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

Philosophiae Doctor (PhD)
Thesis 2019:71

Functional traits across primary producer groups and their effects on micro-arthropod communities in alpine Norway

Funksjonelle trekk hos primærprodusenter og deres effekt på alpine mikroartropod-samfunn i Norge

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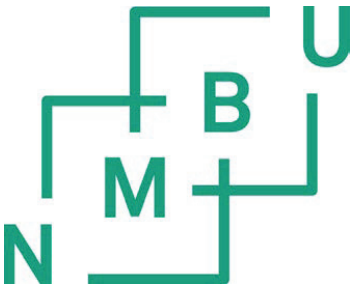
Ås (2019)



Thesis number 2019:71
ISSN 1894-6402
ISBN 978-82-575-1631-4

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Voor mama

Acknowledgements

If there is one thing that academics in general and PhD-students in particular tend to forget, it is the importance of *having a life* outside the workspace. As a result, approximately half of the PhD-students suffers from stress, and a whopping one out of three suffers from serious psychiatric disorders, most notably depression (Levecque *et al.*, 2017). The aim for my three-and-a-bit-more period as PhD-student in Ås was therefore not only to deliver the thesis that now lies in front of you, but also to put into practice a (Scandinavian?) way of life. Now, I do not want to sound like a hipster or guru, but I loosely define this as a way of life that finds inspiration, creativity, and energy from the natural world (and its people) around us, in whatever shape or form that may be. For me personally, this often involved cycling, keeping chickens, ducks and rabbits (thanks Johanna, for all the help and inspiration), hiking mountains, long skiing and awesome ice skating trips, and gardening. During my PhD was fortunate enough to join many amazing field trips, for example to Finse, Svalbard (twice!), and Peru.

That said, a PhD is not easy. The learning curve was steep, and I feel it definitely has not leveled out yet. To those who work outside science, it may be hard to imagine how incredibly critical scientists are towards each other's and their own work. Publishing a paper requires countless rounds of review and revisions, which is a process that can be as frustrating as it is inspiring. However, the product does improve with every round of revision, and I truly look forward to working further on the manuscripts included in this thesis.

I am grateful to all that have helped me get here, who supported me, and whom I could not have done without. First of all mam, thanks for inspiring me, your unconditional confidence and support, and teaching me to enjoy the smallest things in life like the first flower on a favorite Dahlia. Pap, thank you for always encouraging my creativity. Art, photography, drawing: they are not appreciated as much as they should be in modern science with all its coding and computer models. Yet without it, we would be unable to form and express our ideas.

My supervising team was composed of nothing but all-stars. Johan, Kari, and Tone, you were always ready for me and always made my work and troubles your priority. Johan, you are an awesome supervisor and I hope many future PhD-students will be lucky enough to work with you. Kari, nobody climbs mountains like you and, by the way, thanks for warning me for bad Finse-weather already during my job interview. Tone, thanks for many "hyggelig" chats, Christmas dinner, and for trusting me to teach in your courses even though my still crappy Norwegian must have been horrible for the students.

I enjoyed my time at (M)INA because of the amazing colleagues. You are way too many to thank all of you individually, but Kristel, Mari, Yngvild, Vilde, Nathan, Silke, Solrun, Lennart, Rannveig, Lisa, Monica, Ross, Markus, Pablo, Thomas, Fredrick, Erik, Miguel, Mahdieh, Yennie, Tone G., Annie, Paal, Ole Martin, Richard, Line, Anne, and all the others: thanks for a great time! A special shout-out goes to the funniest and best field assistant. Camilla, I have never met anyone who can keep an umbrella up in Finse as well as you (nor have I ever met anyone else who tried…). Linn, thanks for sharing so many hours together in "our" kitchen and living room in Finse, and afterwards. Anne-Sofie, Oda and Julia, thanks for sorting tiny crumbly lichens for a seemingly endless amount of time. I am also grateful to all I had the pleasure to meet during the inspiring

field courses and campaigns on Svalbard and in Peru. Vegard, Aina, when will we go camping and eat ham inside a glacier again?

I would also like to thank all the collaborators and co-authors in my project: Stef, David, Simone, Juha, Peter, Natalia, and Siri. To my master supervisors, Hans and Matty, you have been and always will be a source of inspiration; I am sure we will meet many times and work together in the future. And, I shouldn't forget: Kees, the best biology teacher around. You have inspired me and many others!

For this PhD I left my beloved Amsterdam. However, out of sight is not out of heart. To the friends and family (Jan, Els, Sterre & Vincent) still in the Netherlands: you are still important to me, even a thousand kilometers away. Danny, Richard, Bas, Brie, Dirkje, Ignaz, Aafke, Ruby, Mary, Myrthe, Maartje, studying with you was a blast. En tot slot, de Nieuwe en Oude Helden: Marnick, Judith, Josta, Jolijn, Sonja, Niels, and Frank, bedankt voor alle hilarische uurtjes. Deze winter gaan we schaatsen!

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List of papers

This thesis consists of the following four papers. Throughout the text, Roman numerals (I – IV) are used to refer to these 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, *submitted to Functional Ecology*

Paper II

Ruben E. Roos, Kristel van Zuijlen, Tone Birkemoe, Stef Bokhorst, Johan Asplund, Monocultures of mat-forming lichens support different abundances of associated micro-arthropods, *manuscript*

Paper III

Ruben E. Roos, Tone Birkemoe, Stef Bokhorst, David A. Wardle, Johan Asplund, Synergistic effects of lichen mixtures on associated arthropods, *manuscript*

Paper IV

Ruben E. Roos, Tone Birkemoe, Johan Asplund, Peter Ľuptáčik, Natália Raschmanová, Juha M. Alatalo, Siri Lie Olsen, Kari Klanderud, Recovery of soil micro-arthropod communities after cessation of experimental environmental change, *submitted to Ecosphere*

Summary (in English)

The vegetation of alpine ecosystems, i.e. those above the elevation of the tree line, consists not only of vascular plants, but also of non-vascular primary producers such as lichens and bryophytes. The use of functional traits (characteristics that determine a species' ecological role) allows us to understand how these ecosystems will respond to current and future environmental change. However, we know little about how non-vascular primary producer traits respond across environmental gradients, and whether their drivers differ from those of vascular plants. In addition, there is little knowledge about the associations of lichens and their traits with higher trophic levels such as micro-arthropods. Therefore, this thesis consists of four papers that collectively address several aspects of the ecology of non-vascular primary producers and micro-arthropods in alpine ecosystems.

In paper I, we studied the importance of intraspecific variation versus species turnover as drivers of community-level traits across elevation for three different primary producer groups: vascular plants, bryophytes, and lichens. We found that the importance of intraspecific variation differs between the groups, but also among traits. Intraspecific variation was most important as driver of nutrient traits for vascular plants and lichens.

In paper II and III, we explore the associations between mat-forming lichens and soil micro-arthropods. We found that mat-forming lichen species that differentially affect soil microclimate support different micro-arthropod abundances (paper II). For mat-forming lichens grown in mixture, we found that they often support higher abundances of micro-arthropods than expected

from the individual components of the mixture. The abundance of arthropods at higher trophic levels depended more on lichen water holding capacity and prey availability than lichen diversity or identity.

In paper IV, we assessed the recovery of soil micro-arthropods from experimental environmental change nine years after treatments were ceased. We found that Collembola and Mesostigmata recovered in terms of abundance, but that Collembola community compositions remained affected.

The findings of these studies stress the importance of intraspecific variation as driver of community-level traits in different primary producers, and provide a valuable first insight in the ecology and associations of very common organisms in alpine ecosystems: non-vascular primary producers and micro-arthropods.

Sammendrag (på Norsk)

Vegetasjonen i alpine økosystemer, det vil si over skoggrensen, består ikke bare av karplanter, men også av laver og moser. Bruken av funksjonelle trekk (kjennetegn som har betydning for arters opptreden) gir oss mulighet til å forstå hvordan økosystemer vil respondere på nåværende og kommende miljøendringer. Vi vet imidlertid lite om hvordan trekkene hos primærprodusenter uten ledningsvev (f.eks. laver og moser) responderer langs miljøgradienter, og hvordan dette skiller seg fra hvordan karplanter responderer. Dessuten er det liten kunnskap om hvordan laver og deres trekk samspiller med høyere trofiske nivåer som f.eks. mikroartropoder. Denne avhandlingen består av fire artikler som til sammen tar for seg flere aspekter av økologien til primærprodusenter uten ledningsvev og mikroartropoder i alpine økosystemer.

I artikkel I, studerte vi betydningen av innenartsvariasjon i forhold til forandring i artssammensetning for funksjonelle trekk på samfunnsnivå langs en høydegradient for tre grupper av primærprodusenter: karplanter, moser og laver.

I artikkel II og III, undersøkte vi samspill mellom mattedannende lav og mikroartropoder. Vi fant at ulike arter av mattedannende laver gir forskjellige mengder mikroartropoder (artikkel II). Vi fant også at laver som vokser sammen gir flere mikroartropoder enn ventet basert på mengden i hver art for seg. Abundansen av artropoder fra høyere trofiske nivåer var mer avhengige av lavenes vannlagringspotensiale og tilgjengeligheten av byttedyr enn på diversitet av laver eller type lav.

I artikkel IV, studerte vi hvordan samfunn av mikroartropoder restituerer seg etter at eksperimentelle manipuleringer av miljøet har stanset. I dette forsøket fant vi at abundansen av Collembola og Mesostigmata endret seg tilbake til det opprinnelige ni år etter manipuleringene stoppet, mens artsammensetningen av Collembola var uforandret.

Resultatene av disse studiene gir verdifull innsikt I økologien og samspillet mellom svært vanlige organismer i alpine økosystemer: moser, laver og mikroartropoder

Samenvatting (Nederlandstalig)

De vegetatie in alpiene ecosystemen, dat wil zeggen die ecosystemen die boven de boomgrens liggen, bestaat niet alleen uit vaatplanten, maar voor een groot deel ook uit mossen en kortmossen. Door soorten te omschrijven aan de hand van hun functionele eigenschappen, zogenaamde *functional triats*, is het mogelijk de functie van een soort in ecologische processen te bepalen, en verwachtingen te maken hoe die functie onder toekomstige omstandigheden zal veranderen. Echter, er is slechts weinig bekend over hoe de functional traits van vaatplanten, mossen, en korstmossen fundamenteel verschillen en veranderen over gradiënten in omgevingsfactoren. Bovendien weten we weinig over hoe de in alpiene gebieden zeer algemene korstmossen interacties aangaan met organismen op hogere trofische niveaus, zoals bijvoorbeeld microarthropoden. Dit proefschrift bevat daarom vier manuscripten, die elk een verschillend aspect van de functional traits van alpiene primaire producenten met en zonder vaatsystemen, en hun interacties met microarthropoden behandelen.

In manuscript I onderzochten we in welke mate de variatie binnen soorten (intraspecifiek) ten opzichte van variatie tussen soorten (interspecifiek) bijdraagt tot de algehele variatie in verschillende functional traits over een hoogtegradiënt, en hoe die bijdrage verschilt tussen vaatplanten, mossen, en korstmossen. Onze resultaten laten zien dat het belang van intraspecifieke variatie niet alleen verschilt tussen functional traits, maar ook dat er belangrijke verschillen in de bijdrage van intraspecifieke variatie zijn tussen vaatplanten, mossen, en korstmossen. Zo was intraspecifieke variatie het belangrijkst voor vaatplanten en korstmossen, en in het bijzonder voor functional traits die met nutrienten te maken hebben.

In manuscript II en III verkenden we de associaties tussen matvormende korstmossen en de microarthropoden voor wie zij een habitat vormen. We vonden dat de verschillende korstmossoorten verschillende hoeveelheden microarthropoden bevatten en dat dit te maken kan hebben met hun vermogen water vast te houden, en de manier waarop zij het microklimaat in de bodem beïnvloeden (manuscript II). Wanneer korstmossoorten gemixt voorkomen, ondersteunden zij vaak een hogere abundantie microarthropoden dan verwacht op basis van hun abundantie in de individuele korstmossen waar de mix uit bestond (manuscript III). Voor arthropoden van hogere trofische niveaus is abundantie meer afhankelijk van het vochthoudend vermogen van de korstmossen en de abundantie van prooidieren, dan van de precieze identiteit van de korstmossen.

In manuscript IV vroegen we in welke mate microarthropoden in staat zijn te herstellen na experimentele manipulatie van hun leefomgeving, zoals opwarming en het toevoegen van nutriënten. Negen jaar nadat de experimentele manipulaties beëindigd waren, vonden we dat de abundantie van Collembola en Mesostigmata hersteld was, maar dat de soortensamenstelling van Collembola nog niet was hersteld van de nutriënttoevoegingen.

De bevindingen in dit proefschrift onderschrijven het belang van intraspecifieke variatie voor funtional traits voor verschillende groepen primaire producenten, en zijn een eerste verkenning naar de associaties tussen matvormende korstmossen en microarthropoden in alpiene gebieden.

