of bryophytes result in lower decomposability. The link between tissue pH and decomposability is consistent with previous studies on lichens (Asplund and Wardle 2013) and vascular plants (Cornelissen et al. 2006). While these studies have found that decomposability increases with increasing tissue pH, we found a less straightforward link between tissue pH and decomposability at the community-level, since it was a non-linear relationship and decomposability was relatively high at low tissue pH.

At the individual-level, the relationship between tissue pH and decomposability indicates that decomposability hardly changes at low tissue pH, while it increases with tissue pH above a certain threshold (roughly at pH=4.2). Lang et al. (2009) found that tissue pH related to decomposability in lichens but not in bryophytes. In contrast, we found that the relationship between pH and decomposability is more apparent for bryophytes than for lichens. In lichens, the relationship is weakened by *Flavocetraria nivalis*, which has low tissue

pH and relatively high decomposability (Figure S3), indicating that low pH is not limiting decomposition rate in this species. In another study from the same study area, it was found that *F. nivalis* had a positive effect on decomposition rate of plant litter placed under the lichen mat (Van Zuijlen et al. 2019), indicating that this species not only has high decomposability, but also increases decomposition rates of other litter types.

Species turnover was the main driver of community decomposability across elevation, which is consistent with findings from previous studies (Wardle et al. 2009; Sundqvist et al. 2011b). As such, these studies concluded that community decomposability is more responsive to environmental gradients across which there is a greater shift in community composition, i.e. high species turnover. Thus, the increase in decomposability at higher elevations that we found must be the result of increasing dominance by faster-decomposing lichen and bryophyte species at higher elevations. Consistent with this, slow-decomposing lichens, e.g. *Cladonia arbuscula* and *C. rangiferina/stygia,* dominated the lower elevations, while faster-decomposing *Cladonia* spp. and *Cetraria* spp. were abundant at the higher elevations. Similarly, slow-decomposing *Pleurozium schreberi* dominates the bryophyte community at the lower elevations while faster-decomposing *Polytrichum hyperboreum* was the most abundant bryophyte at higher elevations. Overall, the shift in species composition with increasing elevation that we observed involves a general decrease in boreal species and an increase in species that are associated with alpine and arctic habitats. The smaller stature and more compact growth form of arctic-alpine species might result in less dilution of N (Körner 2003), which could have resulted in the observed higher litter quality and decomposability of these species.

Within-species variability contributed little to variation in decomposability at the community level across the elevational gradient, even though some of the traits that explained community-level decomposability were in a large part determined by intraspecific variation, notably P and N:P ratio. Similarly, Jackson et al. (2013) found that intraspecific variability was an important component of plant functional traits but a poor predictor of litter decomposability, and therefore concluded that within-species trait variation may not necessarily be an important driver of ecosystem processes. However, in the present study, intraspecific variation was an important driver of nutrient release across elevation and greatly enhanced the total variation in P release explained by elevation, while it greatly reduced the

total variation in N release explained by elevation. At the within-taxon level, we only found significant effects of elevation on decomposability of *C. rangiferina/stygia* and *Polytrichum* spp. In our study *Polytrichum* spp. was not separated to species and the increase in decomposability of *Polytrichum* with elevation is therefore likely not a within-species response, but the result of species turnover within the genus. As such, the middle elevation contained only *P. strictum*, while the highest two elevations mainly contained *P. hyperboreum* (Table S1). This is consistent with Lang et al. (2009), who found that *P. strictum* had among the lowest decomposability of all the non-*Sphagnum* mosses, while *P. commune* had the highest. This highlights again the importance of among species variation in decomposability, even among closely related species.

To conclude, we showed that community-level decomposability of lichens and bryophytes increased with increasing elevation, and that variation in both community and individual level decomposability was driven by nutrient concentrations, tissue pH and primary producer group. Our study highlights the importance of among species differences in decomposability, as within-species variation was small and contributed very little to community-level decomposability, in line with previous work (Jackson et al. 2013). Our findings indicate that future climate change, i.e. increasing temperature, might not automatically result in faster decomposition. When lichens and bryophytes from lower elevation move upwards as a result of global warming, their lower litter quality and decomposability might compensate the expected increase in decomposition rates caused by higher decomposer activity, constituting a potential negative feedback on carbon cycling (Cornelissen et al. 2007b). Further, our study shows that under future climate change, decomposability of lichens and bryophytes will change strongest when there is a strong turnover of species.

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Author contributions

JA designed the study in consultation with KvZ, RR, KK, SL and DW. KvZ and RR conducted field and lab work. KvZ analysed the data and led the writing in collaboration with RR, KK, SL, DW and JA.

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Tables and figures

Table 1. Results of the final model selected following multiple regression of community-weighted decomposability (decay rate k (90 d^{-1})) of cryptogams (parameter estimates and standard errors, t statistic and p-value), explained by community-weighted functional traits (N, P, pH) and cover of bryophytes relative to total cryptogam cover. Mixed effects models were used with functional traits and relative bryophyte cover as fixed effects, and elevation as random effect.

	Estimate	*SE*	*t*	*p*
(Intercept)	20.59	7.44	2.77	0.016
Nitrogen	0.48	0.08	6.45	<0.001
Phosphorus	1.03	0.46	2.24	0.043
Tissue pH	-9.49	3.64	-2.61	0.022
Relative bryophyte cover (BRYO)	-4.87	2.14	-2.27	0.041
Tissue pH^2	1.09	0.45	2.45	0.029
Tissue pH × BRYO	1.11	0.52	2.14	0.052

Number of observations (n) = 24, number of groups (elevation) = 5, degrees of freedom (df) = 13. Conditional R^2 = 0.88. Parameters excluded during model selection: water holding capacity (WHC).

Table 2. Results of ANCOVA after model selection of decomposability (decay rate k (90 d^{-1})) of cryptogams at the individual level (numerator and denominator degrees of freedom, F statistic and p-value), explained by primary producer group (lichens versus bryophytes) and functional traits (tissue pH). Mixed effects models were used with primary producer group and traits as fixed factors, and plot nested within elevation as random effects.

	df	*F*	*p*
(Intercept)	1, 114	317.99	<0.001
Primary producer group	1, 114	29.95	<0.001
Tissue pH	1, 114	22.96	<0.001
Tissue pH^2	1, 114	17.38	<0.001

Conditional R^2 = 0.69. Parameters excluded during model selection: nitrogen (N), nitrogen to phosphorous ratio (N:P) and water holding capacity (WHC).

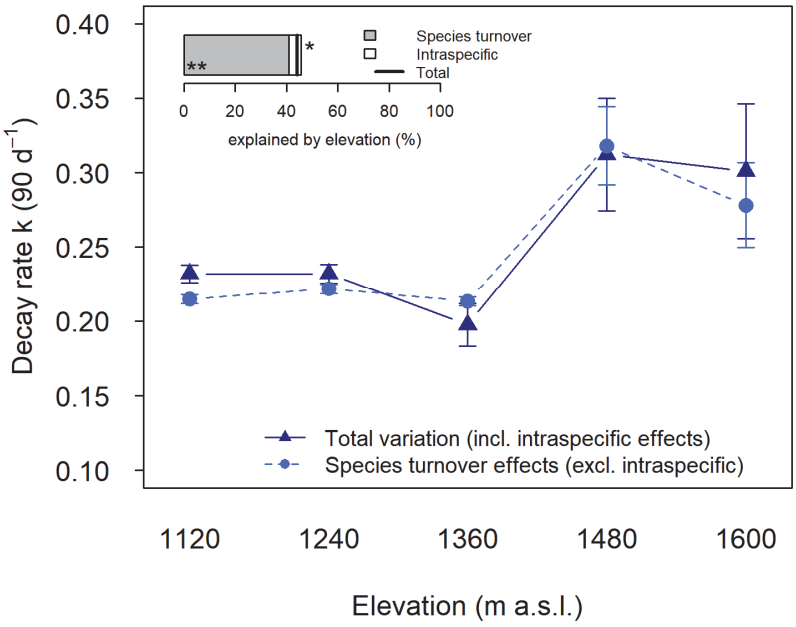

Figure 1. Community-weighted mean decomposability (decay rate k) of lichens and bryophytes across elevation. The solid line with triangles denote total variation, the dotted line with circles denote species turnover effects only (species turnover and changes in species abundance). Variation explained by elevation is shown in the top left corner: the grey part of the column corresponds to species turnover effects, the white part corresponds to intraspecific variability effects and the black bar denotes the total variation, i.e. the sum of species turnover and intraspecific variability and their covariation. Significant differences are denoted with * ($p<0.05$), ** ($p<0.01$) and *** ($p<0.001$).

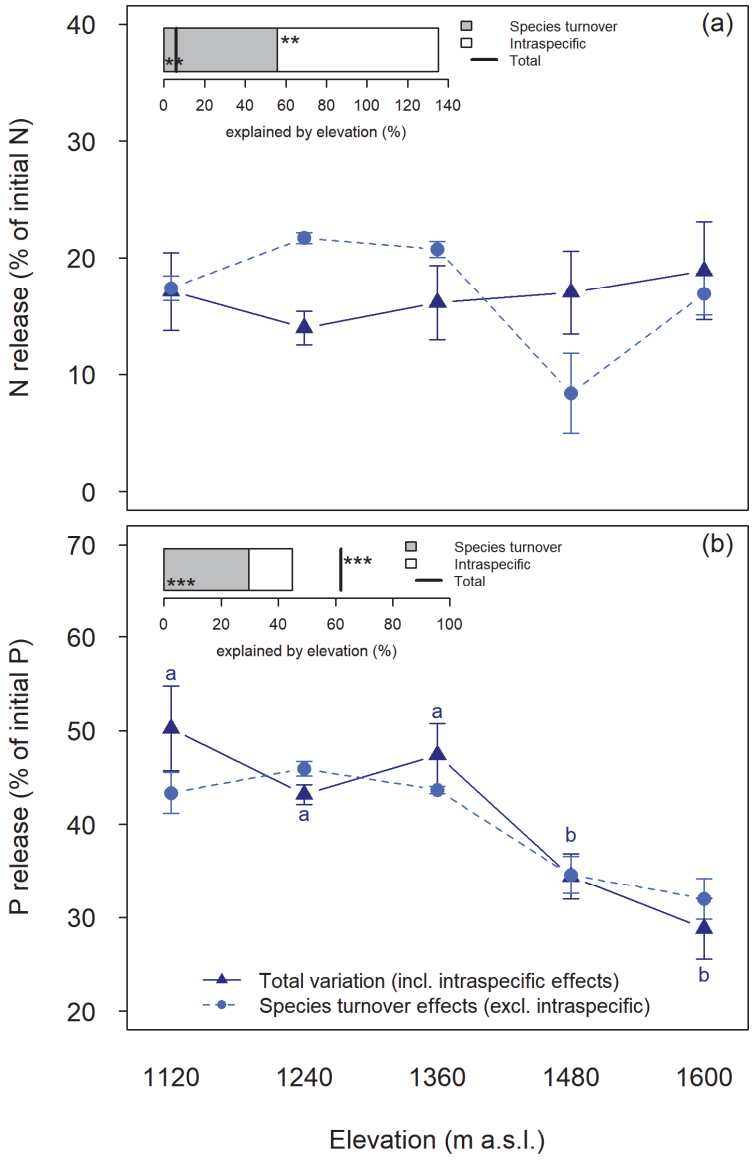

Figure 2. Community-weighted nitrogen (N) release (a) and phosphorous (P) release (b) of lichens and bryophytes across elevation, expressed as percentage of the initial concentration. The solid line with triangles denote total variation, the dotted line with circles denote species turnover effects only (species turnover and changes in species abundance). Variation explained by elevation is shown in the top left corner of each panel: the grey part of the column corresponds to species turnover effects, the white part corresponds to intraspecific variability effects and the black bar denotes the total variation, i.e. the sum of species turnover and intraspecific variability and their covariation. Significant differences are denoted with * ($p<0.05$), ** ($p<0.01$) and *** ($p<0.001$).

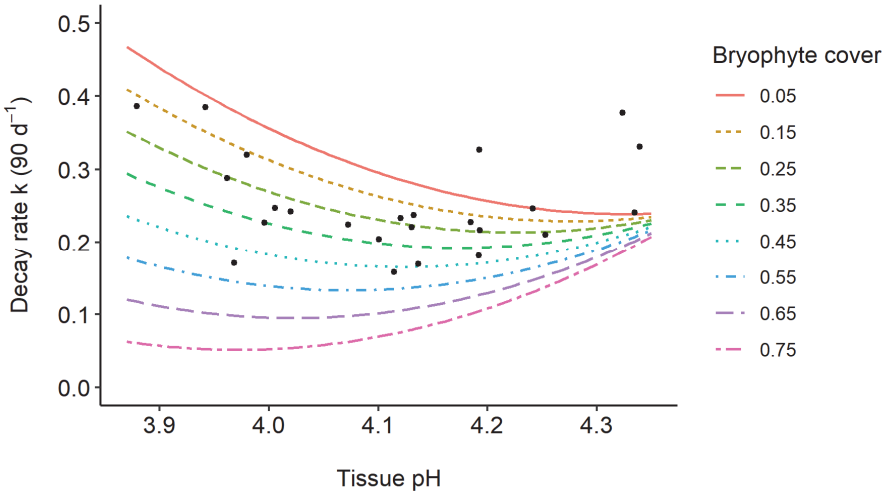

Figure 3. Community-weighted mean decomposability (decay rate k) of lichens and bryophytes explained by community-weighted tissue pH. Black dots denote the actual measurements at plot-level, while lines denote model predictions of the regression model presented in Table 1. Different lines represent predictions with different bryophyte proportions relative to total cryptogam cover. Model predictors not shown in the figure (i.e. tissue nitrogen and phosphorous) were set to mean values.