Synopsis

Introduction

Cool ecosystems

Alpine ecosystems, i.e. those above the elevation of the tree line (Nagy & Grabherr, 2009), are the ultimate playground for ecologists. Here, extreme temperatures, short growing seasons, low nutrient levels, high UV-radiation, and sometimes lack of moisture make organisms struggle for existence. In the alpine, differences in local topography can cause environmental conditions to vary across small scales, making the interactions between living organisms and their environment almost tangible (Figure 1). Yet, the species that call these unhospitable regions home are so well adapted that they would likely perform worse, or get outcompeted by stronger competitors, should they be moved to more favorable conditions (Körner, 2003). At the same time, "cool" ecosystems are among those most severely affected by anthropogenic environmental change. For example, the northern high latitudes warm at a rate more than double the global average (Cohen et al., 2014), a phenomenon known as Arctic amplification, and a similar process occurs at high elevation (Pepin et al., 2015; Wang, Fan & Wang, 2016). Although observed warming already affects alpine plant communities today (Steinbauer et al., 2018), we do not fully comprehend the complexity of their responses and their functioning may be altered by environmental change.

Figure 1. A view into Mälardalen, Svalbard, 78 °N. Organisms living in such ecosystems are adapted to challenging and variable conditions. The landscape topography is heterogeneous and provides strong gradients, for example in temperature, moisture, and snow cover. Photo: Ruben Erik Roos, July 2018.

Functional traits and intraspecific variation

In order for ecologists to understand how alpine communities are structured, how they vary across spatial and temporal scales, and how changes in the environment can affect their functioning, it is necessary to go beyond simple nomenclature approaches. In other words, it is more useful to describe a species or a community by the characteristics that determine how it functions ecologically (McGill *et al.*, 2006), than by species names alone. These *functional traits* are characteristics of a species that impact fitness indirectly via growth, reproduction and survival (Violle *et al.*, 2007). For example, plants can be placed along an "economic spectrum" ranging from slow to fast return on investments by a relatively small set of leaf functional traits, such as leaf area

per unit dry weight, and photosynthetic assimilation rates (Wright *et al.*, 2004). Although the idea of describing and classifying species into groups defined by their characteristics is not new (Raunkiaer, 1934), the use of functional traits has increased considerably in recent years, especially within plant ecology (Figure 2). Trait-based approaches are now used to improve our understanding of community assembly (McGill *et al.*, 2006; 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), and can aid biological conservation (Pollock, Thuiller & Jetz, 2017).

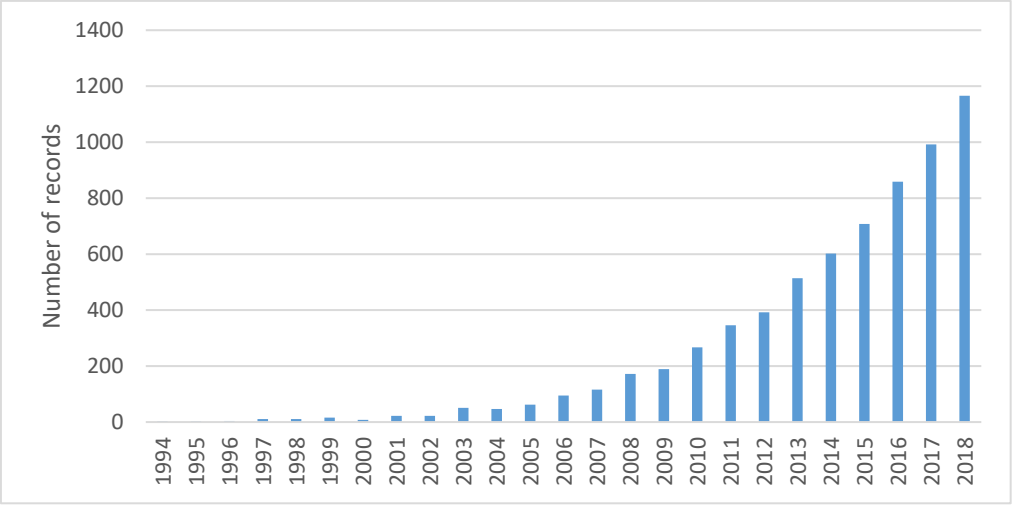


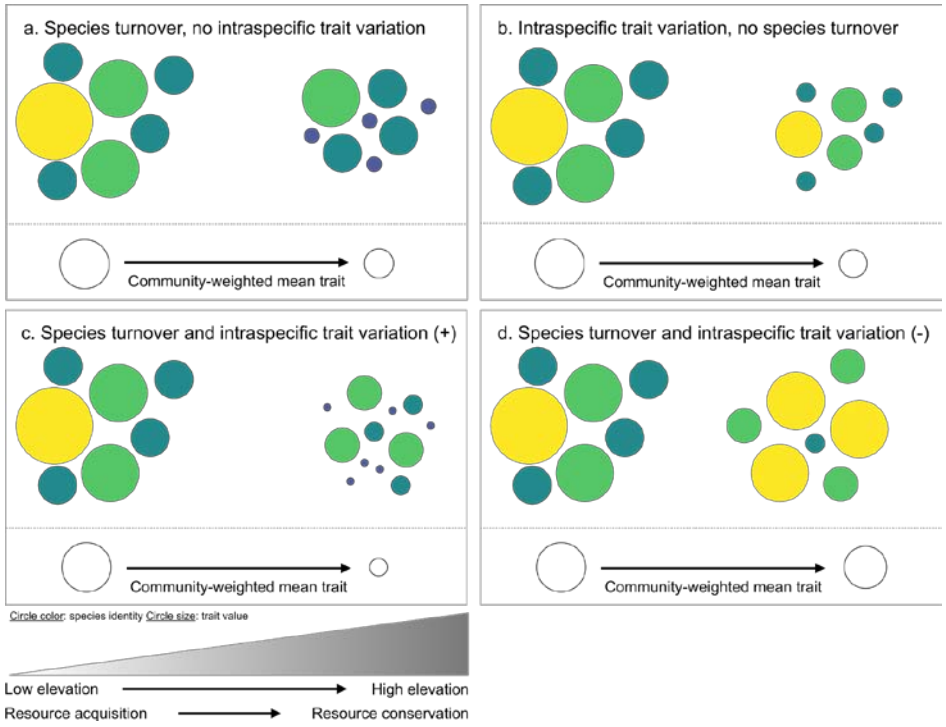
Figure 2. Number of records per year found for a topical search on "functional trait$" in Web of Science. The current year, 2019, was excluded.

The use of trait-based approaches has significantly advanced our ability to describe the functioning of ecosystems and communities (Funk *et al.*, 2017). Although many studies have successfully used mean trait values for each species, a considerable number of studies shows that traits do not only vary among species, but can also vary considerably within species (Siefert *et al.*, 2015; Funk *et al.*, 2017). This intraspecific variation is important for community assembly (Albert *et al.*, 2012; Violle *et al.*, 2012), and essential to the advance of trait-based ecology towards a predictive science (Cadotte *et al.*, 2015). Siefert *et al.*, 2015 found in a global meta-analysis on vascular plant traits that intraspecific variation explains a substantial 25 % of the variation within communities, and 32 % of variation among communities. This then raises questions about whether variation in community-level trait values along environmental 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 (Box 1).

Box 1. Species turnover versus intraspecific trait variation at the community-level

If we know the relative abundance and trait value of each species in an ecological community, we can calculate one trait value at the community level. Specifically, this *community-weighted* trait value is the sum of the relative trait values of all species, but the trait value of each species is weighted by its relative abundance within the community (Garnier *et al.*, 2004). If we then consider that community-level traits change across environmental gradients, we can deduce that such changes can be caused by an alteration in the composition or in the abundances of species in the community (species turnover), by variation in trait values within species themselves (intraspecific variation), or by a combination of both.

For example in the figure below, along an elevational gradient, community-level traits may change from those associated with resource acquisition towards those associated with resource conservation. In (a), the community-weighted trait value (open circle) changes due to changes in species composition (colors) while species' trait values remain the same (size of colored circles). In (b), the community-weighted trait value changes due to intraspecific changes in trait values (circle sizes), while species composition remains the same (circle colors). In (c), both species turnover and intraspecific variation operate simultaneously towards lower trait values (positive covariation), while in (d) both processes operate in opposite direction (negative covariation). Figure adapted from paper I.



Traits along environmental gradients

Environmental gradients can provide useful information on how the occurrence of plant species are filtered by environmental conditions (Cornwell & Ackerly, 2009; Sundqvist, Sanders & Wardle, 2013). In addition, nearly all

plant traits vary systematically along gradients in environmental conditions (Funk *et al.*, 2017), although a significant portion of trait variation occurs within populations as well (Wright *et al.*, 2004). As such, the variation in traits across gradients can be used to predict how communities may respond to future climatic change (McGill *et al.*, 2006; Suding *et al.*, 2008), while variation within communities (and species) may determine their resilience to change (Mori, Furukawa & Sasaki, 2013). Although gradient studies do have their disadvantages (e.g. covariation of other environmental factors than the particular gradient studied), they allow for generalizations across larger temporary and spatial scales than manipulative experiments (Sundqvist, Sanders & Wardle, 2013).

Non-vascular vegetation

Non-vascular primary producers such as lichens and bryophytes are abundant and important components of alpine ecosystems (Figure 3), especially under conditions where vascular plants fail to thrive (Longton, 1988; Longton, 1997; Asplund & Wardle, 2017). They lack the roots and vessels that vascular plants have to distribute nutrients and water, and thus rely directly on their environment for resources (Nash, 1996), although some can fix nitrogen through symbiotic associations with cyanobacteria (Rikkinen, 2017) and lichen species differ considerably in their capacity to hold water and remain photosynthetically active (Gauslaa, Solhaug & Longinotti, 2017; Phinney, Solhaug & Gauslaa, 2018).

The contributions of lichens and bryophytes to ecological functioning are many. For example, they 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). Yet, their functional traits are understudied relative to vascular plants, at least to some degree because of unfamiliarity with taxonomy and relevant traits (Martin & Mallik, 2017), although first attempts towards a clear framework of comparative trait-based ecology for non-vascular primary producers have been made (Cornelissen *et al.*, 2007).

Figure 3. Mat-forming lichens (mostly yellowish-white in color) dominate the landscape at 1100 m a.s.l. in Forollhogna National Park, Trøndelag, Norway. Photo: Ruben Erik Roos, August 2017

Non-vascular primary producers do not only differ from vascular plants in the particular traits that are relevant to their fitness (e.g. traits related to their hydration status; Cornelissen *et al.*, 2007), but recent studies suggest that the two groups also differ in how changes in community-level traits are driven across environmental gradients. For example, intraspecific variation was the main driver of changes in community-level trait values of epiphytic lichens

across a strong successional gradient (Asplund & Wardle, 2014), and phenotypic plasticity allowed lichen species to persist along gradients within forest canopies (Coyle, 2017). These findings suggests that intraspecific variation may be a more important driver of trait variation than species turnover for non-vascular primary producers than for vascular plants.

Lichen – micro-arthropod associations in alpine ecosystems

The traits of non-vascular primary producers do not only respond to the environment, but can also affect the environment (i.e. response and effect traits *sensu* Lavorel & Garnier, 2002) and subsequently biogeochemical and ecological processes such as permafrost thaw (Guglielmin, Evans & Cannone, 2008; Blok *et al.*, 2011; Turetsky *et al.*, 2012) and seedling recruitment (Nystuen *et al.*, 2019). In addition, we know for vascular plants that variation in traits (e.g. leaf palatability) and microhabitat has important consequences for the invertebrate communities of consumers they support (Wardhaugh, Stork & Edwards, 2014). In contrast, we know relatively little about how the traits of non-vascular primary producers affect their associated invertebrate communities, but Mitchell *et al.*, 2016 found that local scale factors such as habitat and food quality drive differences micro-arthropod communities in moss dominated heaths. In addition, Bokhorst *et al.*, 2015 found that lichen traits such as nutrient concentrations and thallus growth form differentially affected associated invertebrate communities.

In alpine ecosystems, soil micro-arthropods such as Collembola (springtails) and Oribatida (mites) are among the most common arthropods and can be present in densities of up to 100.000 individuals m^{-2} (Tolbert, Tolbert & Ambrose, 1977). They contribute to decomposition, nutrient cycling, and

formation of soil structure (Rusek, 1998; Kampichler & Bruckner, 2009). Despite the abundance of both soil micro-arthropods and lichens in alpine ecosystems, we know relatively little of how the two interact, and how lichen traits may drive micro-arthropod community assemblages.