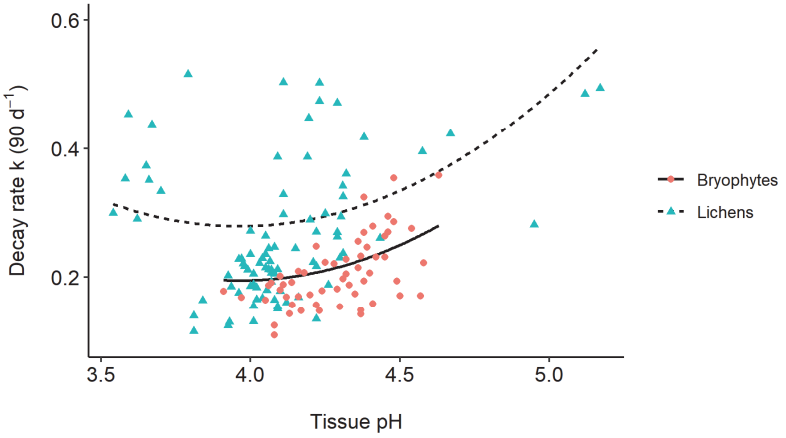

Figure 4. Decomposability (decay rate k) of individual lichens and bryophytes explained by tissue pH. Dots and triangles denote the actual plot-level measurements for each bryophyte and each lichen, respectively, while lines denote model predictions based on the ANCOVA model presented in Table 2.

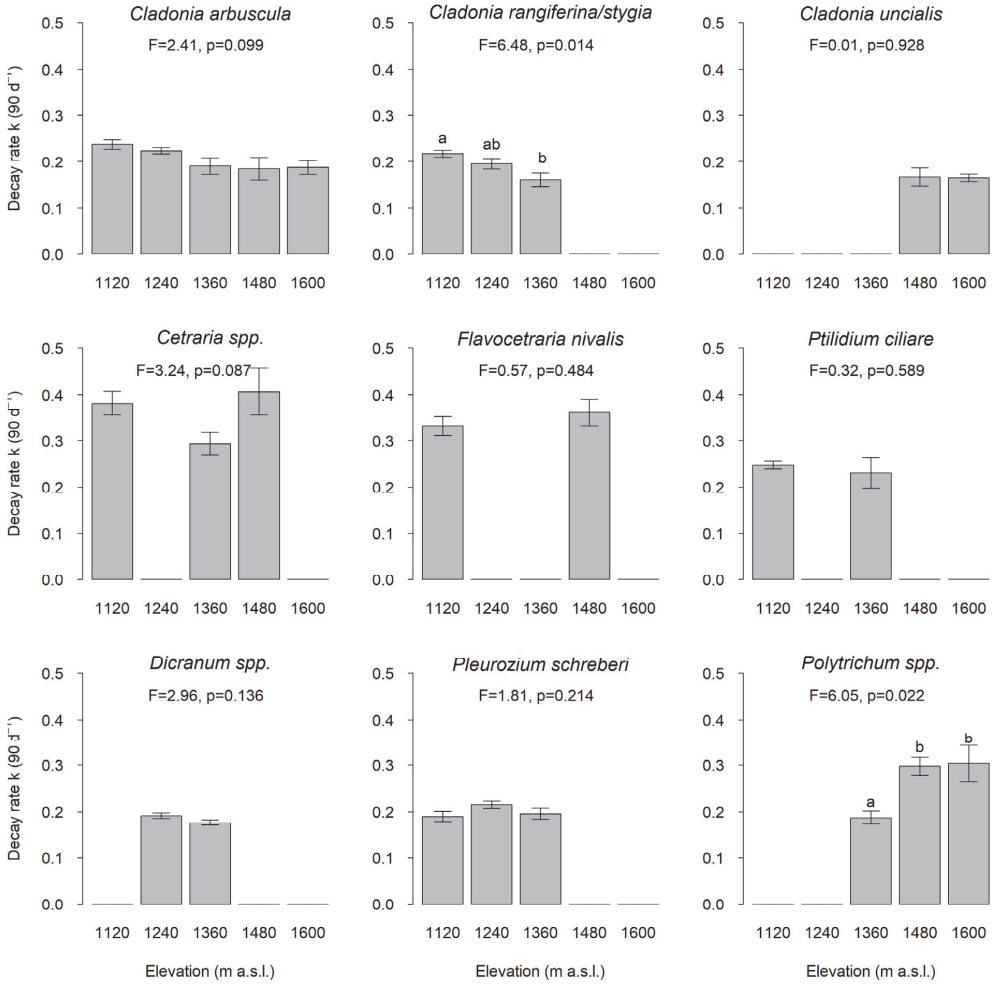

Figure 5. Mean (± SE) decomposability (decay rate k) of each abundant lichen and bryophyte species across elevation. Different letters denote significant differences between elevation levels using Tukey HSD at $\alpha = 0.05$.

Supplementary information

Table S1. Mean (± SE) of lichen and bryophyte decomposability (decay rate k) and relative cover (% of total cover of selected species, covering at least 80% of the community per plot) of species and species groups from five different elevations (m a.s.l.). If cover and/or decay rate are only available for one plot per elevation, no standard error is filled out.

	1120	**1240**	**1360**	**1480**	**1600**
Alectoria ochroleuca					
Relative cover (%)	–	–	–	3.31 (± 1.33)	–
Decay rate k	–	–	–	0.52 (± 0.04)	–
Cetraria spp.					
Relative cover (%)	4.80 (± 0.95)	3.48 (± 2.00)	7.72 (± 3.02)	20.31 (± 4.75)	21.12 (± 6.86)
Decay rate k	0.38 (± 0.03)	0.31 (± 0.05)	0.29 (± 0.02)	0.40 (± 0.03)	0.46 (± 0.03)
Cladonia arbuscula					
Relative cover (%)	31.96 (± 7.68)	50.20 (± 6.19)	55.21 (± 6.67)	17.68 (±12.51)	3.89 (± 0.69)
Decay rate k	0.24 (± 0.01)	0.22 (± 0.01)	0.19 (± 0.02)	0.19 (± 0.02)	0.18 (± 0.01)
Cladonia gracilis					
Relative cover (%)	1.13 (± 0.07)	0.83 (± 0.06)	0.80 (± 0.06)	1.05 (± 0.13)	2.71 (± 0.48)
Decay rate k	0.25 (± 0.01)	0.29 (± 0.02)	0.16 (± 0.00)	0.19 (± 0.01)	0.26 (± 0.02)
Cladonia rangiferina/stygia					
Relative cover (%)	26.41 (± 9.06)	13.81 (± 1.73)	12.13 (± 3.04)	3.62 (± 2.57)	–
Decay rate k	0.22 (± 0.01)	0.20 (± 0.01)	0.15 (± 0.01)	0.17 (± 0.00)	–
Cladonia spp.					
Relative cover (%)	–	–	–	–	15.51 (± 7.89)
Decay rate k	–	–	–	–	0.28 (± 0.02)
Cladonia uncialis					
Relative cover (%)	–	0.43 (± 0.23)	1.25 (± 0.17)	1.98 (± 0.45)	6.99 (± 3.14)
Decay rate k	–	0.17 (± 0.03)	0.12 (± 0.00)	0.16 (± 0.01)	0.16 (± 0.01)
Dicranum spp.					
Relative cover (%)	3.85 (± 1.47)	0.75 (± 0.14)	9.31 (± 5.93)	2.04 (± 1.12)	11.62 (± 5.88)
Decay rate k	0.17 (± 0.01)	0.20 (± 0.00)	0.18 (± 0.01)	0.14 (± 0.02)	0.15 (± 0.02)

Table S1 continued

	1120	1240	1360	1480	1600
Flavocetraria cucullata					
Relative cover (%)	–	1.16 (± 0.80)	1.61 (± 0.96)	1.85 (± 0.81)	–
Decay rate k	–	0.30	0.47	0.50 (± 0.01)	–
Flavocetraria nivalis					
Relative cover (%)	6.56 (± 2.03)	–	–	37.02 (± 9.43)	7.68 (± 2.89)
Decay rate k	0.33 (± 0.02)	–	–	0.36 (± 0.03)	0.39 (± 0.03)
Hylocomium splendens					
Relative cover (%)	4.47 (± 2.61)	0.25	0.50 (± 0.12)	–	–
Decay rate k	0.15 (± 0.01)	0.14 (± 0.00)	0.15 (± 0.00)	0.14 (± 0.01)	–
Paraleucobryum enerve					
Relative cover (%)	–	–	–	0.26 (± 0.01)	2.57 (± 0.87)
Decay rate k	–	–	–	0.15	0.17 (± 0.00)
Pleurozium schreberi					
Relative cover (%)	14.43 (± 6.88)	23.60 (± 5.68)	8.49 (± 2.57)	–	–
Decay rate k	0.19 (± 0.01)	0.22 (± 0.01)	0.20 (± 0.01)	0.18 (± 0.01)	–
Polytrichum alpinum					
Relative cover (%)	–	–	–	3.44 (± 2.12)	8.79 (± 4.55)
Decay rate k	–	–	–	0.32 (± 0.03)	
Polytrichum hyperboreum					
Relative cover (%)	–	–	–	9.08 (± 5.83)	15.28 (± 5.03)
Decay rate k	–	–	–	0.28 (± 0.03)	0.30 (± 0.04)
Polytrichum piliferum					
Relative cover (%)	–	–	–	1.33 (± 0.44)	–
Decay rate k	–	–	–	0.27	–
Polytrichum strictum					
Relative cover (%)	–	0.50	2.11 (± 1.31)	–	–
Decay rate k	–	0.17	0.18 (± 0.01)	–	–

Table S1 continued

	1120	1240	1360	1480	1600
Ptilidium ciliare					
Relative cover (%)	8.61 (± 2.21)	0.56 (± 0.15)	1.28 (± 0.20)	1.10 (± 0.84)	–
Decay rate k	0.25 (± 0.01)	0.22 (± 0.01)	0.21 (± 0.03)	0.26 (± 0.01)	–
Racomitrium lanuginosum					
Relative cover (%)	–	–	–	–	21.16 (± 8.94)
Decay rate k	–	–	–	–	0.14 (± 0.01)
Racomitrium microcarpon					
Relative cover (%)	–	–	–	–	3.09
Decay rate k	–	–	–	–	0.25
Stereocaulon sp.					
Relative cover (%)	–	6.22 (± 2.09)	–	1.00 (± 0.07)	9.05 (± 4.75)
Decay rate k	–	0.39 (± 0.06)	–	0.48 (± 0.01)	0.42 (± 0.01)

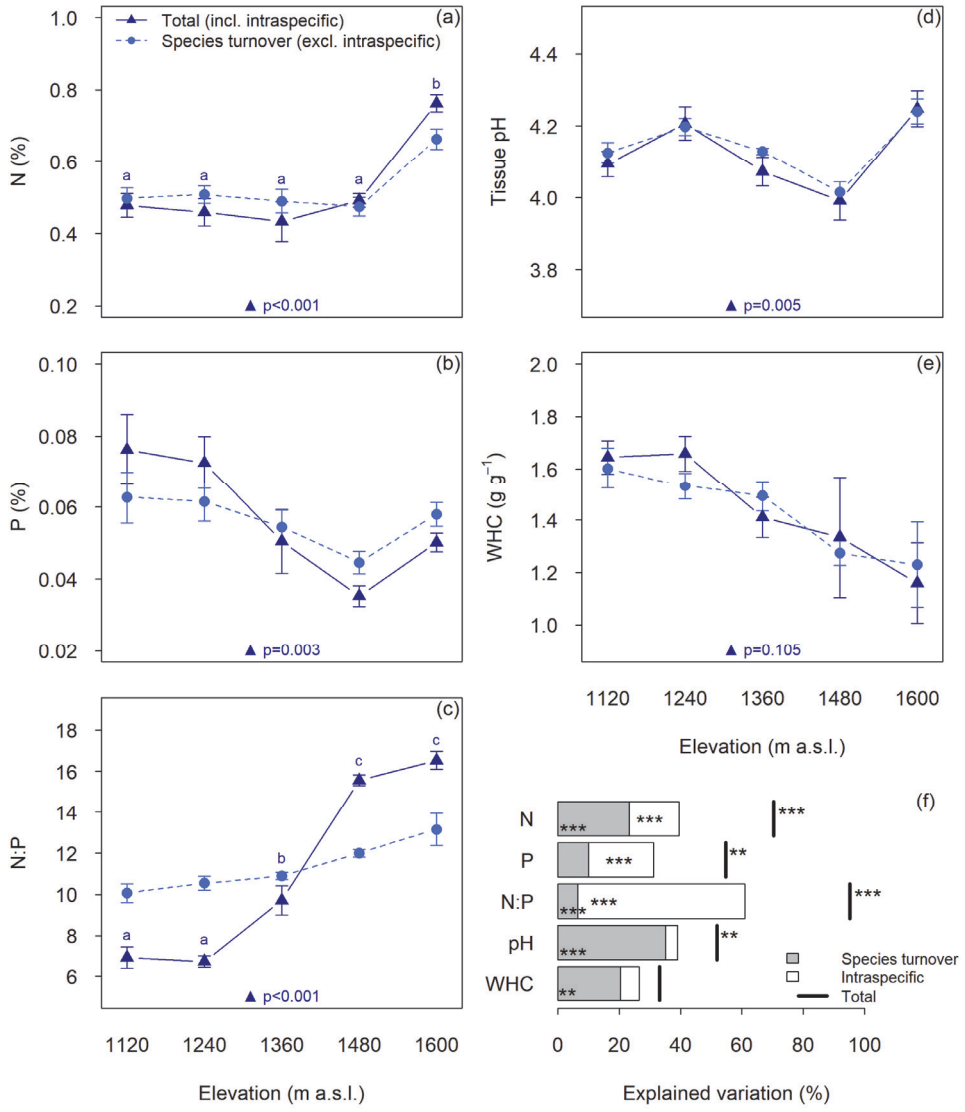

Figure S1. Community weighted mean functional traits of lichens and bryophytes across elevation: (a) nitrogen (N), (b) phosphorous (P), (c) N:P ratio, (d) tissue pH and (e) water holding capacity (WHC). The solid line with triangles denote total variation, the dotted line with circles denote species turnover effects only (species turnover and changes in species abundance). Different letters indicate significant differences in total trait variation between elevation levels at $\alpha = 0.05$, using pairwise permutation tests. The variation explained by elevation is shown in (f): grey parts of the columns correspond to species turnover effects, white parts correspond to intraspecific variability effects and black bars denote the total variation, i.e. the sum of species turnover and intraspecific variability and their covariation. Significant differences are denoted with ** ($p<0.01$) and *** ($p<0.001$).

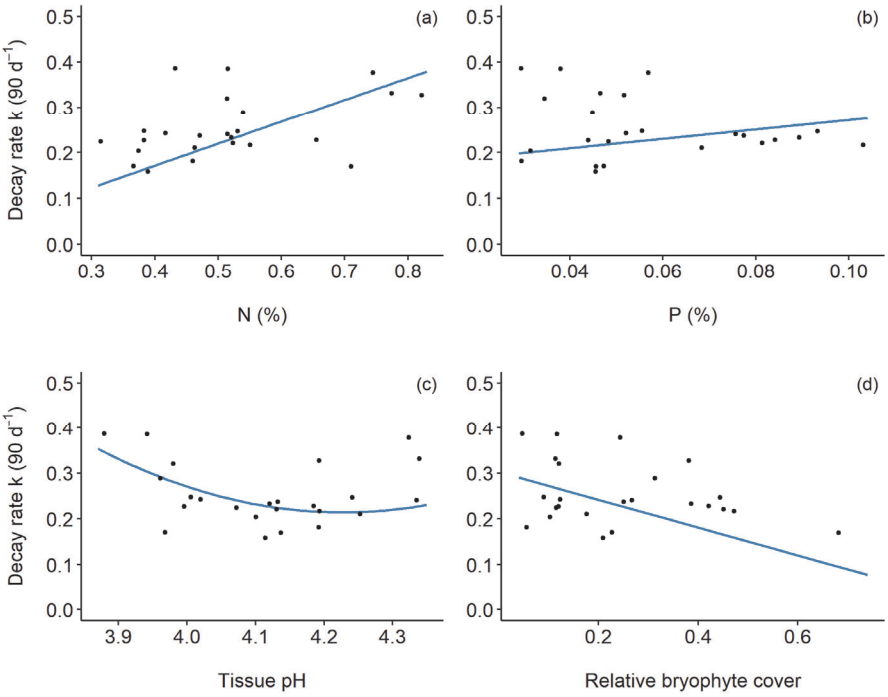

Figure S2. Community-weighted mean decomposability (decay rate k) of cryptogams (lichens and bryophytes) explained by community-weighted (a) nitrogen (N), (b) phosphorous (P), (c) tissue pH and (d) cover of bryophytes relative to total cryptogam cover. Dots denote the actual measurements at plot-level, while lines denote model predictions of the regression model presented in Table 1. For each panel figure, the model predictors not shown in the graph were set to mean values.

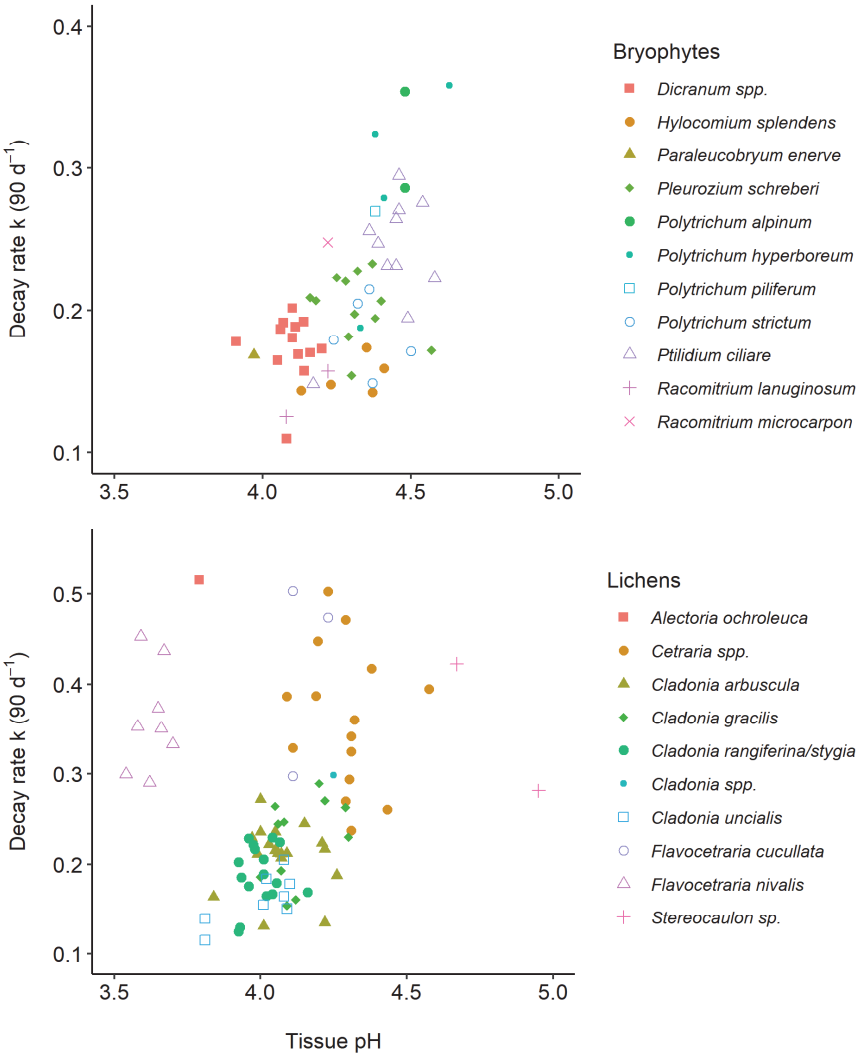

Figure S3. Decomposability (decay rate k) as a function of tissue pH of bryophytes (upper panel) and lichens (lower panel). Different symbols and colours indicate different species.

Paper IV

Contrasting responses of plant and lichen secondary metabolites across an elevational gradient

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Summary

- Vascular plants and lichens often produce a diversity of secondary metabolites to protect them against biotic and abiotic stresses. These compounds play important but often compound-specific roles in community and ecosystem processes by affecting herbivore and decomposer activity. Meanwhile, our current understanding of what drives community-level secondary metabolites among ecosystems or across environmental gradients is limited.
- We measured concentrations and compositions of secondary metabolites for all dominant vascular plant and lichen species across a 500 m alpine elevational gradient. These measurements were combined with data on species composition and abundance to obtain whole-community measures of plant and lichen secondary metabolites across the gradient.
- At the whole community level, plant secondary metabolites had the lowest concentrations while lichen secondary metabolites had the highest concentrations at the highest elevations. Further, plant metabolites shifted from those associated with herbivore defence towards those protecting against light and oxidative stress as elevation increased, while lichen secondary metabolites showed the opposite pattern.

- In conclusion, climate change will have important effects not only on community composition of primary producers but also on secondary chemistry at the whole community scale, which in turn will affect the structure and functioning of communities and ecosystems.

Key-words: alpine ecology; carbon based secondary metabolites; defence; flavonoids; lichens; phenols; tannins; vascular plants

Introduction

Both vascular plants and lichens have evolved a high variety of carbon based secondary metabolites, as defence against herbivores (e.g. Coley *et al.*, 1985; Gauslaa, 2005), pathogens (Witzell & Martín, 2008), oxidative stress, and light damage (Close & McArthur, 2002). These compounds also have after-life effects in senesced litter as they can inhibit decomposer activity and immobilize nitrogen (N) through protein complexation, and thus reduce plant-available N (Fierer *et al.*, 2001; Asplund *et al.*, 2013). Given the importance of secondary metabolites in species-driven ecosystem processes, it is important to understand their effects at the whole community level. Community level measures of plant functional traits have been widely used for inferring ecosystem processes, but these have mainly focused on leaf nutrient concentrations and morphological and ecophysiological characteristics (Garnier *et al.*, 2007; Sundqvist *et al.*, 2013; Mayor *et al.*, 2017). Meanwhile, only a few studies have considered community level measures of secondary metabolites and how they may vary among ecosystems or across environmental gradients (Kichenin *et al.*, 2013; Sundqvist *et al.*, 2013; Siefert *et al.*, 2015).

Those studies that have explicitly considered community-level measures of secondary metabolites (e.g. Sundqvist *et al.*, 2012; Asplund & Wardle, 2014; De Long *et al.*, 2016) have only quantified total amounts of broad classes of compounds like total phenolics or tannins, and not the composition of compounds within these broad classes. However, different compounds and compound groups within these broad classes can have very different biological functions and efficacy. For instance, in vascular plants, some flavonoids such as quercetin and luteolin have a much stronger antioxidant capacity than do other flavonoids, such as kaempferol and apigenin (Agati *et al.*, 2012). In lichens, phenolic compounds such as usnic acid and atranorin, which are both situated in the cortical layer, are considered to have

a photo protective role, while other phenolics such as fumarprotocetraric acid and lecanoric acid are more involved in protecting the lichen from other stressors such as herbivory (Solhaug & Gauslaa, 2012). Further, these protective phenolic compounds in lichen thalli can vary greatly in their efficacy (Asplund & Wardle, 2013). This highlights the importance of studying the composition of individual compounds or specific compound groups, rather than simply total amounts of very broad classes of compounds, such as total phenolics, in plant and lichen material.

At high latitudes and elevations, temperature and low nutrient availability limit plant growth, and the primary producer communities are often dominated by lichens (Matveyeva & Chernov, 2000). With increasing elevation, vascular plants and lichens are predicted to invest more into carbon-based secondary defences because of a surplus of fixed carbon (C) when low nutrient availability limits C use for growth (Herms & Mattson, 1992; Stamp, 2003). In addition, a general increase in oxidative stress with increasing elevation could also result in further induction of phenolic antioxidants (Close & McArthur, 2002). In contrast, as invertebrate herbivore pressure decreases with increasing elevation, vascular plants and lichens might allocate less to secondary defence compounds (Descombes *et al.*, 2017; Galmán *et al.*, 2017; Moreira *et al.*, 2018). As such, Zidorn (2010) suggested that while there should be an increase in radical scavenging and UV-B protective secondary compounds with increasing elevation, there should also be a decrease in allelopathic and anti-herbivory secondary compounds such as tannins and stilbenes.

In this study, we investigated the concentrations of secondary metabolites of individual plant and lichen species along an elevational gradient spanning 500 m in the Norwegian alpine zone. These measurements were combined with data on species composition and abundance to obtain whole community measures of plant and lichen secondary metabolites (PSM and LSM, respectively). We used this system to test the following two hypotheses: (i) with increasing elevation, there will be a shift towards overall higher concentrations of plant and lichen secondary metabolites when quantified at the whole community level; and (ii) at the whole community level, the composition of secondary metabolites will shift from those associated with herbivore defence to those associated with light protection and antioxidative capacity with increasing elevation. Because of the variable role that different secondary metabolites play in driving ecosystem processes, understanding

how they individually respond to a strong natural gradient at the whole community level will advance knowledge of how vascular plants and lichens may contribute to ecological processes across contrasting environmental conditions.