Micro-arthropod responses to environmental change

Alpine ecosystems face environmental changes such as increased temperatures (Rizzi *et al.*, 2017), and higher nitrogen availability due to faster mineralization rates (Rustad *et al.*, 2001), increased atmospheric deposition (Hole & Engardt, 2008) and agricultural activity (Vitousek *et al.*, 1997). A large number of studies has addressed the effects of increased temperature and nutrients on alpine plants (e.g. the ITEX-project; Elmendorf *et al.*, 2012), but there are relatively few that study the effects on associated micro-arthropods. In fact, the responses of micro-arthropods to experimental warming are inconsistent (Nash, Griffin & Hoffmann, 2013), and may be species or trait dependent (Makkonen *et al.*, 2011). However, Hågvar & Klanderud, 2009 found strong responses of soil micro-arthropods to nutrient addition treatments with and without additional warming in an alpine *Dryas*-heath in Finse, Norway. In the same system, Olsen & Klanderud, 2014 found limited recovery of the vegetation five years after environmental treatments were stopped. Because micro-arthropods are often linked to vegetation (Coulson, Hodkinson & Webb, 2003), this suggests that environmental effects on soil micro-arthropod communities may be long lasting.

Research aim of thesis

This thesis deals with several aspects of trait-based ecology in alpine ecosystems (Figure 4). First, we studied the importance of species turnover and intraspecific variation as drivers of community-level traits across elevation for three different primary producer groups: vascular plants, bryophytes, and lichens (paper I). Then, two papers explore the associations between mat-forming lichens and soil micro-arthropods. In paper II, we studied whether lichen monocultures with different lichen traits and different effects on soil microclimate support different micro-arthropod communities. In paper III, we examined whether diverse lichen patches support more diverse and abundant arthropod communities. Last, we investigated to what extend soil micro-arthropods are able to recover from experimental environmental change (paper IV). The specific research questions addressed are:

1. Are changes in vascular plant, lichen, and bryophyte community-level traits across an elevational gradient driven by species turnover or intraspecific variation?
2. Do lichen monocultures that differentially affect soil microclimate support different micro-arthropod abundances?
3. Do more diverse lichen communities support more abundant and diverse arthropod communities?
4. Can micro-arthropod communities recover after cessation of experimental climate change?

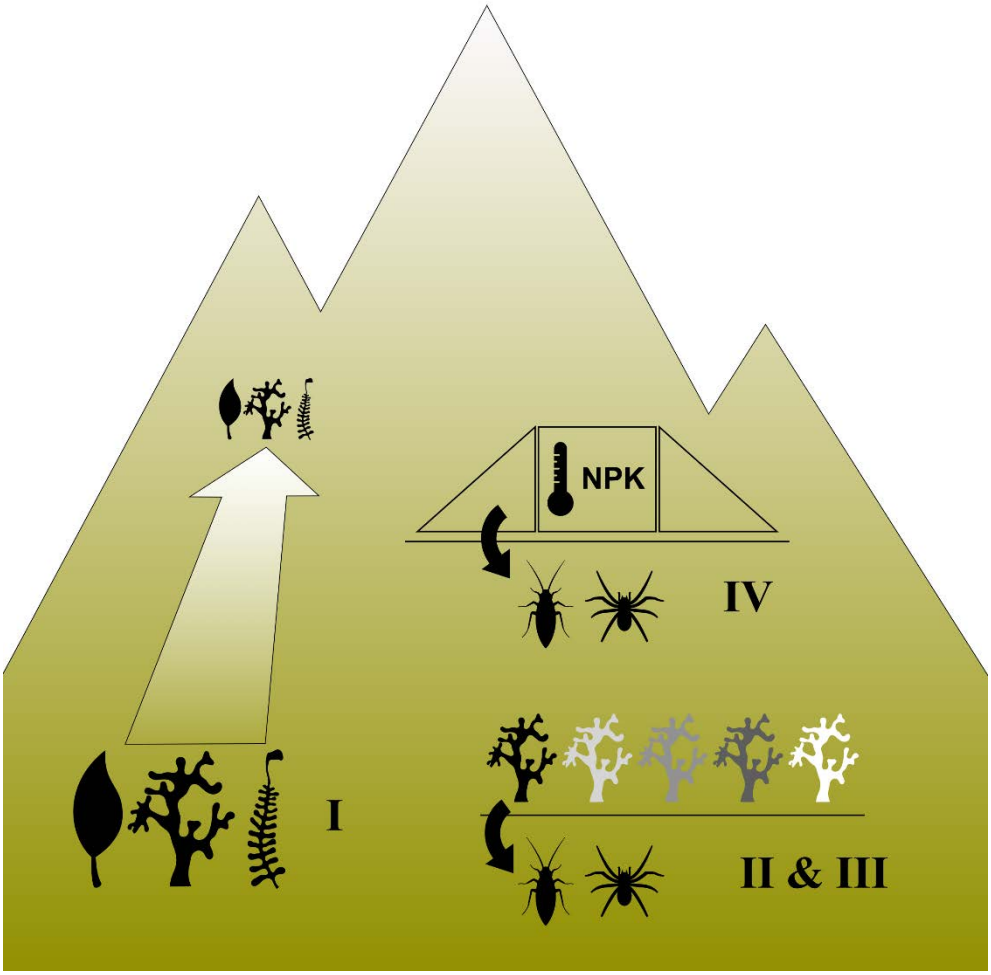


Figure 4. This thesis combines several aspects of trait-based ecology in alpine ecosystems. In paper I, we study the importance of intraspecific variation as driver of community-level traits for vascular plants, lichens, and bryophytes. In paper II and III, we study the associations between arthropods and lichens in monocultures and mixtures. In paper IV we assess to what extend arthropod communities are able to recover from experimental environmental change.

Methods

Study sites

The studies included for this thesis were performed at two different sites. Paper I, II, and IV were performed near Finse, southern Norway, and paper III at Kollåsen, southeastern Norway (Figure 5).

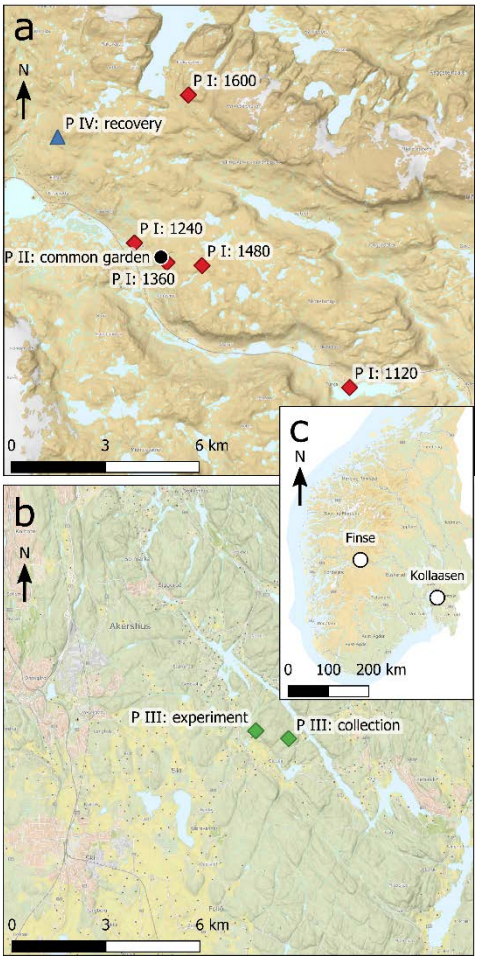


Figure 5. The field sites for paper I, II, and IV are located near (a) Finse, southern Norway, and (b) the site for paper III in Kollåsen, southeastern Norway.

Finse (paper I, II, IV)

Finse is located just north of mainland Norway's sixth largest glacier, Hardangerjøkulen, and south of Hallingskarvet national park at an elevation of 1222 m a.s.l. The Finse Alpine Research Center (Figure 6), run by the University of Oslo and the University of Bergen, hosts a meteorological station at 1210 m a.s.l. The average yearly temperature measured at this station is -2.1 °C with 1030 mm yearly precipitation (Aune, 1993; Førland, 1993). The weather conditions at Finse can be very challenging to ecologists (personal observation).

Kollåsen (paper III)

The fieldwork for paper III was performed in the Kollåsen nature reserve in Ski, southeastern Norway. This relatively young reserve includes one complete hill with many small crevices, and thus hosts a variety of habitats. Our sites however, were located near the hilltop at approximately 190 m a.s.l. in forest dominated by Scots pine pine forests (*Pinus sylvestris*). Here, dense lichen mats cover rocky outcrops, while vascular plants dominate depressions in the landscape. The nearest weather station is located in Ås at 92 m a.s.l., with an annual mean temperature of 5.3 °C and 785 mm precipitation (Aune, 1993; Førland, 1993).

Figure 6. The Finse Alpine Research Center at the foot of the Hardangerjøkul glacier, June 2018. Photo: Ruben Erik Roos

Experimental designs

Elevational gradient (paper I)

In paper I, we studied the importance of species turnover versus intraspecific variation as drivers of vascular plant, lichen, and bryophytes community-level trait variation across elevation. The elevational gradient consisted of five sites, spanning 480 m of elevation; at 1120, 1240, 1360, 1480, and 1600 m a.s.l. All sites were located on similar bedrock within the great Finse area (Figure 5), southwest exposed, and had similar inclination. The sites showed a distinct temperature gradient with elevation (Figure 7). At each site, five plots were selected on the condition that all primary producer groups of interest, i.e. vascular plants, lichens, and bryophytes were present. Topography in the alpine landscape in Finse varies across small scales (Opedal, Armbruster & Graae,

2015), for example between wind-exposed ridges and depressions where snow can accumulate. As such, snow is an important predictor of vegetation composition (Niittynen & Luoto, 2018), and communities in snow beds are distinctly different from those at more wind exposed (and thus free of snow) ridges. Therefore, all plots were located at dry ridges or mesic zonal sites *sensu* Walker, 2000.

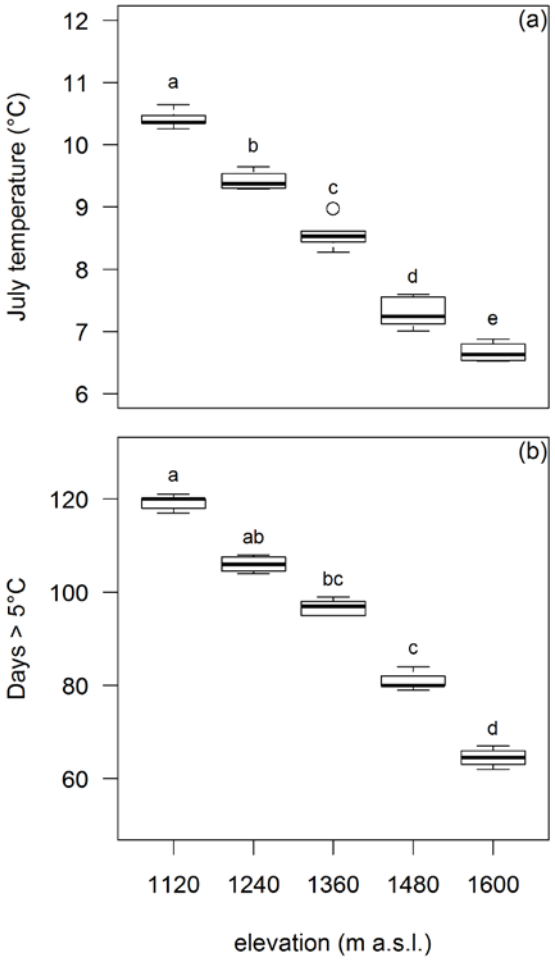


Figure 7. The mean July temperature (a) and the number of days with a daily average exceeding +5 °C (b) for each elevation (site). Figure adapted from paper I.

Lichen monoculture gardens and species mixtures (paper II, III)

In paper II and III, we explored the associations between lichens and soil micro-arthropods. In both papers, we took advantage of the ability of lichens to withstand abuse. When dry, lichens become photosynthetically inactive, and can withstand extreme low temperatures (Bjerke, 2009). These characteristics make lichens ideal organisms for experimental studies, as they can be harvested and stored dried or frozen. Lichens can then be moved and manipulated (e.g. Asplund *et al.*, 2015) without causing them any harm.

For paper II, we established six blocks with five different monoculture lichen garden plots each. We removed all vegetation from 50 × 50 cm plots and fenced them with 10 cm high plastic insect netting (mesh size 2.5 mm). Then, the plots were planted with *Alectoria ochroleuca* (Hoffm.), *Cetraria islandica* (L.) Ach., and *Flavocetraria nivalis* (L.). The fourth plot was planted with a mixture of *Cladonia rangiferina* (L.) and *Cladonia stygia* (Fr.) Ruoss, as these species grow intermixed and have similar growth forms and secondary chemistry (Ahti *et al.*, 2013). The fifth and final garden contained only bare soil and was added as a control. The lichens were transplanted from the immediate surroundings of the plots, cleaned from debris but not dried or defaunated. All of the lichens survived the first year after transplant, but one block was destroyed by domestic sheep. In each lichen garden, we placed a soil moisture and temperature logger (ECH$_2$O 5TM) three cm below the soil surface, connected to Em50 data loggers (Decagon Devices Inc., WA, USA). Measurements were taken and logged every 30 minutes over the course of 14 months. From these measurements, the number of diurnal freeze-thaw cycles during 15 October 2016 – 19 October 2017, was calculated as described by Van Zuijlen *et al.*, 2019.