Materials and methods

This study was performed along an elevational gradient consisting of five sites ranging from approximately 1120 to 1600 m a.s.l. with 120 m difference between elevationson south-facing slopes on acidic granite and gneiss bedrock near Finse, alpine Norway (N 60°33'–60°38'; E 7°35'–7°42') (Roos *et al.*, 2019). The air temperature in July decreases on average by 0.9 °C with each level (120 m) of increasing elevation, and the growing season is almost half the length at the highest site compared to the lowest site (Roos *et al*, 2019). The study sites are on exposed ridges and have a mixed cover of vascular plants, lichens and bryophytes, but are dominated by ericaceous dwarf shrubs and fruticose mat-forming lichen species. The lowest site is situated approximately 150 m above the nearest tree line, which is dominated by *Betula pubescens* ssp. *czerepanovii*.

To quantify species composition along the gradient, vascular plant and lichen cover were estimated in five 1 m^2 plots at the five elevations between 11 and 24 July 2016. The plots were selected within a 100 m radius at each elevation by randomly throwing an object, provided that all functional groups were present (vascular plants, lichens and bryophytes). The median distance between plots within elevations was ca. 43 m, which is sufficient to ensure adequate independence among plots, considered the small-scale spatial heterogeneity in these communities (Björk *et al.*, 2007; Opedal *et al.*, 2015), and is in line with previous studies along elevation gradients in tundra environments (e.g. Veen *et al.*, 2015). The cover was estimated visually for each of four 50x50 cm quadrants per plot; the whole-plot cover was then calculated as the average across the four quadrants. One quadrant per plot was destructively harvested between 28 July and 18 August 2016: all aboveground material was collected and sorted to species. In case insufficient material was available for a given species, extra material was harvested from the other quadrants or the immediate surroundings of the same plot. The most abundant species that composed at least 80% of the cover per group per plot were used (Pakeman & Quested, 2007).

For vascular plants, 30 young but fully developed (i.e. current growing season) and undamaged leaves were sampled from 15 shoots per species, except for small leaves species (leaf length <0.5 cm) for which 150 leaves were used. For lichens, 10 intact thalli of each species were selected and cleaned. The material was air-dried and stored at -18°C until analysis of secondary metabolites. All samples were ground to powder with a ball mill (Retsch MM400, Retsch, Haan, Germany).

For analysis of the secondary metabolites of the thallus material from each lichen species in each plot (lichen secondary compounds: LSM), we extracted approximately 15 mg of lichen powder in 2 ml acetone for 3 × 30 min. The combined supernatants were evaporated and re-dissolved in 1000 µl methanol.

For analysis of the secondary metabolites of the leaves from each vascular plant species of each plot (vascular plant secondary compounds: PSM), approximately 10 mg plant powder was added to 600 µl methanol and homogenized on a Precellys homogenizer (Bertin Technologies, Montigny-le-Bretonneux, France) for 20s at 5400 rpm. The samples were then left for 15 min on ice, and centrifuged for 3 min at 1500 rpm (Eppendorf centrifuge 5417C, Eppendorf, Hamburg, Germany) before the supernatant was poured off and the residue re-extracted three times (excluding the 15 min on ice).

For each of the lichen and plant extracts, secondary compounds were then quantified by HPLC (Agilent Series 1200, Agilent Technologies, Waldbronn, Germany) with an ODS Hypersil column, 50 × 4.6 mm using 0.25% orthophosphoric acid and 1.5% tetrahydrofuran in Millipore water (A) and 100% methanol (B) as mobile phases at 2 ml min^{-1}, following the gradient described in Nybakken *et al.* (2007). When analysing LSMs, we used UV-detection at 245 nm, while PSMs were run with detection at 220, 270, 320 and 360 nm. Compound identification was based on retention times, online UV spectra and co-chromatography of commercial standards.

Due to the high diversity of PSMs both within and between species, including of the glycosylated flavonoids, not all compounds were identified down to the specific compound. Further, because some compounds (e.g, chlorogenic acid) appear in many plant species while others in only one, it was necessary to perform some grouping of compounds to allow for comparisons of PSMs across species and across communities. As such, we firstly grouped PSM

by their chemical classes, which is reflective of molecular complexity, molecule size and the position at which they are synthesized along the phenylpropanoid pathway; the groups we used were phenolic acids (including all chlorogenic acid derivatives, hydroxycinnamic acids and unclassified phenolic acids), flavonoids (with the subgroups flavonols and flavones), stilbenes, and condensed tannins. Flavonoids are known to vary greatly with regards to their antioxidant capacity, and the capacity is primarily decided by the amount of hydroxy (-OH) groups on the B-ring (the central of the three phenol-rings that form the typical flavonoid structure) (Agati *et al.* 2012). This means that dihydroxy B-ring substituted flavonoids (e.g. luteolin and quercetin derivatives) are stronger antioxidants than monohydroxy substituted ones (e.g. apigenin and kaempferol derivatives). Therefore, we chose to further classify flavonoids by their aglycon and look at the differences between these; as such, all quercetin glycosides were classified as "quercetins", all luteolin glycosides as "luteolins" etc.

Concentrations of both MeOH-soluble and MeOH-insoluble condensed tannins (CTs) were identified using the acid butanol assay for proanthocyanidins described in Hagerman (2002). MeOH-soluble CTs were analysed from the HPLC extract, while the amount of MeOH-insoluble CTs were analysed from the residues left after the extraction process. Purified tannins from spruce needles were used as standards to calculate concentrations.

Lichen secondary metabolites were grouped according to their placement in the lichen thallus following Ahti *et al.* (2007, 2013) and Thell & Moberg (2011). This grouping was made because LSMs in the cortical layer are assumed to primarily function as light screeners while the LSMs in the medulla defend against other stressors such as herbivory, pathogens and harmful metals (Solhaug & Gauslaa, 2012). We further grouped LSMs according to their chemical structure into aliphatic compounds, depsides, depsidones and dibenzurans. Depsides and depsidones are the most common groups and are composed of two (or three) aromatic rings joined by ester linkages. Unlike depsides, depsidones have an ether linkage in addition to the ester linkage and are considered to be weaker antioxidants (Hidalgo *et al.*, 1994; Lohézic-Le Dévéhat *et al.*, 2007; Atalay *et al.*, 2011; Brisdelli *et al.*, 2013). Some lichen species produce melanic compounds, which function as sunscreens, instead of cortical LSMs. These compounds are not easy to extract and quantify. In order to account for the importance melanic species at the community level we calculated the relative abundance of melanic species.

Data analysis

All collected species (collectively composing >80% of total lichen or plant cover) within each plot were weighted according to their relative abundance in that plot. For each individual secondary compound, we calculated community-weighted average for each plot following Garnier *et al.* (2007) and Fortunel *et al.* (2009):

$$\mathrm{SM}_{\mathrm{weighted}} = \sum_{i=1}^{n} p_i \times \mathrm{SM}_i$$

Where p_i is the cover of species *i* as a proportion of the total cover of all collected plant or lichen species, and SM_i is the secondary metabolite concentration of species *i*. For each secondary metabolite, the relative importance of intra- and interspecific variability effects in explaining variation in specific community-weighted averages across the five elevations was assessed using sum of squares (SS) decomposition following the procedure of Lepš *et al.* (2011), using the R package cati (Taudiere & Violle, 2016). As such, total SS (SSspecific) of the plot-level secondary metabolite variance related to elevation was decomposed into 'fixed' (SSfixed), 'intraspecific'(SSintraspecific) and 'covariation' (SScov) effects, so that SSspecific = SSfixed + SSintraspecific + SScov. For each plot and secondary metabolite, we calculated the 'specific' community average secondary metabolite concentration using the species metabolite concentration recorded on the specific plot (both inter and intraspecific effects), and 'fixed' community average metabolite concentration using the mean concentration for all plots (which removes the intraspecific variability effect). Intraspecific community averages were then calculated by subtracting the fixed community average from the specific community average (which removes the interspecific variability). For each secondary metabolite, we ran three one-way ANOVAs (Lepš *et al.*, 2011), one for each of the 'specific', 'fixed' and 'intraspecific' community average measures with elevation as factor, and extracted the SS for each of the tree measurements (SSspecific, SSfixed and SSintraspecific) explained by elevation. Finally, we subtracted SSfixed and SSintraspecific from SSspecific to yield SScov, which is the effect of covariation between interspecific metabolite concentration variability and intraspecific metabolite concentration variability. We fitted and tested the ANOVAs with permutation tests (5000 iterations) using the aovp function of the R package lmPerm (Wheeler & Torchiano, 2016), when residuals were not normally distributed.

We used non-metric multidimensional scaling (NMDS) on the basis of a Bray-Curtis distance matrix, using the metaMDS function in the R package vegan (Oksanen *et al.*, 2016), to depict the composition of secondary metabolites at the community level, separately for vascular plants and lichens. For both PSMs and LSMs, we performed two separate PERMANOVAs with a Bray-Curtis distance matrix and 999 permutations, using the adonis function in the R package vegan to test for the effect of elevation on 'specific' community weighted SM (both inter and intraspecific effects) and 'fixed' community weighted SM (only species turnover effects). All analyses were performed in R 3.5.0 (R Core Team, 2018).

Results

Plant secondary metabolites

All PSM groups varied significantly with elevation (Fig. 1). The community-weighted concentration of total phenols was higher at 1240 m than at the two highest elevations (Fig. 1a). Condensed tannins were 1.8 times greater at the lowest elevation than at the highest (Fig. 1b), and this was almost entirely driven by a shift in species composition (Fig. 2). For total low molecular phenolics, total phenolic acids and total flavonols, the 1240 m site had significantly higher concentrations than some of the higher elevations, while concentrations at 1120 m were not significantly different from those at the higher elevations (Fig. 1b-d). For these compounds, the responses were stronger when within-species variation was included, as shown by the strong positive covariation of within and between species variability (Fig. 1, 2). Total flavones responded differently to the other types of PSM, with a strong increase with increasing elevation. Further, within-species variation contributed significantly, but in the opposite direction to the effect of species turnover, to this response; this yielded a negative covariation (Fig. 1f, 2). Total stilbenes decreased with elevation and were 42 times higher at the lowest elevation than at the highest (Fig. 1g). Concentrations of individual compounds in all species are given in Table S3.

There was a significant shift in the composition of PSMs with elevation at the whole community level (Table 1, Fig. 3a, 4a). The PERMANOVAs showed a significant effect of elevation on the composition of community weighted PSMs both when accounting for within-species variation and when only accounting for species turnover (Table 1). Flavones (luteolins

and apigenins) increased in concentration with increasing elevation while most other PSMs decreased (Fig. 4a, Table S1). The ratio of concentrations of flavonoids to condensed tannins at the whole community level increased with elevation (Fig. S1a). As such, the concentrations of condensed tannins was higher than flavonoids at the two lower elevations and less than flavonoids at the higher sites.

Lichen secondary metabolites

The community-weighted concentration of total, cortical and medullary LSMs varied significantly with elevation (Fig. 5). As such, medullary and total concentration were 3.4 times and 2.0 times greater respectively at the highest than the lowest elevation (Fig. 5a,c). Meanwhile, cortical secondary metabolites peaked at the 1480 m elevation (Fig. 5b). The variation in medullary compounds with elevation was almost entirely driven by species turnover (Fig. 2b). By contrast, intraspecific variation was almost equally as important as species turnover in explaining the change in community-weighted cortical LSMs, and it also contributed significantly to the change in total LSMs (Fig. 2b). The relative abundance of species with melanin, a dark non-phenolic compound functioning as sunscreen instead of cortical LSMs, increased significantly with elevation (Fig. S2). Concentrations of individual compounds in all species are given in Table S4.

The NMDS ordination of the community-weighted averages of LSMs showed a separation between the three lower elevations and the two upper elevations on the primary axis (Fig. 3b). The PERMANOVAs showed a significant effect of elevation on the composition of community weighted LSMs both when accounting for within-species variation and when only accounting for species turnover (Table 1). The change in composition of LSMs with elevation was partly driven by a strong increase of several depsides (e.g. squamatic acid, alectorialic acid, baemycesic acid and barbatolic acid) with increasing elevation (Fig. 3b, 4b, Table S2). As such, the ratio of concentrations of depsides to depsidones at the whole community level increased significantly with elevation (Fig. S1b).

Discussion

We found mixed support for our hypotheses. As such, our first hypothesis predicting a shift towards overall higher concentrations of secondary metabolites with higher elevation was supported for lichens but not for vascular plants. Meanwhile, our second hypothesis that with

increasing elevation the composition of secondary metabolites will shift from those associated with herbivore defence to those associated with light protection and antioxidative capacity was supported for plants but not for lichens. We now explore the mechanisms behind the contrasting behaviour of secondary metabolites in vascular plants and lichens and then discuss possible implications.