For paper III, we collected lichens of four different species just outside the Kollåsen nature reserve at similar elevation and habitat (Figure 5). We consider the lichen mats in this open pine forests similar to those found above the tree line. The species used were *Cladonia arbuscula* (Wallr.) Flot., *Cladonia stellaris* (Opiz) Pouzar & Vezda, *Cladonia uncialis* (L.) Wigg., and *Cetraria islandica* (L.) Ach. We created ⌀ 15 cm lichen patches of different species mixtures; four mixtures consisted of a single species (monocultures), six mixtures had two species, four had three species and one mixture contained all lichen species – adding up to 15 different mixtures in total. Subsequently, the lichen patches were incubated within lichen mats in the field from 21 June to 4 October 2017 (Figure 8). With 10 blocks each containing 15 patches with a different lichen mixture, the experiment counted 150 lichen patches in total.

Figure 8. The mixed lichen patches were incubated in lichen mats at Kollåsen, southeastern Norway. A ring of nylon insect netting without bottom (mesh size 2.5 mm) held the patches together. Photo: Ruben Erik Roos, 2017

Experimental environmental change (paper IV)

In paper IV, we studied if micro-arthropod communities are able to recover from environmental change after conditions have returned to normal. We resampled soil micro-arthropods from an experiment that had previously received environmental treatments (Klanderud & Totland, 2005). The treatments were ceased nine years before the current study. The original study was established in 2000 and consisted of ten blocks of four plots, each of which received either warming, nutrient addition, combined warming and nutrient addition, or a control treatment. For the warming treatment, Open Top Chambers (OTCs) were set up to simulate climate warming (Henry & Molau, 1997). Although this treatment is referred to as "warming" in paper IV and previous publications, it is important to recognize that greenhouses like OTCs can influence multiple climatic variables other than temperature, such as for example humidity, wind speed, and snow accumulation (Kennedy, 1995). For the nutrient addition treatment, a slow-release granular NPK fertilizer (~10 g N, 2 g P, and 8 g K m^{-2} per growing season) was added.

After four years of treatment, significant shifts in community composition and diversity of the vegetation were detected (Klanderud & Totland, 2005) and micro-arthropods responded distinctly to nutrient addition with and without warming (Hågvar & Klanderud, 2009). In 2007, the treatments were ceased and herbivory exclosures were erected around half of the plots. Five years after cessation of the treatments, Olsen and Klanderud (2014) found incomplete recovery of the vegetation but that herbivory increased recovery rates compared to ungrazed plots. The herbivore exclosures were left up and running until the fieldwork for paper IV. We sampled for soil micro-arthropods approximately 20 cm from the original sampling locations, to avoid sampling from disturbed soil.

Vegetation recordings and harvesting (paper I)

For paper I, vegetation recordings were performed by estimating cover between 11 and 24 July, 2016 with a 1 × 1 m metal frame subdivided into four 50 × 50 cm quadrats. In addition to vascular plant, lichen, and bryophyte species cover, we registered the cover of litter, bare soil, biological crust, and rock. Then, between July 28 and August 18 2016, one quadrat per plot was destructively harvested and all aboveground vegetation was collected and subsequently sorted to species for functional trait measurements. For rare species, additional material was collected from the immediate surroundings of the plots. Even then, for some rare species it was not possible to collect ample material for, for example, chemical analysis. Analyses were therefore restricted to those species covering at least 80 % of the cover of the particular primary producer group. This "80 %-rule" is in line with other studies (Pakeman & Quested, 2007). Vascular plant samples were stored in moist, sealed plastic bags at 4 °C until trait measurements, while lichen and bryophyte samples were stored in paper bags and air dried at room temperature.

Functional trait selection and measurements (paper I)

We selected easy to measure (see Hodgson *et al.*, 1999) eco-physiological traits that exert a strong impact on ecosystem C and N cycling (Perez-Harguindeguy *et al.*, 2013), and that determine a species position within the fast-slow continuum of plant strategies (Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016). For vascular plants and lichens, we measured N and P concentrations and their ratio, and specific leaf area (SLA). In addition, we measured specific thallus area (STA, the lichen equivalent to SLA) for lichens, leaf dry matter content (LDMC) for vascular plants, and water holding capacity (WHC) for lichens and bryophytes. In addition, we measured tissue pH for all primary

producer groups as this is considered a proxy for decomposability and acidification potential (Cornelissen *et al.*, 2006). Trait measurements were performed in accordance to the protocols of Perez-Harguindeguy *et al.*, 2013, and any deviations are further addressed in paper I.

Micro-arthropod extraction and identification (paper II – IV)

The arthropods for paper II – IV were sampled from either lichen or soil with soil corers. After sampling, the cores were immediately stored in plastic bags and kept cool (approximately + 5 °C). Subsequently, the lichen or soil samples were placed in high-gradient extraction apparatuses where temperatures were gradually increased from 30 to 70 °C during the first five days of extractions, and remained at 70 °C until samples dried completely. The arthropods were extracted onto a saturated solution of NaCl, or water saturated with benzoic acid. The latter is recommended as hypertonic NaCl solutions may damage fragile Collembola. Arthropods for paper IV were identified by Dr. Peter Ľuptáčik (Oribatida) and Dr. Natália Raschmanová (Collembola), while arthropods (Collembola) for paper II and paper III were identified by Dr. Stef Bokhorst. Identifications of Oribatida followed Weigmann, 2006, and identifications of Collembola followed Fjellberg, 1998, Bretfeld, 1999, Potapov, 2001, Hopkin, 2007, and Dunger & Schlitt, 2011.

Statistical analyses (paper I – IV)

For paper I, we performed a two-dimensional Non-Metric Dimensional Scaling analysis (NMDS) to illustrate differences with elevation in vascular plant, lichen, and bryophyte communities using the R-package vegan (Oksanen *et al.*, 2015). In addition, we used permutational ANOVAs to test for the response of total trait variation to elevation. In case these were significant, we then used

permutational pairwise comparisons to check for differences between elevation levels. Further, we used the Sum of Squares decomposition method described by Lepš *et al.*, 2011 to quantify how much variability in traits was accounted for by species turnover or intraspecific variation.

In paper II, we tested how micro-arthropod abundances in soil and in lichen differed between lichen monocultures, and how abundance responded to lichen WHC and the number of freeze-thaw cycles, with linear mixed effect models using the lme4-package (Bates *et al.*, 2014) in R v. 3.5.2 (R Core Team, 2018). In paper III, we used similar models to test the difference between the expected and observed arthropod abundance in lichen mixtures, except that here the model intercepts were set to zero, as our interest was specifically to test whether the model estimates differed from zero. For effects on species richness, we used generalized mixed-effect models (Poisson family).

In paper IV, we used mixed effect models to examine the effect of environmental treatment, sampling year, and herbivory on Collembola and Acari abundance and richness. Further, we used two-dimensional NMDS to examine the recovery trajectory of Collembola and Oribatida communities. In addition, we used constrained multivariate ordination techniques (Redundancy Analysis, RDA) to test for environmental treatment effects on community composition.

Table 1. provides a summary of the experimental designs, data collected, and analyses performed for the papers included in this thesis.

Methodology summary

Table 1. Summary of the data collected, the experimental design, and statistical analyses for each of the papers presented in this thesis.

	Experimental design	Data collected	Data analysis
PAPER I	Elevational gradient in Finse. 25 plots across five sites: 1120, 1240, 1360, 1480, and 1600 m a.s.l.	Plant, lichen, and bryophyte cover Functional traits: N, P, N:P, SLA/STA, LDMC/ WHC, pH	GNMDS (Permutational) ANOVA Linear mixed-effect models Sum of squares decomposition *sensu* Lepš *et al.*, 2011
PAPER II	Four different species monoculture gardens, one control with bare soil near Finse at 1400 m a.s.l. 30 plots, 6 blocks	Collembola and Oribatida in lichen and soil, soil microclimate data, lichen WHC	Linear mixed-effect models
PAPER III	Patches of 15 different lichen mixtures (one to four species) incubated in natural lichen mats at Kollåsen 10 blocks with 15 mixtures each	Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Aranaea in lichen Lichen WHC	Linear mixed-effect models
PAPER IV	10 blocks with four plots with either control, warming, nutrient, or nutrient + warming treatment (ceased nine years before current sampling) at Sanddalsnuten, Finse, 1500 m a.s.l.	Collembola, Oribatida, and Mesostigmata in soil	Linear mixed-effect models GNMDS RDA

Main results

Species turnover versus intraspecific variation (paper I)

We found that species turnover is the most important driver of community-level trait variation across elevation for most of the vascular plant and bryophyte traits. However, some of the vascular plant and lichen traits, specifically the tissue nutrient traits (N, P, and N:P), were significantly affected by intraspecific variation. The non-chemical traits (SLA/STA, LDMC/WHC) and tissue pH were mainly driven by species turnover for all primary producer groups (Figure 10). In addition, we found that some traits change towards being more resource conservative with increasing elevation, while others showed opposite responses.

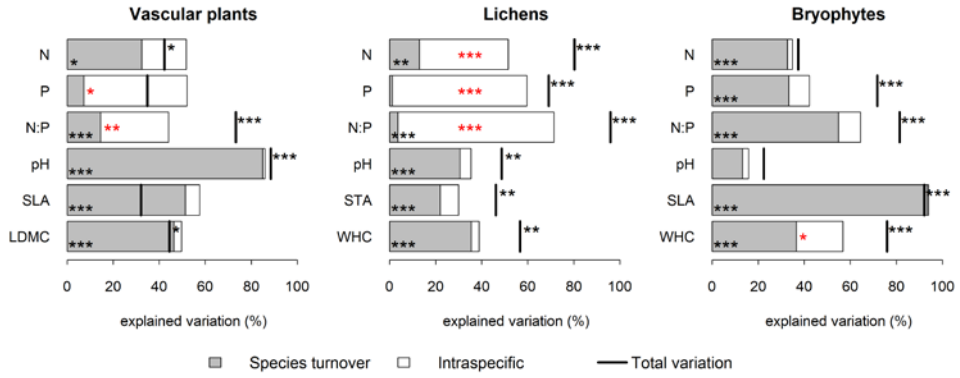


Figure 10. The contributions of species turnover and intraspecific variation to variation in tissue nitrogen (N) and phosphorous (P), N:P ratio, pH, specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC), and water holding capacity (WHC). Grey bars indicate the variation explained by species turnover (as percentage of total trait variation including variation not explained by elevation), white bars show the contribution of intraspecific variation. Black lines denote the sum of species turnover and intraspecific variability effects. In those cases where the total variation exceeds (falls below) the sum of species turnover and intraspecific variability effects, covariation is positive (negative). Significance responses to elevation are denoted with * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$). Figure adapted from paper I.

Micro-arthropods in lichen monocultures (paper II)

We found that monocultures of different mat-forming lichen species support different abundances of micro-arthropods. Specifically, Collembola were most abundant in *Cladonia rangiferina*/*stygia*, the lichen species with the highest water holding capacity and coolest but most stable soil climate (Figure 11). However, we found no significant effect on micro-arthropod abundance in the soil. Although Collembola abundance and the ratio between Collembola in the lichen versus soil showed negative trends with the number of freeze-thaw cycles, this was not statistically significant. In general, Oribatida were less responsive than Collembola.

Arthropods in lichen mixtures (paper III)

We found that in many cases, lichen mixtures contain higher abundances of arthropods than expected from the individual (monoculture) components of the mixture. In other words, mixing lichens often had non-additive, synergistic effects. However, not every specific mixture showed such synergistic effects, and synergistic effects were more common in micro-arthropods such as Collembola, Oribatida, and Mesostigmata than in arthropods at higher trophic levels such as Pseudoscorpiones and Araneae (Figure 12). In none of the mixtures did we find a negative effect on arthropod abundance. In addition, we did not find any effect of lichen mixture on Collembola species richness. Lichen mixture identity predicted abundance of Collembola and Oribatida well, but lichen water holding capacity and prey abundance become increasingly more important drivers of abundance for arthropods higher up the food chain, i.e. for Mesostigmata, Pseudoscorpiones, and Araneae.