Our finding that community-level concentrations of PSMs were lower at higher elevations than at some of the lower elevations was most pronounced for condensed tannins and stilbenes. This result was largely driven by a switch from a plant community dominated by ericaceous shrubs (which generally have high concentrations of PSMs) to one dominated by graminoids (with lower PSM concentrations) as elevation increased and as conditions become too harsh for woody plants. In contrast to our results, De Long *et al.* (2016) found increasing concentrations of total phenols and condensed tannins at the community level with increasing elevation, but in their study ericaceous shrubs increased with higher elevation. In our study, the increasing ratio of flavonoids to condensed tannins at the whole community level with elevation, driven by a relative decrease in ericaceous shrubs, suggests a shift from protection against herbivory (e.g. by tannins and stilbenes) at lower elevations to protection against photodamage (by antioxidants) at higher elevations. This is in line with our second hypothesis predicting a decrease in biotic stressors (e.g. competition and herbivory) and an increase in abiotic stressors (e.g. oxidative stress) with increasing elevation (Moreira *et al.*, 2018). The increase in antioxidants with increasing elevation was driven in part by a relative increase in species containing luteolins (i.e. graminoids); these compounds have two hydroxyl groups on the B-ring, and are much stronger antioxidants than are flavonoids with only one hydroxyl group such as kaempferols and apigenins (Agati *et al.*, 2012). However, quercetins, which are also strong antioxidants with two hydroxyl groups, decreased with elevation. Changes in PSMs were mainly driven by species turnover, but for several compounds there were also strong effects of covariation between turnover and variation within species, pointing to a role of intraspecific variation also contributing to the overall community-level response.

The increase in total LSMs with increasing elevation that we observed is consistent with lower temperatures slowing down growth, resulting in a surplus of carbon that can be used for producing secondary metabolites. This is consistent with plant defence theories

suggesting that environmental constraints are more limiting to growth than to defence (Herms & Mattson, 1992; Stamp, 2003). Our findings, which included an increase in concentrations of usnic acid with elevation, are in line with Bjerke *et al.* (2004) who also found increasing usnic acid in lichens at higher elevations, and who attributed this to declining temperature and increasing frost-sums. Further, Nybakken *et al.* (2011) ran an open top chamber-experiment in the same area as our study, and showed that warming led to lower concentrations of usnic acid in *Cladonia arbuscula*, but no changes in other compounds in that species or any compounds in other lichen species (Nybakken *et al.*, 2011). In our study, the community level increase in usnic acid as elevation increased was primarily driven by changes within species, which indicates physiological responses of species to lower temperatures. The changes in other LSMs were primarily driven by species turnover.

The increase in LSM concentration with elevation was more pronounced for compounds in the medullary layer that are known to deter herbivores, than for cortical compounds that are recognized as protecting the lichen against damage by sunlight. This is in contrast to our second hypothesis (Solhaug & Gauslaa, 2012). However, even though medullary compounds do not screen light, they do protect against light-induced oxidative stress. Thus, the very large increase in medullary compounds with elevation suggests that the lichen community is increasingly investing in protection against oxidative stress. Still, we did not find support for a shift towards antioxidants, because lichen communities at higher elevations were characterized by an increase in depsides, which are considered to be less efficient scavengers of radicals than are depsidones such as fumarprotocetraric acid (Hidalgo *et al.*, 1994; Lohézic-Le Dévéhat *et al.*, 2007; Atalay *et al.*, 2011; Brisdelli *et al.*, 2013). The low concentrations of cortical LSMs at the highest elevation can in part be explained by an increase in the relative abundance of brown melanic species such as *Cetraria islandica,* which do not produce cortical LSMs. These lichens instead rely on melanins for light protection; this leads to them having a higher surface temperature due to absorbance of visible and near-infrared light (Gauslaa, 1984), and therefore being more susceptible to heating by excess light (Gauslaa & Solhaug, 1999). Because of their light absorbance, these lichens can also melt snow during winter, causing hydration and thus activation of photosynthesis (Coxson & Coyle, 2003), and they are therefore often restricted to colder environments.

Conclusions

In this study, we show that responses of plant and lichen secondary metabolites to elevation at the whole community level is compound-specific. These compound-specific changes can to some extent be understood from a functional perspective, i.e. the shift from those protecting against herbivory at lower elevations to those protecting from oxidative stress at higher elevations, although this pattern was less pronounced for lichens. As such, our findings highlight the importance of studying qualitative as well quantitative changes in SMs in response to environmental factors or gradients.

The fact that with increasing elevation, the vascular plant community has lower levels of herbivore defence compounds while the lichen community has more, suggests a shift with increasing elevation in the relative palatability of these two groups. This has potentially important trophic implications in that generalist herbivores may switch from a lichen based diet to a vascular plant based diet with increasing elevation. The changed relative palatability of vascular plants and lichens may also promote a shift in herbivore community composition from those that specialize on vascular plants to those that specialize on lichens. Furthermore, the changes in LSM and PSM composition may also impact carbon and nutrient fluxes. For instance, the decrease in tannin concentration in the vascular plant community with elevation will presumably result in decreased carbon sequestration and increased N mineralization (Hättenschwiler & Vitousek, 2000). In contrast, the large increase in SMs in the lichen community may reduce decomposition rates (Asplund & Wardle, 2013). Finally, climate change will have important effects not only on community composition of primary producers but also on secondary chemistry at the whole community scale, which in turn will affect the structure and functioning of communities and ecosystems.

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Author contributions

JA designed the study in consultation with KvZ, RR, TB, KK, SIL and DAW. Field and lab work was conducted by KvZ and RR. Data analyses was done by JA and LN. JA led the writing in collaboration with KvZ, RR, TB, KK, SIL, DAW and LN.

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Tables and figures

Table 1. Permutational multivariate analyses of variance (PERMANOVA; using 999 permutations) testing for the effect of elevation on the composition plant and lichen secondary metabolites at the community level. Specific community weighted (CW) values include both species turnover and within-species variability while Fixed CW values assume that there is no within-species variation.

	SS	MS	$F_{4,20}$	R^2	*P*
Specific community weighted plant secondary metabolites					
Elevation	0.45	0.11	9.13	0.646	<0.001
Residuals	0.25	0.01			
Fixed community weighted plant secondary metabolites					
Elevation	0.44	0.11	14.41	0.742	<0.001
Residuals	0.15	0.01			
Specific community weighted lichen secondary metabolites					
Elevation	0.84	0.21	4.39	0.468	0.001
Residuals	0.96	0.048			
Fixed community weighted lichen secondary metabolites					
Elevation	0.60	0.15	4.60	0.479	0.001
Residuals	0.65	0.03			

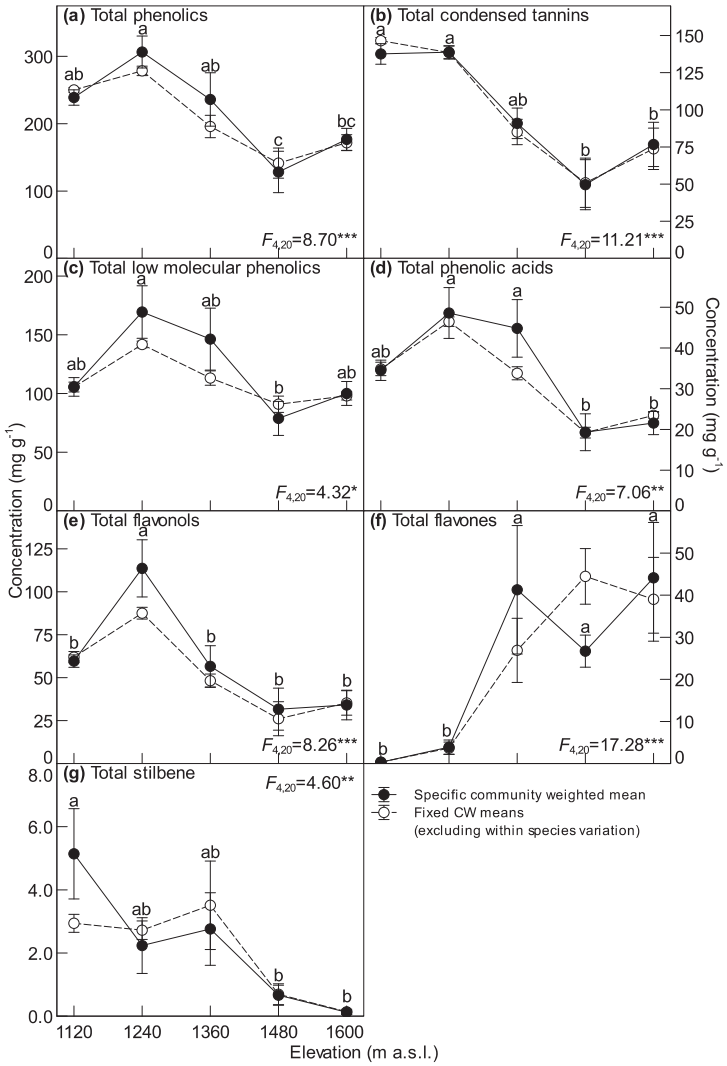


Figure 1. Community-weighted averages (± SE) of plant secondary metabolites divided into (a) total phenolics, (b) condensed tannins and (c) low molecular phenolics. The low molecular phenolics include: (d) phenolic acids, (e) flavonols, (f) flavones and (g) stilbenes. Specific community averages (which include species turnover and intraspecific trait variability) and fixed community averages (which do not take intraspecific trait variability into account) are calculated from plot-specific and plot-independent trait values, respectively (see Materials and Methods). *F* values are derived from ANOVAs testing for the effect of elevation. *F*-values for fixed CW means are not presented. *, ** and *** denote that *F* value differs from 0 at $p < 0.05$, <0.01 and <0.001, respectively. Within each panel, dots topped with the same letter are not significantly different according to Tukey's HSD test at p=0.05.

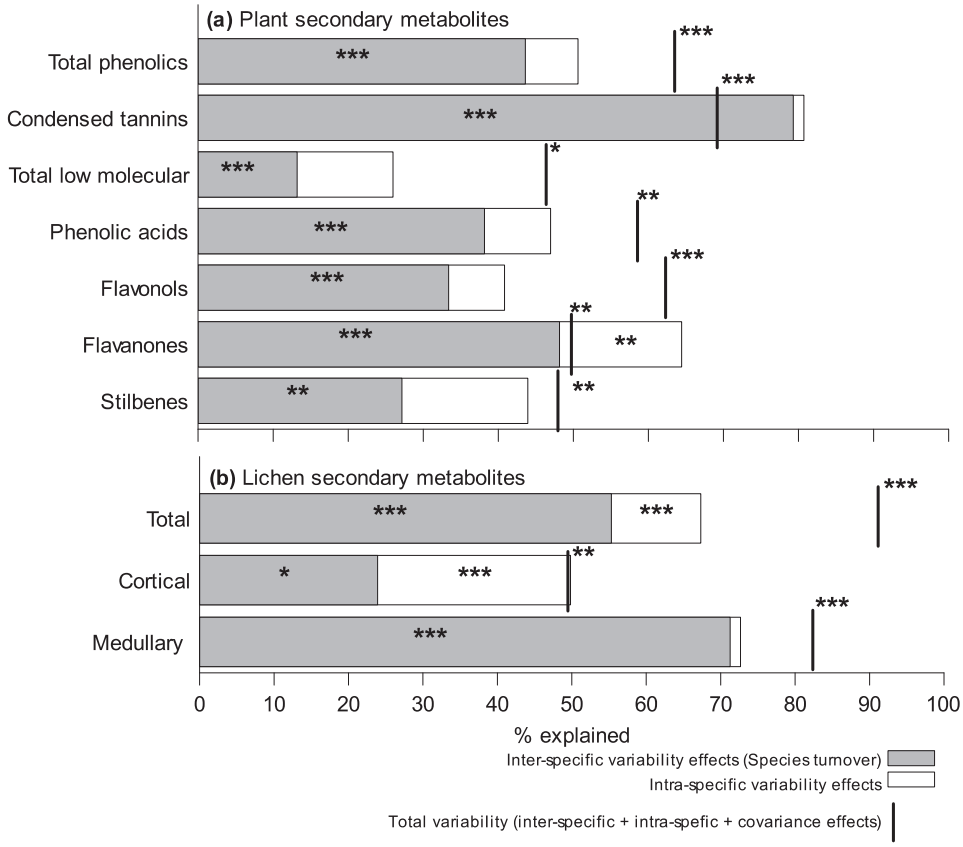


Figure 2. Decomposition of the total variability of (a) plant and (b) lichen secondary metabolites explained by elevation into interspecific (species turnover), intraspecific effects and total variability (specific average), depicted using the style of Lepš *et al.* (2011). Covariation strength is represented by the interval between the total variability and the sum of inter- and intraspecific variability effects. Covariation is negative when total variability is lower than the sum of interspecific variation and intraspecific variation and positive when the total variability is higher than the sum of interspecific variation and intraspecific variation. Lichen secondary metabolites are divided into those present in the cortical layer and those present in the medullary layer. *, ** and *** denotes significant effects of interspecific variability, intraspecific variability and total variability at p <0.05, <0.01 and <0.001, respectively.

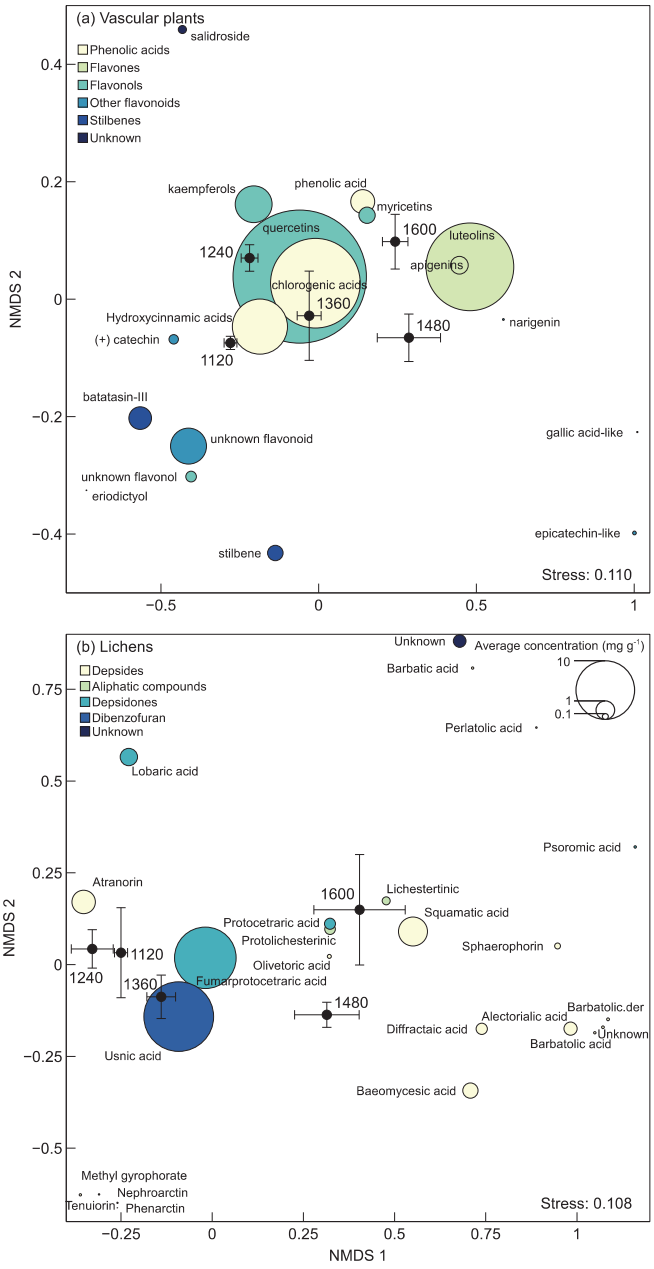


Figure 3. Ordination plot derived from a non-metric multidimensional scaling (NMDS) of community-weighted averages of (a) low molecular plant secondary metabolites and (b) lichen secondary metabolites, across an elevational gradient from 1120 to 1600 m a.s.l. The area of the circles indicate the community-weighted concentration of each secondary metabolite averaged across the entire gradient. Black dots and error bars represent centroids (± SE) of plots at each elevation.

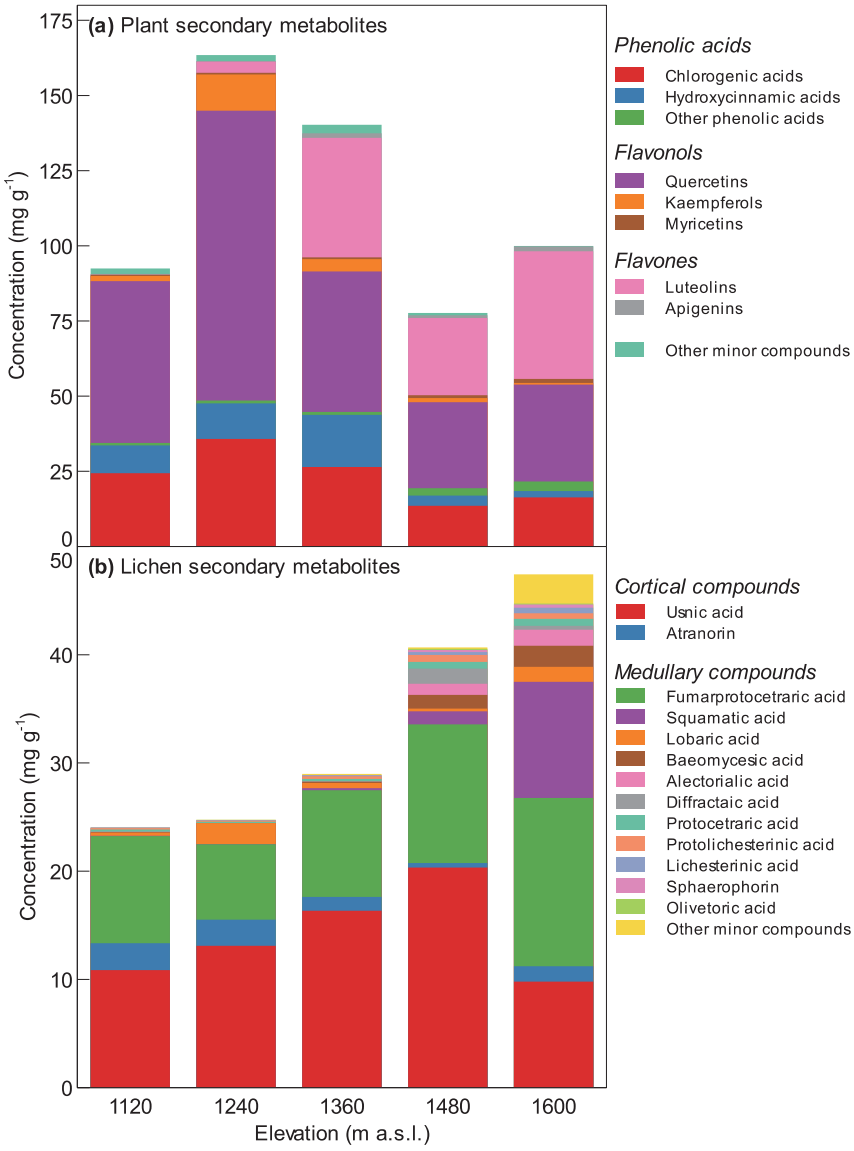


Figure 4. Mean values of individual (a) plant and (b) lichen secondary metabolites across elevation. See Table S1 and S2 for mean ±SE-values and relative contributions of within species variability and species turnover.

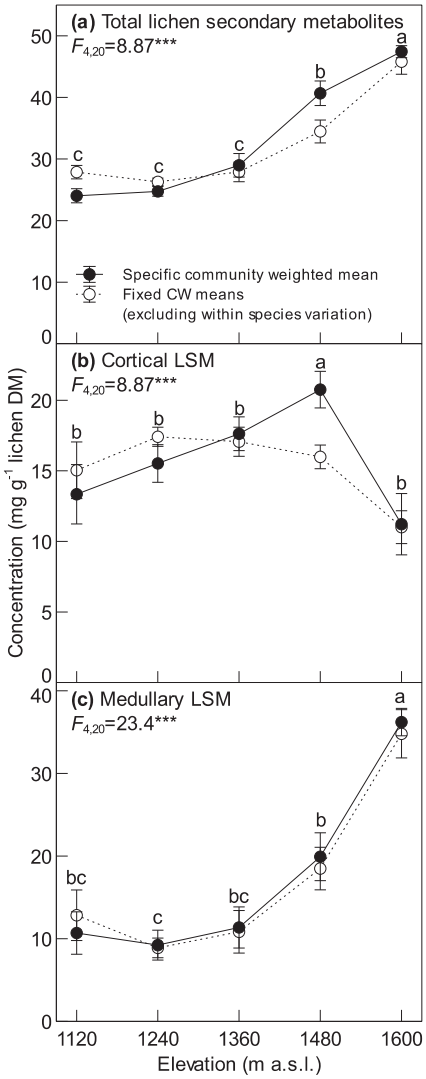


Figure 5. Community-weighted averages (± SE) of (a) total lichen secondary metabolites (LSMs), (b) LSMs in the lichen cortex and (c) LSMs in the lichen medulla. Specific community averages (which include species turnover and intraspecific trait variability) and fixed community averages (which do not take intraspecific trait variability into account) are calculated from plot-specific and plot-independent trait values, respectively (see Materials and Methods). *F*-values are derived from ANOVAs testing for the effect of elevation. *F*-values for fixed CW means are not presented. *, ** and *** denote that *F* value differs from 0 at $p < 0.05$, <0.01 and <0.001, respectively. Within each panel, dots topped with the same letter are not significantly different according to Tukey's HSD test at p=0.05.

Supplementary information

Table S1. Community weighted mean (± SE) concentrations of plant secondary metabolites at five elevations. The left part of the table gives the actual concentrations and the right part presents the decomposition of the total variability explained by elevation into interspecific (species turnover), intraspecific effects and total variability (specific average). Covariation is negative when total variability is lower than the sum of interspecific variation and intraspecific variation and positive when the total variability is higher than the sum of interspecific variation and intraspecific variation. Within each row, values with the same letter are not significantly different according to Tukey's HSD test at p=0.05. Bold letters denote significant effects of elevation. *, ** and *** denote significant effects of interspecific variability and intraspecific variability at p <0.05, <0.01 and <0.001, respectively.

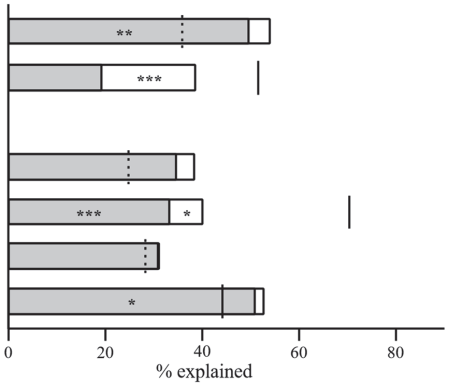
	Community weighted mean concentration (mg g^{-1})						Relative contribution of species turnover, (▭) intraspecific variation (▭) and total variability |
	1120	1240	1360	1480	1600	$F_{4,20}(P)$	
Condensed tannins (CT)							
MeOH-soluble CT	119.3±6.3ab	121.6±4.8a	75.2±8.0bc	43.1±14.7c	67.1±15.0c	**10.3 (<0.001)**	***
MeOH-insoluble CT	18.3±1.0a	17.2±1.3ab	15.7±2.8ab	6.6±2.2c	9.6±1.0bc	**8.1 (<0.001)**	***
Phenolic acids							
Chlorogenic acids	24.4±2.7ab	35.8±5.5a	26.4±6.5ab	13.5±2.7b	16.3±2.4b	**4.2 (0.013)**	***
Hydroxycinnamic acids	9.2±0.9ab	11.8±1.6ab	17.4±5.2a	3.4±1.9b	2.1±0.3b	**5.7 (0.003)**	***
Flavonols							
Quercetins	53.8±3.9ab	96.4±14.7a	46.7±10.8b	28.6±11.9b	32.2±8.3b	**6.6 (0.001)**	***
Kaempferols	1.7±0.6b	12.0±2.6a	4.1±2.2ab	1.4±0.5b	0.56±0.2b	**† (<0.001)**	***
Myricetins	0.37±0.04b	0.58±0.1ab	0.60±0.1ab	0.94±0.3ab	1.3±0.3a	**† (0.036)**	*** *
Flavones							
Luteolins	–	3.7±1.6b	39.8±14.6ab	25.7±3.7ab	42.5±12.6b	**† (0.006)**	*** ***
Apigenins	0.31±0.1a	0.21±0.1a	1.5±0.6a	0.89±0.2a	1.6±0.6a	**† (0.045)**	*** *

0 20 40 60 80
% explained

† *P-values from permutation tests due to non-normal residuals*

Table S2. Community weighted mean (± SE) concentrations of lichen secondary metabolites at five elevations. The left part of the table gives the actual concentrations and the right part presents the decomposition of the total variability explained by elevation into interspecific (species turnover), intraspecific effects and total variability (specific average). Covariation is negative when total variability is lower than the sum of interspecific variation and intraspecific variation and positive when the total variability is higher than the sum of interspecific variation and intraspecific variation. Within each row, values with the same letter are not significantly different according to Tukey's HSD test at p=0.05. Bold letters denote significant effects of elevation. *, ** and *** denotes significant effects of interspecific variability and intraspecific variability at p<0.05, <0.01 and <0.001, respectively.