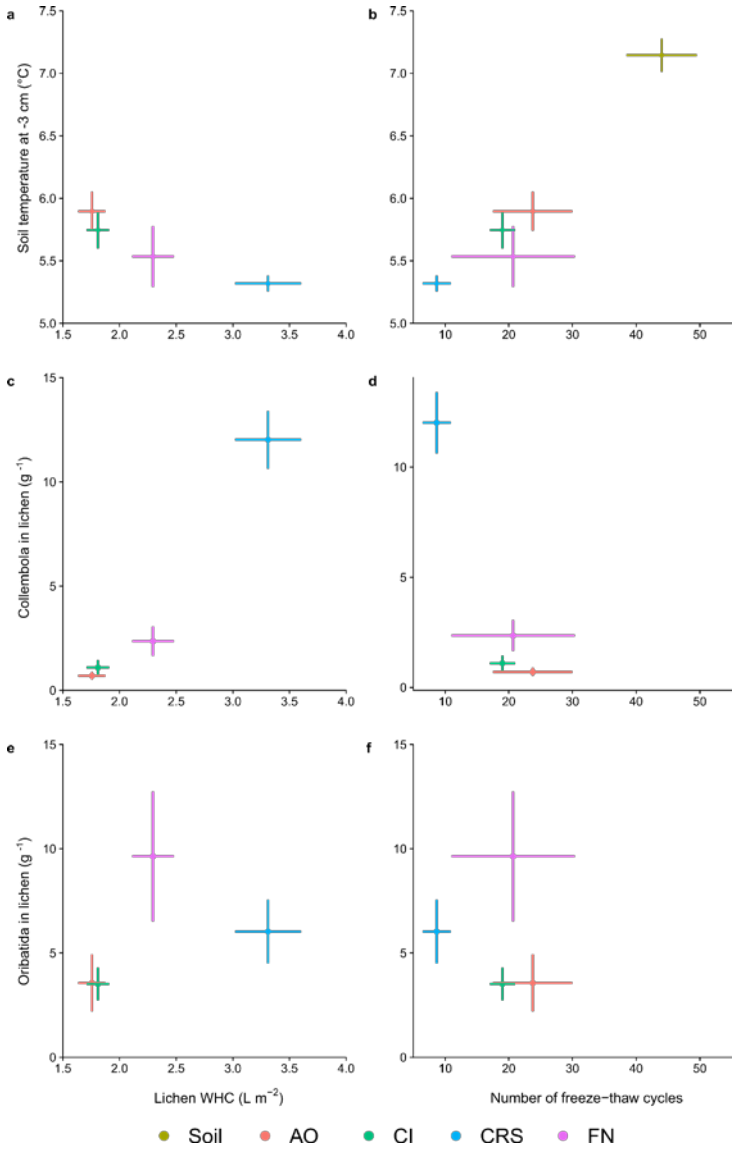


Figure 11. Mat-forming lichens differentially affect soil temperature during the growing season and the frequency of freeze-thaw cycles (panel a and b). Collembola abundance in lichen increased with water lichen water holding capacity (WHC) and was highest in *Cladonia rangiferina/stygia*, but abundance tends to decrease with increasing frequency of freeze-thaw cycles (panel b and c). Oribatida (panel e and f) show less clear trends with WHC and freeze-thaw cycles. Panel a and b are adapted from Van Zuijlen *et al.*, 2019, panel b – f from paper II.

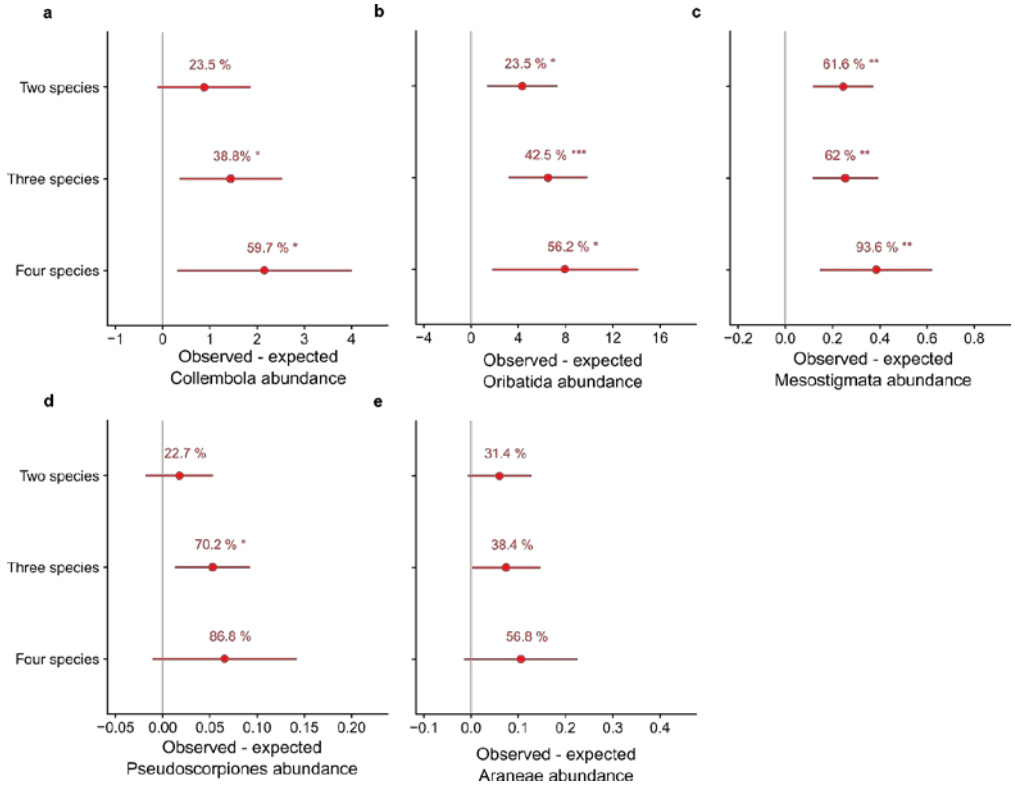


Figure 12. Model estimates +/- 95% CIs of the observed – expected abundances of Collembola (a), Oribatida (b), Mesostigmata (c), Pseudoscorpiones (d), and Araneae (e) per lichen dry weight for lichen patches with mixtures of two, three, or four species. Asterisks denote a significant difference of the estimate from zero ('*'p = 0.05, '**' p= 0.001, '***' p < 0.001). The percentages denote the model estimated observed – expected abundance per gram lichen dry weight, expressed as percentage of the observed abundance per gram lichen dry weight. Figure adapted from paper III.

Micro-arthropod recovery from environmental change (paper IV)

We found that soil micro-arthropods only partly recovered from their initial responses to environmental treatments nine years after those treatments were ceased. In terms of abundance, Collembola and Mesostigmata responded most strongly to the original nutrient addition treatments with and without warming, and their abundances had recovered during the recovery period (Figure 13). However, the Collembola community composition in nutrient addition with and without warming treatments differed from the controls after the recovery period. Oribatida were generally less responsive than Collembola, but their community structure was altered by nutrient addition after four years of treatment, and by warming nine years after cessation of the treatments (Table 2).

Table 2. *F* and *P*-values (significance levels: **P* < 0.05, ***P* < 0.01, ****P* < 0.001) of RDA analysis testing the effects of nutrient addition (N), warming (W), and warming combined with nutrient addition (NW) on species composition of the Collembola and mite communities at Finse, Norway, in 2004 (during treatments) and 2016 (nine years after treatments). Significant effects at *P*<0.05 are printed in bold. The table is adapted from paper IV, where effects of herbivory and interactions with treatments can be found.

	Collembola		**Oribatida**	
Treatment	**2004**	**2016**	**2004**	**2016**
N	**6.03 ****	**3.79 ***	**3.42***	1.39
NW	**10.66 *****	**4.70 ***	1.60	0.30
W	**3.96 ***	0.62	0.54	**4.40***

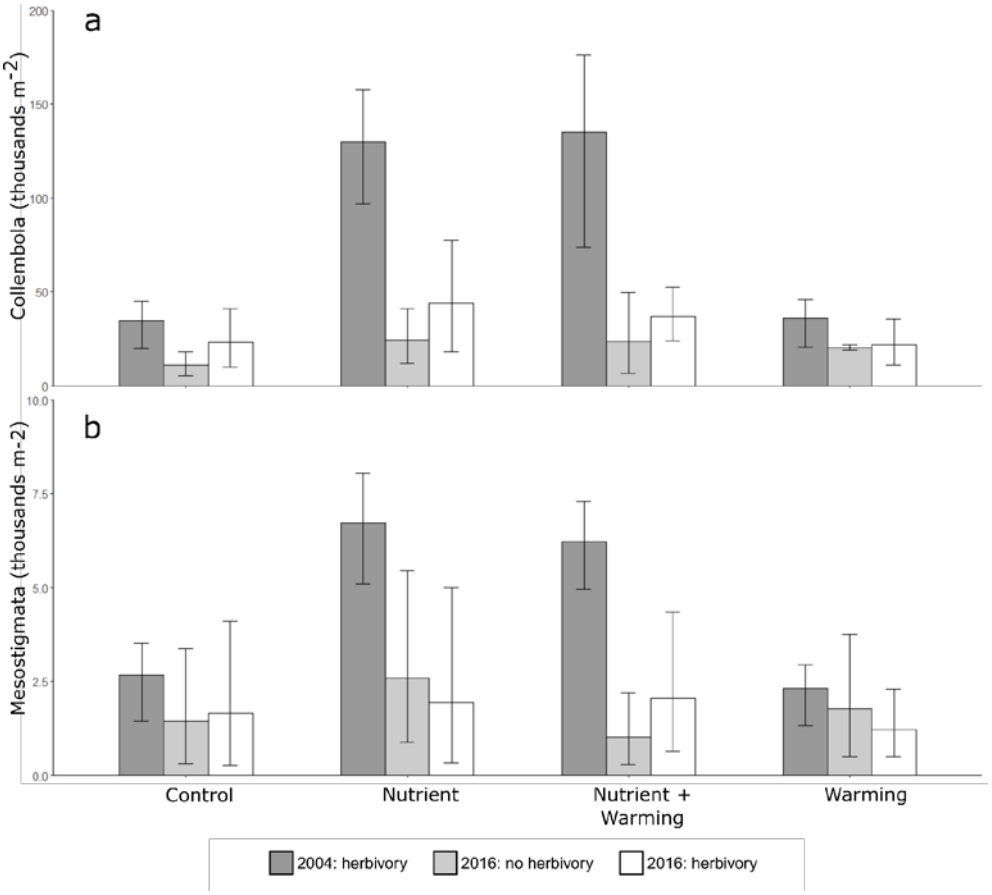


Figure 13. Mean abundance (in thousands m^{-2}) for all Collembola (a) and Mesostigmata (b) per treatment (control, nutrient addition, warming, and nutrient addition + warming) per sampled year. Data are shown on the non-transformed scale but error bars indicate exponentiated 95% confidence intervals calculated on natural log transformed data. Figure adapted from paper IV.

Discussion and further perspectives

The works collected in this thesis show that the importance of intraspecific variation as driver of community-level trait variability across elevation differs among primary producer groups and among traits (paper I); that mat-forming lichen traits and diversity affect soil arthropod communities (paper II and III); and that soil micro-arthropod communities may be slow to recover from environmental change (paper IV).

Traits and its variation for non-vascular primary producers

Although our study (paper I) does not allow for a generic statement such as "all traits of non-vascular primary producers are mainly driven by intraspecific variation across elevation", it stresses the importance of intraspecific variation as its contribution to trait variability differed greatly among primary producer groups and traits. Other studies on vascular plants support that the contribution of intraspecific variation differs among traits (Siefert *et al.*, 2015; Derroire *et al.*, 2018), but to our knowledge, this had not previously been compared among different primary producer groups simultaneously.

Given their abundance in alpine and other ecosystems (e.g. cloud forests; Nadkarni *et al.*, 2004), their association with many ecological and biogeochemical processes (Turetsky, 2003; Asplund & Wardle, 2017), and their susceptibility to environmental change (Elmendorf *et al.*, 2012), there is a real need for the further development of a comprehensive trait-framework that includes intraspecific variation for non-vascular primary producers (Cornelissen *et al.*, 2007; Martin & Mallik, 2017). Some attempts have now been made towards an economic spectrum *sensu* Wright *et al.*, 2004 for non-vascular

primary producers, but they are not yet conclusive. For example, Wang *et al.*, 2017 report similar trait relationships in bryophytes as found for vascular plant leaves. Contrastingly, Rice, Aclander & Hanson, 2008 report clear economic strategies for *Sphagnum* species, but also that these differ fundamentally from those in vascular plant leaves and canopies. As such, their findings stress the importance of including traits that describe bryophytes' water content or water holding capacity (for which paper I found a significant contribution of intraspecific variation), as these were the strongest predictors of photosynthetic activity. Similar mechanisms will most likely drive trait associations and economic strategies for lichens species, which differ greatly in their capacity to hold water (Gauslaa & Coxson, 2011; Phinney, Solhaug & Gauslaa, 2018).

Intraspecific trait variation and environmental change

If the climate in alpine ecosystem changes, primary producer communities may no longer be optimally adapted to their environment (Shaw & Etterson, 2012), and greater intraspecific variability in traits may enable species to adapt to a wider range of conditions (Sides *et al.*, 2014). Following this train of thought, lichen communities with high intraspecific variation would be better able to adapt to environmental change, which seemingly contradicts the general consensus that the diversity and abundance of non-vascular primary producers declines under climate change scenarios (Elmendorf *et al.*, 2012). However, the increase of competition from vascular plants is an important cause of such negative responses of non-vascular primary producers to climate change (Joly, Jandt & Klein, 2009), and lichen communities would thus only benefit from their intraspecific variation if conditions remain too harsh for vascular plants to establish and dominate. Further, in a transplant experiment, Henn *et al.*, 2018

show that the vascular plant traits with the largest amount of intraspecific variation were not necessarily those with the highest plasticity under new environmental conditions. Whether such responses in primary producer traits have a genetic basis, or depend on phenotypic plasticity (Franks, Weber & Aitken, 2014), and whether primary producer communities are able to keep up with the current rapid changes in environmental conditions (Shaw & Etterson, 2012) remains an active field of research.

Gradient studies and their limitations

Elevational gradients such as used in paper I are powerful ecological tools as they capture community and ecosystem dynamics across larger scales and/or longer timeframes than can generally be achieved by experimental studies (Sundqvist, Sanders & Wardle, 2013). However, it is important to recognize that environmental conditions across elevation may not only depend on the physical parameters tied to elevation (such as temperature focused on here), but also depend on other site-specific abiotic conditions (Körner, 2007) or biotic interactions. For example, precipitation may increase with elevation. In our study area near Finse, average annual precipitation (1986-2015) increases from 843 mm at 1120 m a.s.l. to 1026 mm at 1600 m a.s.l. (data adjusted from Lussana *et al.*, 2018). Also, in Finse, domestic sheep are the most common grazers at low elevation, while wild reindeer (*Rangifer tarandus tarandus*) graze at high elevation and farther from human presence. Because sheep and reindeer have different dietary preferences (Staaland *et al.*, 1995), they may differentially affect vegetation. Such covariables make it hard to identify specific mechanisms underlying observed changes in (plant) communities across elevation (Dunne *et al.*, 2004) and may limit the generality of gradient studies unless covariables are specifically addressed. However, it was beyond

the scope of paper I to disentangle all of such effects, and we thus considered elevation as a "complex" of environmental conditions. In future research, it could be fruitful to test the importance of intraspecific variation as driver of community-level traits among primary producer groups across other gradients, such as for instance nutrient availability.

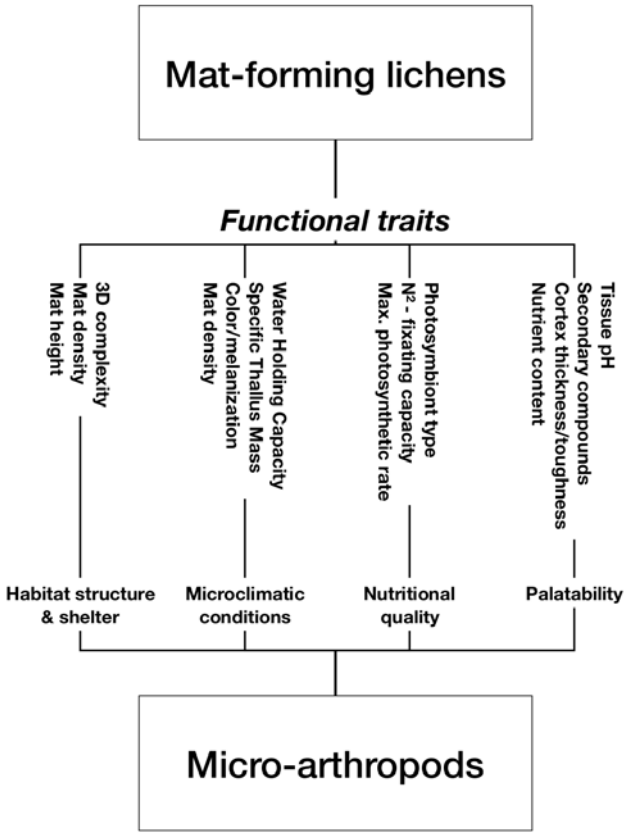
Lichen-arthropod associations

In paper II and III, we found that mat-forming lichen traits and diversity influence the abundance of associated (micro)-arthropods. These findings are supported by Bokhorst *et al.*, 2015, who reported that lichen growth form and traits affect invertebrate communities, and that different invertebrate groups respond contrastingly to lichen traits. Yet, we still know relatively little about how arthropods associate with mat-forming lichens, and whether these associations are based primarily on nutrition/diet, the provision of shelter, or microclimatic conditions (Box 2). Although some cases of direct feeding of micro-arthropods on lichens have been documented (Behan & Hill, 1978; Reutimann & Scheidegger, 1987; Meier, Scherrer & Honegger, 2002; Bokhorst *et al.*, 2007), the species found in paper II and III may not be among those feeding on lichen directly. We found (paper II) that arthropod abundance may be linked to the water holding capacity of lichen mats, and subsequently their microclimatic conditions. However, lichens are poikilohydric and lichen mats may dry out under unfavorable conditions, suggesting that micro-arthropods have to deal with substantial temporal variation in suitability of their habitat by either migration towards the soil or adaptation to drought. In paper II, III, and IV we found little responses of micro-arthropod species richness, most likely because many are generalist feeders (Hopkin, 1997; Scheu & Maraun, 2004) and show little habitat specialization (Wehner *et al.*, 2016). Because of the

abundance of both mat-forming lichens and micro-arthropods such as Collembola and Oribatida in alpine ecosystems, their interactions deserve more attention in future studies.

Box 2. Associations between mat-forming lichens and micro-arthropods

Mat-forming lichens support micro-arthropod communities, but their abundance varies considerably between lichen species (paper II). As illustrated by the conceptual framework below, mat-forming lichens may influence their associated micro-arthropod communities through several trait-based interactions. First, traits such as thallus 3D complexity and mat density may determine habitat structure and how much habitat is available to arthropods of particular body sizes (Shorrocks *et al.*, 1991) and the shelter the lichen provides against predators.



Second, lichen traits such as water holding capacity may influence microclimate in lichen mats and in the soil below (paper II) and thereby the (vertical) distribution of micro-arthropods. Third, traits that determine the nutritional quality of lichens may influence those micro-arthropods that directly feed on lichen thalli, and indirectly micro-arthropods that feed on lichen microbial communities or lichen litter. Finally, lichen traits such as secondary chemical composition can influence the palatability of lichens for micro-arthropods. Ultimately, such trait-based frameworks may allow predictions of micro-arthropod community composition and abundance in mat-forming lichens under environmental change. For example, in the elevational gradient in paper I, lichen water holding capacity (WHC) decreased with elevation, while lichen tissue N concentration increased. In theory, such changes in trait attributes would have a negative (WHC: less favorable microclimatic conditions) and positive (tissue N: increased nutritional quality and palatability) effects on micro-arthropod communities. Further studies are required to elucidate trait-based interactions between mat-forming lichens and associated micro-arthropods and to quantify the relative strength of such trait-based interactions.

Micro-arthropod recovery

In paper IV, we studied the recovery of soil micro-arthropod communities from experimental environmental change. The initial responses of Collembola and Oribatida to warming treatment alone were limited (Hågvar & Klanderud, 2009). Although there are few studies on micro-arthropod responses to environmental change, insignificant responses to warming have been reported before (Nielsen & Wall, 2013; Alatalo, Jägerbrand & Čuchta, 2015), suggesting that micro-arthropod communities are relatively resilient to warming. However, the Collembola communities responded strongly to nutrient addition, and their community structure did not completely recover nine years after cessation of the treatments. This pattern is on par with the vegetation in this system, which also showed slow recovery rates (Olsen & Klanderud, 2014). This suggests that micro-arthropods are either directly linked to vegetation

(Coulson, Hodkinson & Webb, 2003; Eisenhauer *et al.*, 2013) or that vegetation and micro-arthropods respond similarly to other factors influenced by nutrient addition, such as for instance the microbial community (Rinnan *et al.*, 2007; Nemergut *et al.*, 2008). In either case, it further emphasizes the need to study through what mechanisms soil micro-arthropods are associated to primary producers and their traits, and how these associations depend on environmental conditions.

Future directions

Based on the work in this thesis, I recommend several directions for further research.

First, to improve our understanding of alpine and Arctic ecosystem functioning, further studies on functional traits of non-vascular primary producers across different environmental gradients are essential. The scarcity of data on non-vascular primary producer traits (especially compared to vascular plants) has slowed the development of a comprehensive trait-framework. Traits related to water holding capacity should receive special attention, as these seem fundamental in determining photosynthetic activity and thus productivity.

Second, studies of how vascular and non-vascular primary producer community compositions and community-level traits respond to environmental changes should include some parameterization of intraspecific variation. Including measures of intraspecific variation would likely also improve model predictions of ecological functioning under future conditions.

Third, further studies should elucidate the drivers of lichen – arthropod associations so ubiquitous in alpine ecosystems, and how such associations depend on community-level trait variability of primary producers across environmental gradients.

Conferences and outreach contributions

Ruben E. Roos, Kristel van Zuijlen, Tone Birkemoe, Kari Klanderud, Simone I. Lang, Stef Bokhorst, David A. Wardle, Johan Asplund, *Functional traits across primary producer groups and their effects on alpine arthropod communities*, talk at the Ecological Climatology network seminar in Oslo, 2016

Ruben E. Roos, Kristel van Zuijlen, Tone Birkemoe, Kari Klanderud, Simone I. Lang, Stef Bokhorst, David A. Wardle, Johan Asplund, *Primary producer functional traits across an environmental gradient*, talk at the NØF conference in Oslo, 2017

Ruben E. Roos, Tone Birkemoe, Johan Asplund, Peter Ľuptáčik, Natália Raschmanová, Juha M. Alatalo, Siri Lie Olsen, and Kari Klanderud, *Recovery of soil micro-arthropods after cessation of experimental environmental change*, talk at the NØF conference in Tromsø, 2019

Ruben E. Roos, Kristel van Zuijlen, Tone Birkemoe, Stef Bokhorst, David Wardle, and Johan Asplund, *Lichen and arthropod studies in Finse*, talk at the Finse Alpine Research Seminar, 2018

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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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Pages: 39

Word count: 11229

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 phosphorous (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

70 the relative abundance of each species within that community to yield a 'community weighted' trait
71 value (Garnier *et al.*, 2004). To understand how these community-weighted trait values respond to
72 environmental change, gradients provide powerful tools (Malhi *et al.*, 2010). For example, lower
73 temperatures with increasing elevation (Körner, 2007), and subsequent declining availability of
74 nutrients (notably nitrogen (N) and phosphorus (P), see Huber *et al.*, 2007), lead to a shift in
75 community-weighted trait values from those associated with rapid resource acquisition to resource
76 conservation in vascular plants (Sundqvist, Sanders & Wardle, 2013; Read *et al.*, 2014). As such, plants
77 at higher elevations generally have leaves with lower tissue nutrient concentrations and low specific
78 leaf area (SLA), although there are many exceptions (Reich & Oleksyn, 2004; van de Weg *et al.*, 2009;
79 Sundqvist, Giesler & Wardle, 2011; Read *et al.*, 2014).
80
81 An increasing number of studies over the past decade have contributed to the realization that traits
82 can vary considerably within as well as between species (Kraft, Valencia & Ackerly, 2008; Messier,
83 McGill & Lechowicz, 2010; Violle *et al.*, 2012; Adler *et al.*, 2013; Enquist *et al.*, 2015; Kuebbing,
84 Maynard & Bradford, 2018). This poses questions about whether variation in community-level trait
85 values along gradients is driven primarily by species turnover (which incorporates both the
86 presence/absence of species in the community and the abundance structure of species that are
87 present) or intraspecific trait variation. In most studies on vascular plants, species turnover is the main
88 driver of community-weighted mean trait values, but intraspecific variation often plays an important
89 role (Albert *et al.*, 2010a; Albert *et al.*, 2010b; Messier, McGill & Lechowicz, 2010; Lepš *et al.*, 2011;
90 Kichenin *et al.*, 2013; Siefert *et al.*, 2015; Mayor *et al.*, 2017), depending on the trait considered
91 (Derroire *et al.*, 2018). In contrast to vascular plants, a limited number of studies suggest that
92 intraspecific variation in other primary producers such as lichens, may be more important than
93 changes in species composition. For example, Asplund & Wardle (2014) showed that intraspecific
94 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