	Community weighted mean concentration (mg g^{-1})						Relative contribution of species turnover, (▭) intraspecific variation (▭) and total variability
	1120	1240	1360	1480	1600	$F_{4,20}$ (P)	
Cortical compounds							
Atranorin†	2.48±0.8	2.41±0.3	1.28±0.2	0.41±0.2	1.43±0.7	† (0.051)	
Usnic acid	10.9±2.9b	13.1±1.5ab	16.4±1.2ab	20.3±1.3a	8.79±2.0b	**5.3 (0.004)**	
Medullary compounds							
Fumarprotocetraric acid	9.90±2.3	6.96±1.8	9.85±2.0	12.8±2.2	15.5±3.9	† (0.190)	
Squamatic acid	0.035±0.04c	0.028±0.02c	0.20±0.08c	1.21±0.2b	10.7±3.0a	**† (<0.001)**	
Lobaric acid	0.29±0.3	1.94±0.7	0.47±0.4	0.24±0.1	1.39±0.9	28.2 (0.140)	
Baeomycesic acid	0.05±0.05b	-	0.12±0.09b	1.26±0.2a	1.94±1.0a	**† (0.010)**	
Alectorialic acid	-	-	-	1.04±0.3	1.49±1.2		
Diffractaic acid	0.07±0.07	-	-	1.40±0.6	0.36±0.2		



† *P-values from permutation tests due to non-normal residuals*

Table S3. Mean (± SE) of plant secondary compounds (mg g^{-1}) and relative cover (%) of vascular plants at five different elevations.

	1120	1240	1360	1480	1600
Arctostaphylos alpinus					
Relative cover (%)	1.17±0.63	–	–	–	–
Condensed tannins (CT; total)	25.4±4.4	–	–	–	–
MeOH-soluble CT	14.4±2.0	–	–	–	–
MeOH-insoluble CT	11.0±2.4	–	–	–	–
Eriodictyol	0.49±0.23	–	–	–	–
Hydroxycinnamic acid	19.6±3.0	–	–	–	–
Quercetins	58.3±5.5	–	–	–	–
Sum phenolic acids	19.6±3.0	–	–	–	–
Sum flavonols	58.8±5.7	–	–	–	–
Sum low molecular	78.4±8.3	–	–	–	–
Avenella flexuosa					
Relative cover (%)	–	0.98±0.49	1.77±0.89	–	–
Chlorogenic acid	–	5.68±0.95	5.09±0.94	–	–
Unknown phenolic acid	–	0.45±0.12	0.17±0.10	–	–
Quercetins	–	57.3±9.0	63.7±12.8	–	–
Kaempferols	–	9.8±1.4	8.7±0.9	–	–
Sum phenolic acids	–	6.1±1.1	5.3±1.0	–	–
Sum flavonols	–	67.2±10.4	72.5±13.6	–	–
Sum low molecular	–	73.3±11.5	77.7±14.6	–	–
Betula nana					
Relative cover (%)	45.2±6.8	–	–	–	–
Condensed tannins (CT; total)	168.6±19.8	–	–	–	–
MeOH-soluble CT	152.2±17.2	–	–	–	–
MeOH-insoluble CT	16.4±2.7	–	–	–	–
Apigenins	0.74±0.22	–	–	–	–
Chlorogenic acids	29.1±6.6	–	–	–	–
Hydroxycinnamic acid	0.44±0.10	–	–	–	–
Kaempferols	0.19±0.08	–	–	–	–
Quercetins	52.7±9.8	–	–	–	–

Table S3 continued

	1120	1240	1360	1480	1600
Unknown flavonoid	11.3±3.1	–	–	–	–
Sum phenolic acids	29.6±6.7	–	–	–	–
Sum flavonols	52.9±9.7	–	–	–	–
Sum flavones	0.74±0.22	–	–	–	–
Sum low molecular	94.5±18.9	–	–	–	–
Bistorta vivipara					
Relative cover (%)	–	–	3.78±2.47	8.84±7.94	–
Condensed tannins (CT; total)	–	–	96.7±2.8	119±1.2	–
MeOH-soluble CT	–	–	70.5±0.6	99.2±0.04	–
MeOH-insoluble CT	–	–	26.3±3.0	19.8±1.2	–
Apigenins	–	–	0.90±0.05	0.35±0.05	–
Chlorogenic acids	–	–	10.9±1.9	12.5±1.4	–
Hydroxycinnamic acid	–	–	0.91±0.06	1.21±0.17	–
Kaempferols	–	–	0.71±0.33	0.12±0.03	–
Luteolins	–	–	54.4±10.2	32.2±1.5	–
Quercetins	–	–	66.4±13.9	86.9±16.2	–
Unknown flavonoid	–	–	1.65±0.27	2.80±0.16	–
Sum phenolic acids	–	–	11.8±1.9	13.7±1.5	–
Sum flavonols	–	–	67.1±14.2	87.0±16.3	–
Sum flavones	–	–	55.3±10.2	32.6±1.5	–
Sum low molecular	–	–	135.8±26.0	136.1±19.5	–
Carex bigelowii					
Relative cover (%)	–	3.98±1.58	25.3±8.4	25.5±8.0	35.8±10.7
Apigenins	–	4.74±0.97	4.76±0.72	2.06±0.11	3.55±0.51
Chlorogenic acids	–	32.8±6.0	26.1±2.4	15.4±1.7	20.0±7.4
Hydroxycinnamic acid	–	0.72±0.13	1.07±0.16	0.43±0.09	1.39±0.64
Luteolins	–	87.5±13.9	120.1±15.8	46.3±7.3	99.4±7.7
Unknown phenolic acid	–	0.63±0.05	0.88±0.18	0.34±0.16	1.13±0.40
Sum phenolic acids	–	34.1±6.1	28.0±2.5	16.2±1.9	22.5±7.9
Sum flavones	–	92.3±14.7	124.8±16.5	48.3±7.4	102.9±8.2
Sum low molecular	–	126.4±15.8	152.8±18.5	64.5±9.0	125.4±15.7

Table S3 continued

	1120	1240	1360	1480	1600
Empetrum nigrum					
Relative cover (%)	34.5±3.3	31.9±3.4	41.2±16.4	6.0±3.7	–
Condensed tannins (CT; total)	93.3±5.4	110.3±6.8	121.6±2.3	132.5±0.5	–
MeOH-soluble CT	71.6±5.4	90.7±6.9	95.1±3.5	111.0±3.3	–
MeOH-insoluble CT	21.7±1.3	19.5±1.2	26.5±2.7	21.4±4.7	–
Batatasin III	11.35±4.15	6.59±4.10	4.34±1.30	2.71±1.08	–
Chlorogenic acids	13.9±3.0	13.0±2.6	8.7±0.6	14.5±3.9	–
Hydroxycinnamic acid	22.6±5.7	21.3±3.3	27.4±4.1	36.9±20.0	–
Kaempferols	0.63±0.25	0.57±0.27	0.25±0.07	0.83±0.42	–
Myricetins	0.65±0.03	0.53±0.10	0.61±0.11	0.66±0.32	–
Quercetins	43.8±10.5	40.0±5.8	31.1±9.6	49.6±23.8	–
Stilbenes	2.58±1.48	1.51±0.38	2.91±1.33	4.97±4.00	–
Unknown flavonoid	9.94±1.30	13.2±0.7	10.3±1.0	11.0±0.6	–
Sum phenolic acids	36.8±8.7	34.5±5.2	36.1±3.9	51.5±23.7	–
Sum flavonols	56.4±12.3	55.5±6.1	43.5±10.5	64.2±24.2	–
Sum stilbenes					–
Sum low molecular	95.7±20.9	91.5±10.9	82.6±15.6	120.6±43.9	–
Festuca vivipara					
Relative cover (%)	–	–	0.89±0.64	14.0±5.6	2.99±1.32
Apigenins	–	–	1.77	0.66±0.24	1.88±0.62
Chlorogenic acids	–	–	17.9	7.1±1.4	14.3±2.3
Hydroxycinnamic acid	–	–	0.60	0.29±0.13	0.81±0.40
Luteolins	–	–	49.7	30.3±9.6	60.0±11.3
Unknown flavonoid	–	–	3.61	1.31±0.54	1.80±0.72
Sum phenolic acids	–	–	18.1	7.2±1.4	14.4±2.8
Sum flavones	–	–	55.0	32.3±10.3	63.6±12.6
Sum low molecular	–	–	73.5	39.7±11.7	78.7±15.2
Juncus trifudus					
Relative cover (%)	–	–	–	16.5±7.0	3.9±1.6
Apigenins	–	–	–	0.69±0.39	0.91±0.44

Table S3 continued

	1120	1240	1360	1480	1600
Chlorogenic acids	–	–	–	6.8±2.1	6.8±2.1
Epicatechin	–	–	–	1.02±0.17	0.78±0.41
Gallic acid	–	–	–	0.10±0.02	0.18±0.05
Kaempferols	–	–	–	1.53±1.34	0.52±0.44
Luteolins	–	–	–	27.8±15.0	27.9±12.1
Narigenin	–	–	–	0.24±0.11	0.19±0.12
Phenolic acids	–	–	–	1.40±0.42	1.45±0.59
Sum phenolic acids	–	–	–	8.34±2.52	8.42±2.74
Sum flavonols	–	–	–	1.53±1.34	0.52±0.44
Sum flavones	–	–	–	28.8±15.5	29.0±12.7
Sum low molecular	–	–	–	39.7±17.5	38.7±15.6
Luzula sp.					
Relative cover (%)	–	–	–	8.26±3.81	5.19±3.02
Apigenins	–	–	–	2.03±0.25	1.97±0.64
Chlorogenic acids	–	–	–	8.21±0.68	5.86±0.50
Kaempferols	–	–	–	4.77±1.67	5.19±3.03
Luteolins	–	–	–	59.5±8.5	60.8±25.7
Stilbenes	–	–	–	2.76±0.69	2.54±0.21
Sum phenolic acids	–	–	–	8.21±0.68	5.86±0.50
Sum flavonols	–	–	–	4.77±1.67	5.19±3.03
Sum flavones	–	–	–	61.5±8.5	62.8±26.4
Sum low molecular	–	–	–	77.2±8.1	76.4±29.5
Salix herbacea					
Relative cover (%)	–	–	3.28±0.59	17.6±8.1	44.0±9.0
Condensed tannins (CT; total)	–	–	144.8±13.4	121.0±13.2	131.1±6.0
MeOH-soluble CT	–	–	130.2±12.9	112.6±13.1	117.9±6.5
MeOH-insoluble CT	–	–	14.6±1.0	8.44±0.50	13.2±1.1
Chlorogenic acids	–	–	27.7±5.3	24.4±3.6	18.6±1.0
Quercetins	–	–	64.1±13.6	67.2±10.0	54.2±4.5
Hydroxycinnamic acid	–	–	3.24±0.44	2.95±0.46	2.12±0.29
Kaempferols	–	–	0.57±0.08	1.47±0.22	0.57±0.17

Table S3 continued

	1120	1240	1360	1480	1600
Myricetins	–	–	3.97±1.29	3.51±1.04	2.54±0.17
Phenolic acids	–	–	0.70±0.18	0.56±0.13	0.38±0.04
Sum phenolic acids	–	–	31.7±5.9	27.9±4.0	21.1±1.3
Sum flavonols	–	–	68.6±14.9	72.1±11.0	57.3±4.6
Sum low molecular	–	–	100.3±20.4	100.1±14.4	78.4±4.5
Vaccinium myrtillus					
Relative cover (%)	1.23±1.09	4.11±0.57	2.66±0.56	–	–
Condensed tannins (CT; total)	122.3±14.9	113.7±5.8	137.9±6.3	–	–
MeOH-soluble CT	104.5±16.2	98.7±7.5	124.8±6.3	–	–
MeOH-insoluble CT	17.8±2.6	15.1±1.8	13.0±1.1	–	–
(+)catechin	22.2±2.2	12.6±1.3	16.6±3.2	–	–
Chlorogenic acids	93.5±6.3	109.9±7.7	125.4±33.6	–	–
Hydroxycinnamic acid	23.5±4.8	38.5±7.1	19.0±5.1	–	–
Kaempferols	5.06±0.93	5.42±1.78	4.22±0.77	–	–
Phenolic acids	2.10±0.24	3.33±0.77	2.94±0.87	–	–
Quercetins	106.8±19.1	188.5±83.0	119.6±21.0	–	–
Sum phenolic acids	119.1±10.4	151.7±14.9	147.3±37.9	–	–
Sum flavonols	111.9±19.7	193.9±83.4	123.8±21.7	–	–
Sum low molecular	253.3±31.6	358.2±87.2	287.7±58.3	–	–
Vaccinium uliginosum					
Relative cover (%)	12.8±6.1	54.6±3.6	13.1±7.6	–	–
Condensed tannins (CT; total)	157.7±10.3	164.8±4.9	178.1±7.5	–	–
MeOH-soluble CT	142.4±10.7	146.9±5.4	162.9±6.6	–	–
MeOH-insoluble CT	15.1±2.1	17.9±2.0	15.2±1.9	–	–
Chlorogenic acids	26.5±7.4	47.4±6.7	54.5±14.1	–	–
Hydroxycinnamic acid	6.94±1.96	5.68±0.80	18.3±5.9	–	–
Kaempferols	8.00±2.08	21.4±4.5	19.9±5.2	–	–
Myricetins	0.23±0.11	0.64±0.19	0.71±0.12	–	–
Phenolic acids	0.34±0.10	0.45±0.14	0.50±0.21	–	–
Quercetins	52.8±13.5	132.1±17.9	109.9±26.4	–	–
Salidroside	1.20±0.61	0.95±0.20	1.60±0.62	–	–