144 Institute). The average summer (June-August) temperature in 2016 was 7.3°C and total summer
145 precipitation was 303.9 mm (Norwegian Meteorological Institute, 2016).
146
147 We selected five sites along an elevational gradient spanning 480 m, at approximately 1120, 1240,
148 1360, 1480 and 1600 m a.s.l., all on south-facing slopes on acidic granite and gneiss bedrock. The
149 lowest site is situated approximately 150 m above the nearest tree line (*Betula pubescens* ssp.
150 *czerepanovii*). Because most lichens respond negatively to snow cover (Bidussi, Solhaug & Gauslaa,
151 2016; Niittynen & Luoto, 2018) and are therefore absent from depressions in the landscape where
152 snow accumulates, we selected sites on exposed ridges that support communities with a mixed cover
153 of vascular plants, lichens and bryophytes. The vascular plant communities are relatively species poor,
154 with *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* as most common at the lowest
155 elevations, and *Carex bigelowii* and *Salix herbacea* at the higher elevations. Common lichen species
156 are *Cladonia arbuscula s. lat.*, *C. rangiferina* and *Flavocetraria nivalis*. The bryophyte species
157 *Pleurozium schreberi* and *Dicranum acutifolium* are common at lower elevations, while *Polytrichum*
158 *hyperboreum*, *P. alpinum* and *Racomitrium lanuginosum* are common at higher elevations. At each
159 site, we selected five 1 m^2 plots within a 100 m radius by randomly throwing an object, on the
160 condition that all three groups (i.e. vascular plants, lichens and bryophytes) were present. Within
161 elevations, the median distance between replicate plots was ca. 43 m. Because of the high small-scale
162 spatial heterogeneity (e.g. in topography, microclimate, soil fertility and biodiversity) in these
163 communities, which occurs over the meter scale (Björk *et al.*, 2007; Opedal, Armbruster & Graae,
164 2015), this distance is sufficient to ensure adequate independence among plots and is in line with
165 previous studies along elevational gradients in these types of environments (e.g. Veen *et al.*, 2017).
166

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

241 weighed (using a Sartorius ED224S scale). Finally, thalli were dried at room temperature and stored in
242 desiccators with silica gel 48 hours prior to weighing dry mass. We calculated STA as thallus area
243 divided by dry mass (expressed in in mm^2 mg^{-1}), and WHC was calculated as '(wet mass – dry mass) /
244 area' (expressed in mg mm^{-2}; water per thallus area).
245

246 ## Specific leaf area and water holding capacity in bryophytes

247 SLA of bryophytes was measured using an adapted version of the protocol of Lang *et al*. (in prep.)
248 which provides more accurate measurements than previous bryophyte SLA-protocols that measure
249 shoot area rather than leaf area (Bond-Lamberty & Gower, 2007). Leaves were picked carefully from
250 the bryophytes by using extremely fine anti-magnetic tweezers (Dumont Swissmade type 5, Electron
251 Microscopy Sciences, USA) and a dissecting microscope. For larger-leaved mosses (such as *Polytrichum*
252 spp. and *Dicranum* spp.), we selected 20 leaves from three shoots, while for small-leaved species (such
253 as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilidium ciliare*), we selected 45 leaves from
254 three shoots. We selected young but fully developed leaves from the upper one-third of the shoots.
255 For branched species, leaves were selected from both the main stem and side branches. These leaves
256 were then prepared on microscope slides and flattened with a cover glass. Pictures were taken using
257 a Leica DFC320 digital camera mounted on a Leica MS5 stereo microscope (Leica Microsystems GmbH,
258 Germany), using a 0.63x objective together with a 1.0x 0.63x camera objective and a light table.
259 Photoshop Elements 14 and ImageJ v1.51k were used to select and measure leaf area (mm^2). Since
260 bryophyte leaves were often curled and folded under the cover glass, the area of all double parts was
261 measured twice. To allow comparisons of bryophyte SLA with vascular plant SLA, we oven-dried the
262 leaves at 50°C for 24 hours and weighed using a Mettler Toledo UMX2 ultra-microbalance (1 µg
263 readability, Mettler Toledo, Switzerland). We calculated SLA as leaf area divided by dry mass
264 (expressed in mm^2 mg^{-1}).
265

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 phosphorous 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.

Acknowledgements

Anne-Sofie Bergene Strømme, Julia Cuypers, Oda Sofie Dahle, and Annie Aasen assisted in lab work, while Ellen Haakonsen Karr, Jon Hagelin, Stine Wiger Elvigen, and Camilla Lorange Lindberg assisted in the field. We thank Matthias Ahrens for help with bryophyte identification. We thank the Finse Alpine Research Center and Erika Leslie for hospitality. This work was supported by a grant from the Research Council of Norway (249902/F20) to JA.

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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Figures & Tables

Tables

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		**Phosphorous**		**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 legends

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), 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 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 $\alpha=0.05$, permutational pairwise comparisons). Note that the scales and units may differ among the three groups.

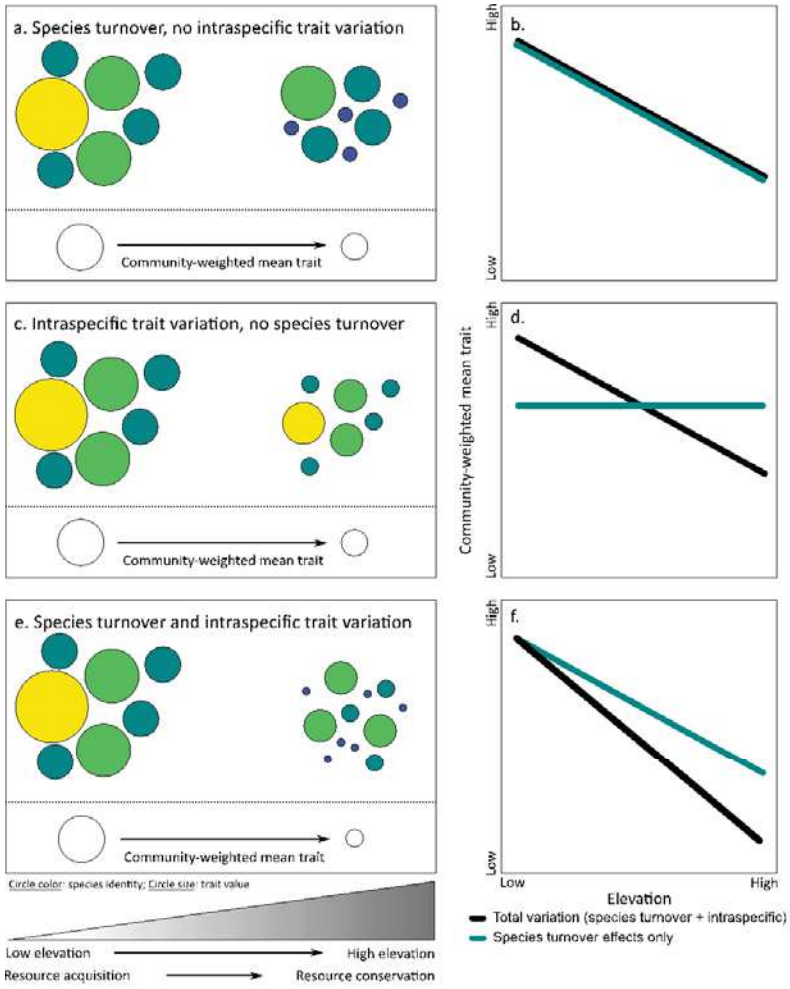
a. Species turnover, no intraspecific trait variation
Community-weighted mean trait
b.
High
Low
c. Intraspecific trait variation, no species turnover
Community-weighted mean trait
d.
High
Low
Community-weighted mean trait
e. Species turnover and intraspecific trait variation
Community-weighted mean trait
f.
High
Low
Low
High
Elevation
Total variation (species turnover + intraspecific)
Species turnover effects only
Circle color: species identity; Circle size: trait value
Low elevation
High elevation
Resource acquisition
Resource conservation

Figure 1.

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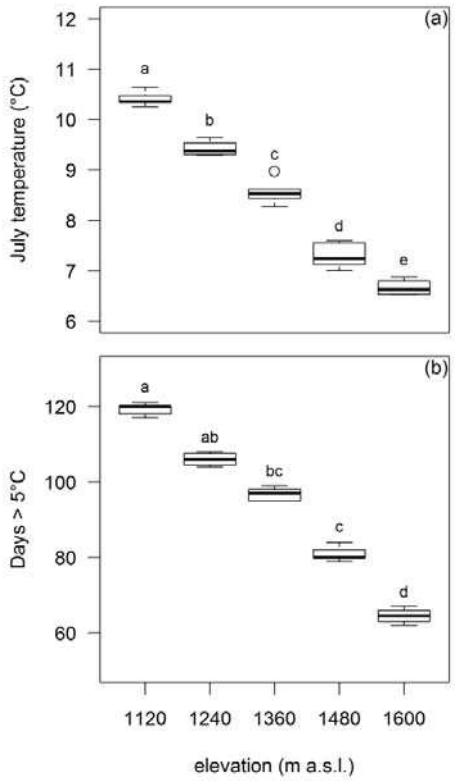

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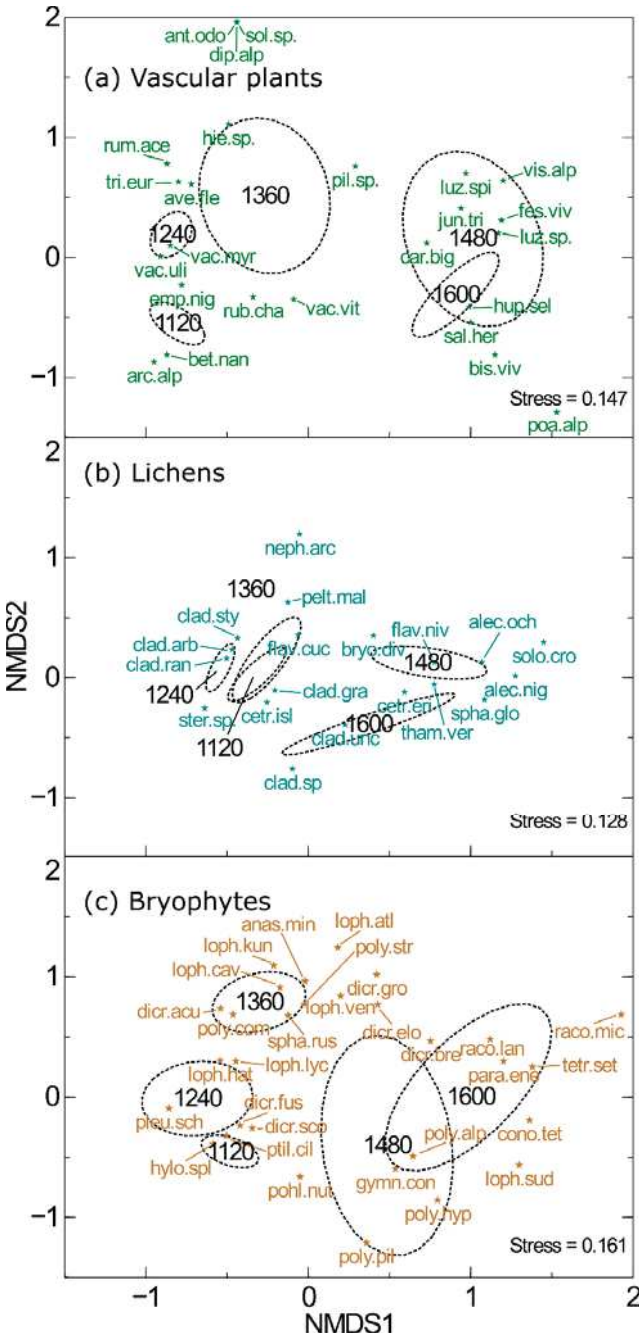

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925 Figure 3.