Table S3 continued

	1120	1240	1360	1480	1600
Sum phenolic acids	33.8±8.9	53.5±6.8	73.3±19.7	–	–
Sum flavonols	61.0±15.6	154.1±22.2	130.5±31.6	–	–
Sum low molecular	96.0±24.0	208.6±28.4	205.3±51.4	–	–
Vaccinium vitis-idaea					
Relative cover (%)	5.06±1.16	4.44±2.47	3.97±0.83	5.92±4.90	8.16±2.90
Condensed tannins (CT; total)	152.1±5.8	154.2±5.9	144.5±13.6	175.1±14.2	172.8±4.8
MeOH-soluble CT	136.1±5.3	143.0±6.0	130.1±13.1	158.2±14.8	157.5±4.9
MeOH-insoluble CT	16.0±1.4	11.2±1.0	14.4±0.6	16.9±2.8	15.3±1.5
Hydroxycinnamic acid	2.97±1.22	1.15±0.27	0.70±0.09	2.21±0.47	5.05±2.31
Kaempferols	1.49±0.35	1.17±0.10	1.07±0.11	1.40±0.51	1.59±0.35
Myricetins	2.17±0.57	1.51±0.22	1.93±0.42	2.56±0.42	2.90±1.12
Phenolic acids	16.0±3.6	11.8±2.0	9.0±0.8	18.9±6.5	27.4±9.1
Quercetins	81.1±22.9	60.1±5.4	48.2±6.4	73.0±15.2	93.0±21.6
Sum phenolic acids	18.9±4.8	13.0±2.3	10.6±0.8	21.1±7.0	32.5±11.3
Sum flavonols	84.4±23.6	62.6±5.4	50.9±6.4	76.4±15.8	97.3±22.4
Sum low molecular	103.7±28.2	75.8±7.1	61.7±6.9	98.0±22.9	130.0±30.9
Viscaria alpina					
Relative cover (%)	–	–	–	1.46±0.54	–
Condensed tannins (CT; total)	–	–	–	7.16±0.62	–
MeOH-soluble CT	–	–	–	3.05±0.28	–
MeOH-insoluble CT	–	–	–	4.11±0.35	–
Apigenins	–	–	–	3.39±0.90	–
Chlorogenic acids	–	–	–	12.0±1.2	–
Hydroxycinnamic acid	–	–	–	2.10±0.34	–
Luteolins	–	–	–	69.3±14.0	–
Sum phenolic acids	–	–	–	12.9±1.1	–
Sum flavones	–	–	–	72.7±14.9	–
Sum low molecular	–	–	–	86.8±16.3	–

Table S4. Mean (± SE) of lichen secondary compounds (mg g^{-1}) and relative cover (%) of lichens at five different elevations.

	1120	1240	1360	1480	1600
Alectoria ocroleuca					
Relative cover (%)	0.15±0.15	–	–	2.87±1.28	1.60±0.87
Diffractaic acid	49.5	–	–	52.4±4.4	24.6±3.5
Usnic acid	12.8	–	–	25.2±5.5	26.8±2.7
Total compounds	62.3	–	–	77.6±5.9	51.4±0.8
Bryocaulon divergens					
Relative cover (%)	0.07±0.07	–	–	0.38±0.21	0.24
Olivetoric acid	60.0	–	–	28.7±0.4	36.5
Cetraria islandica					
Relative cover (%)	6.96±1.91	3.61±2.28	10.5±5.0	22.2±4.8	28.2±7.8
Fumarprotocetraric	44.5±3.8	57.0±8.2	52.3±7.2	51.2±2.2	40.5±3.2
Lichesterinic acid	0.43±0.06	0.52±0.02	0.55±0.08	1.01±0.05	1.37±0.38
Protocetraric acid	2.50±0.18	3.47±0.31	2.34±0.53	2.65±0.25	2.24±0.17
Protolichesterinic acid	2.05±0.18	2.76±0.35	2.41±0.67	2.64±0.38	1.98±0.24
Total compounds	49.5±4.1	63.7±8.5	57.6±8.2	57.5±2.4	46.1±3.6
Cladonia spp.					
Relative cover (%)	–	–	–	–	19.7±8.8
Atranorin	–	–	–	–	0.75±0.42
Barbatic acid	–	–	–	–	55.5±2.5
Fumarprotocetraric acid	–	–	–	–	4.9±1.4
Perlatolic acid	–	–	–	–	0.42±0.25
Psoromic acid	–	–	–	–	0.98±0.53
Squamatic acid	–	–	–	–	23.3±3.4
Unknown	–	–	–	–	10.8±4.0
Usnic acid	–	–	–	–	13.9±0.9
Cladonia mitis					
Relative cover (%)	43.7±10.5	65.8±4.3	66.5±5.0	18.9±12.8	6.5±2.3
Fumarprotocetraric acid	0.49±0.15	0.39±0.21	0.82±0.16	0.40±0.07	0.59±0.11

Table S4 continued

	1120	1240	1360	1480	1600
Usnic acid	18.8±1.3	19.3±1.3	23.4±1.3	29.2±2.6	21.6±2.4
Total compounds	19.2±1.2	19.7±1.2	24.2±1.2	29.6±2.7	22.2±2.5
Cladonia gracilis					
Relative cover (%)	1.63±0.23	1.13±0.11	0.99±0.08	1.17±0.16	3.83±0.41
Atranorin	3.03±1.49	6.32±0.72	5.47±1.84	1.28±0.70	6.52±3.74
Fumarprotocetraric acid	34.6±2.9	35.8±4.8	24.8±2.2	39.2±3.1	41.6±10.4
Total compounds	38.3±3.8	44.6±6.0	36.0±7.2	40.4±2.9	48.1±12.3
Cladonia rangiferina					
Relative cover (%)	29.8±9.6	12.7±1.8	5.10±1.74	2.44±1.98	1.98±1.98
Atranorin	6.51±0.95	9.48±0.38	8.67±1.19	6.58±1.25	NA
Fumarprotocetraric acid	16.1±2.2	21.1±0.6	22.3±2.3	19.5±2.3	NA
Total compounds	22.6±3.0	30.6±0.6	31.0±3.4	26.1±3.4	NA
Cladonia stygia					
Relative cover (%)	7.23±1.28	6.44±2.85	9.32±2.64	1.35±0.70	2.67±0.75
Atranorin	5.76±0.70	5.90±1.10	7.43±0.36	8.11	NA
Fumarprotocetraric acid	17.0±1.4	19.0±1.6	28.9±4.5	22.6	NA
Total compounds	22.7±1.1	24.9±2.1	36.4±4.6	30.7	NA
Cladonia uncialis					
Relative cover (%)	0.78±0.52	0.22±0.15	1.56±0.25	2.30±0.62	11.3±7.7
Squamatic acid	0	1.69±1.64	1.91±0.96	9.39±2.28	32.6±1.7
Usnic acid	18.5±5.0	16.8±7.0	19.9±3.5	21.5±1.2	23.5±2.3
Total compounds	18.5±5.0	18.5±8.6	21.8±3.2	30.9±1.9	56.1±3.0
Flavocetraria cucullata					
Relative cover (%)	2.16±1.25	1.14±0.74	1.55±0.99	2.05±0.86	2.00±0.80
Lichesterinic acid	1.13±0.12	1.51±0.16	1.12±0.18	1.48±0.17	1.29±0.18
Usnic acid	24.8±2.4	24.9±3.9	21.2±4.4	25.9±2.8	24.4±1.5
Total compounds	26.0±2.3	26.4±4.0	22.3±4.6	27.4±2.8	25.7±1.7

Table S4 continued

	1120	1240	1360	1480	1600
Flavocetraria nivalis					
Relative cover (%)	6.44±2.22	0.14±0.14	0.45±0.14	41.8±10.5	10.4±3.8
Usnic acid	27.7±2.5	30.7	20.7±3.7	28.3±3.2	14.3±1.3
Gowardia nigricans					
Relative cover (%)	–	–	–	0.99±0.28	1.18±0.91
Alectorialic acid	–	–	–	108.0±10.5	126.4
Barbatolic acid	–	–	–	3.92±0.42	3.89
Unknown	–	–	–	4.67±0.16	5.98
Unknown	–	–	–	4.23±0.40	4.89
Total compounds	–	–	–	120.8±11.4	141.1
Peltigera malacea					
Relative cover (%)	–	–	1.25±0.76	0.07	–
Tenuiorin	–	–	5.24±2.56	NA	–
Methyl gyrophorate	–	–	2.63±0.95	NA	–
Total compounds	–	–	7.86±3.33	NA	–
Sphaerophorus globosus					
Relative cover (%)	–	–	–	1.14±0.29	2.30±1.12
Squamatic acid	–	–	–	0.30±0.18	0.24
Sphaerophorin	–	–	–	16.9±0.6	12.9
Total compounds	–	–	–	17.2±0.43	13.2
Stereocaulon spp.					
Relative cover (%)	1.14±1.08	8.76±2.90	2.48±1.92	0.92±0.25	6.42±3.84
Atranorin	10.14±0.46	6.73±1.51	6.20±0.99	9.60±0.49	9.55±0.03
Lobaric acid	24.2±3.3	19.9±3.1	19.0±3.2	25.8±1.7	21.7±0.6
Total compounds	34.4±3.6	26.6±3.7	25.2±3.4	35.4±2.0	31.3±0.6
Thamnolia vermicularis					
Relative cover (%)	0.06±0.06	–	0.21±0.13	1.29±0.11	2.76±1.13
Baeomycesic acid	NA	–	55.5±17.9	95.8±13.9	69.8±20.0

Table S4 continued

	1120	1240	1360	1480	1600
Squamatic acid	NA	–	35.3±10.9	64.9±9.6	52.1±15.6
Total compounds	NA	–	90.8±28.8	160.7±23.3	121.8±35.6

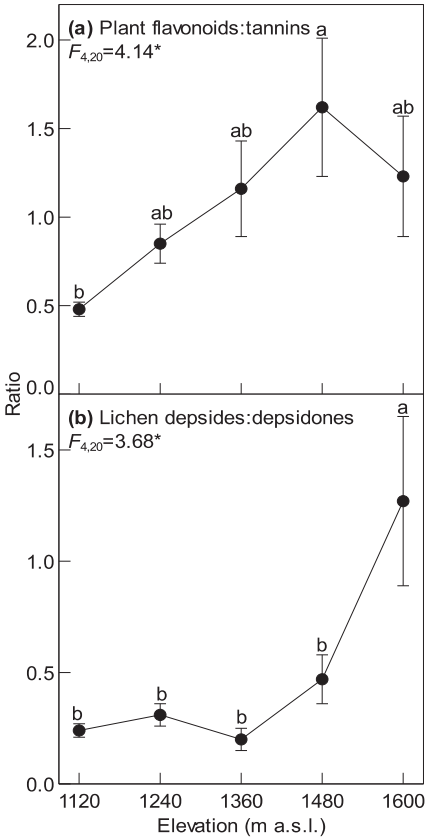


Figure S1. Ratios (mean ± SE) of (a) community-weighted flavonoids to tannins in plant communities and (b) community weighted depsides to depsidones in lichen communitites, at five different elevations. *F* values are derived from ANOVAs testing for the effect of elevation. * denotes that *F* value differs from 0 at $p < 0.05$. Within each panel, dots topped with the same letter are not significantly different according to Tukey's HSD test at p=0.05.

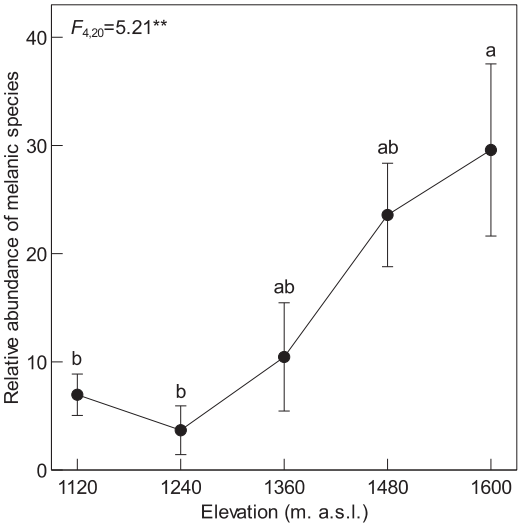


Figure S2. Relative abundance (mean ± SE) of brown melanic species. *F* value is from ANOVAs testing for the effect of elevation. ** denotes that *F* value differs from 0 at $p < 0.01$. Dots topped with the same letter are not significantly different according to Tukey's HSD test at p=0.05.

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