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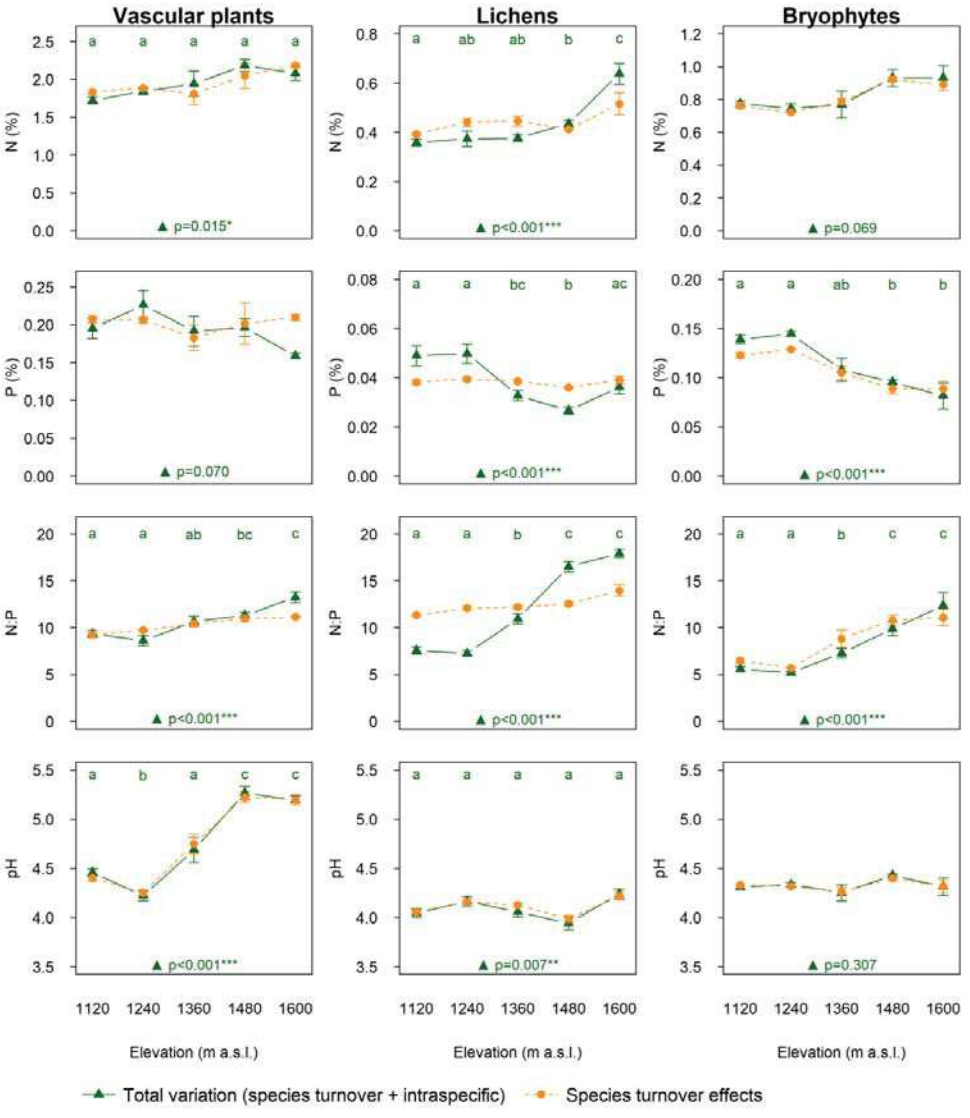

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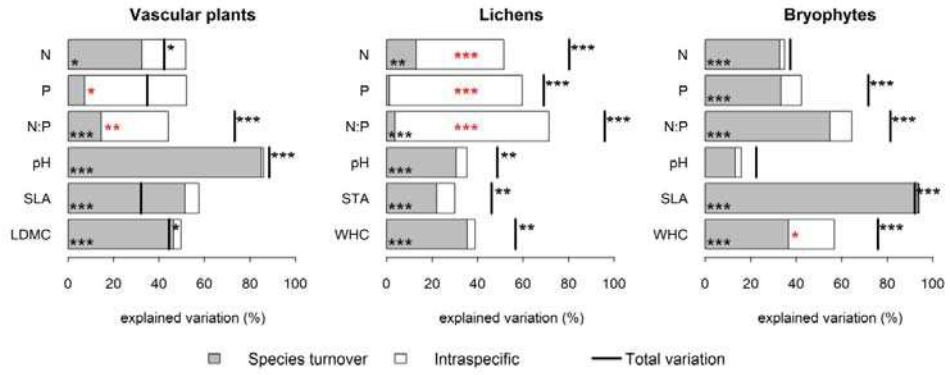
928 Figure 4.



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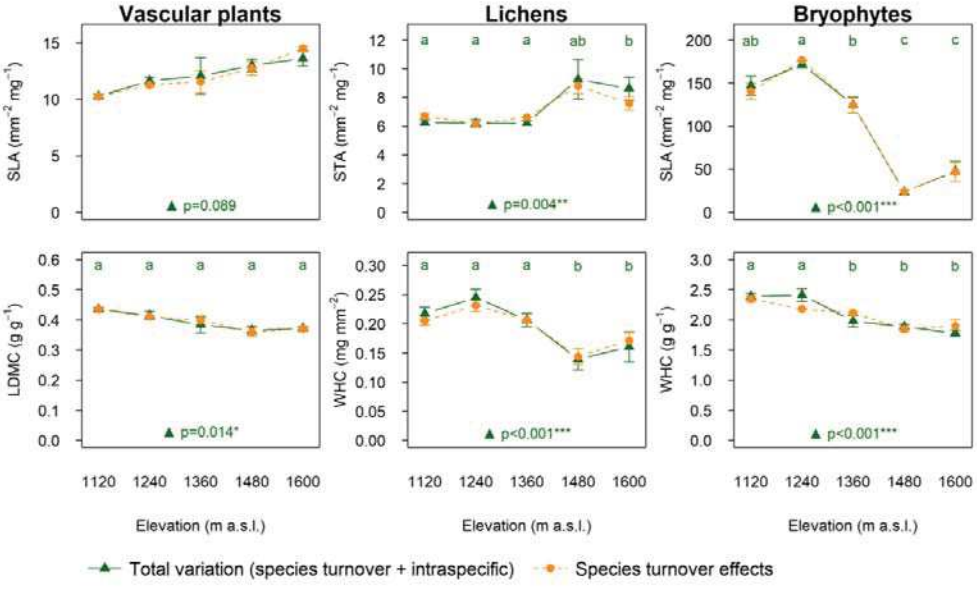
930 Figure 5.



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932 Figure 6.

Supplementary material

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	-	-
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

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
BRYO	spha.rus	*Sphagnum russowii*	-	-	1.3±1.3	-	-
BRYO	tetr.set	*Tetralophozia setifromis*	-	-	-	-	4.8±4.2

15

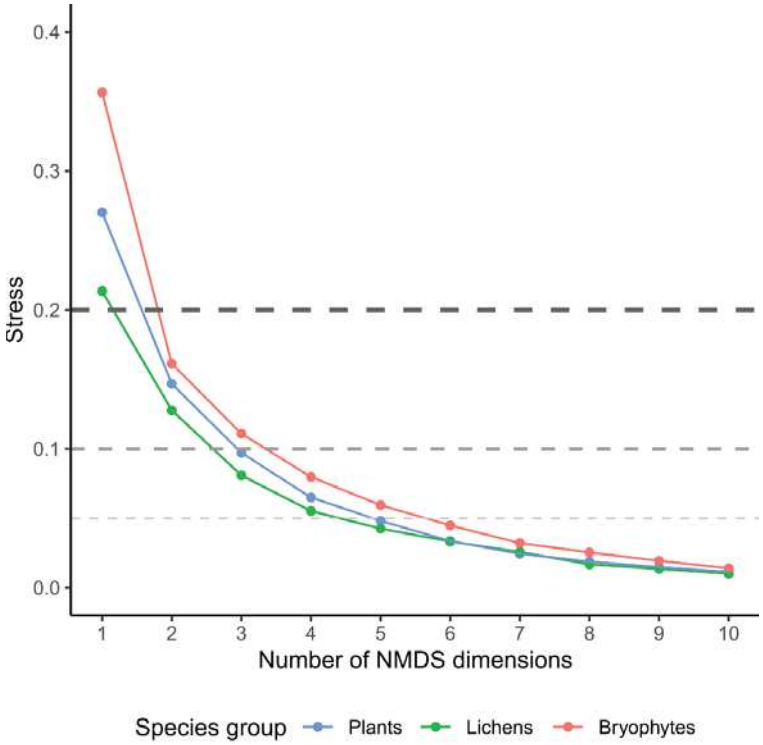

Figure S1. Stress or scree plot of stress versus dimension for Non-Metric Multidimentional Scaling (NMDS) analyses used to illustrate differences in community composition with elevation for vascular plants, lichens, and bryophytes. Increasing the number of dimensions lowers stress, indicating a better 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.

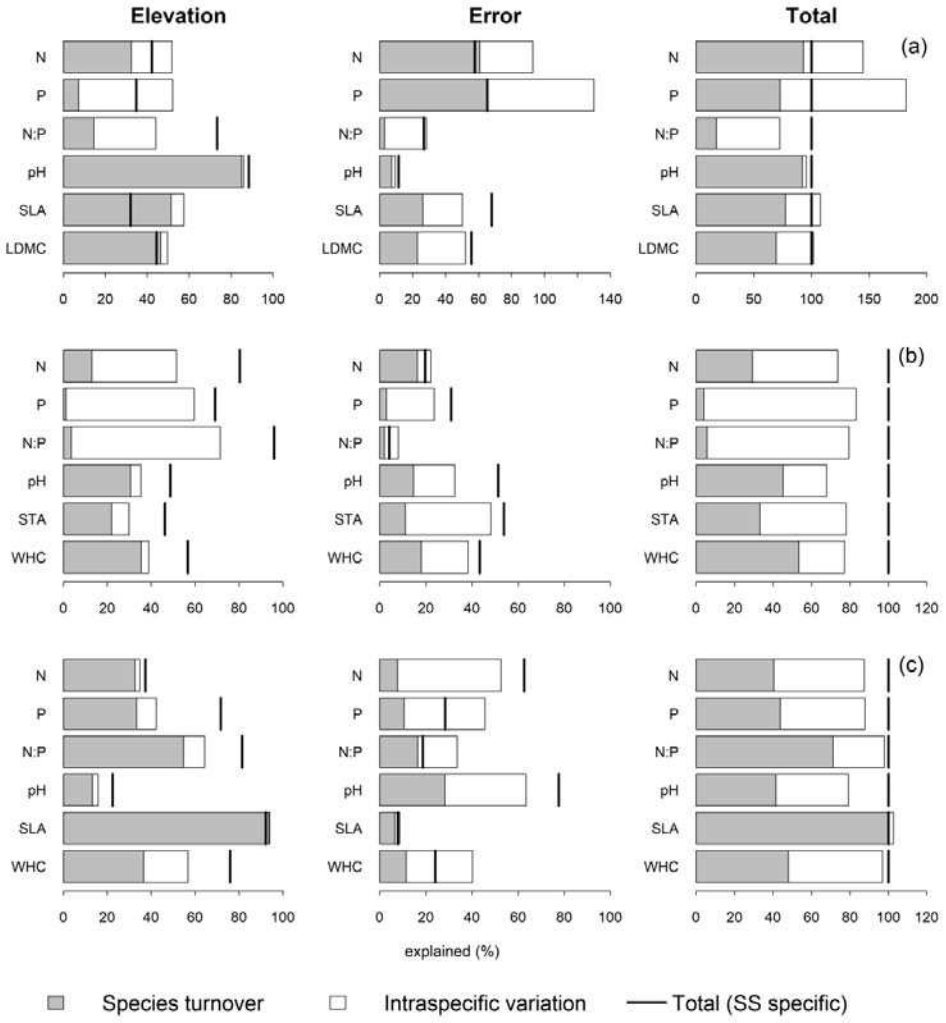

Figure S2. Decomposition of trait variability into: variation explained by elevation, error (residuals) and total (elevation + error) for vascular plant, lichen and bryophyte functional traits: nitrogen concentration (N), phosphorous concentration (P), N:P ratio, pH, specific leaf area (SLA), specific 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.

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Paper II

Monocultures of mat-forming lichens support different abundances of associated micro-arthropods

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https://orcid.org/0000-0002-1580-6424

Pages: 19

Word count: 3844

Abstract

Non-vascular vegetation such as mat-forming lichens can affect soil microclimatic conditions in alpine ecosystems, which in turn could influence the micro-arthropod communities they support. In this study, we explore how monocultures of different mat-forming lichens affect the abundance of lichen- and soil-dwelling Collembola and Oribatida at Finse, southern Norway. The monocultures consisted of *Alectoria ochroleuca*, *Cetraria islandica*, *Cladonia rangiferina*/*stygia*, and *Flavocetraria nivalis*, which differ in their water holding capacity (WHC) and differentially affect the number of freeze-cycles in the soil. We hypothesized that the lichen with the highest WHC and the lowest number of freeze-thaw cycles sustains the highest micro-arthropod abundances in lichen and soil, and that these favorable lichen species support relatively higher abundance in the lichen, than the associated soil. Our results suggest that mat-forming lichens can sustain high abundances of Collembola and Oribatida, but that their abundance may differ considerably among lichen species. *Cladonia rangiferina*/*stygia* supported the highest abundance of Collembola, and lichens with high WHC supported higher abundances in the lichen mat as well as a higher proportion of the species in the lichens versus the soil underneath. Oribatida were less responsive than the Collembola, but increased in the lichens mat relative to the soil with increasing WHC. We found no effect of freeze thaw cycles on micro-arthropod abundance.

Keywords: Collembola, Oribatida, lichen transplants, microclimate, soil arthropod communities

Introduction

Together with topography and soil characteristics, vegetation drives soil microclimatic parameters such as temperature and moisture in alpine ecosystems [1, 2]. For example, shrubs can shade the ground in summer and trap snow in winter, thus affecting both summer and winter microclimate [3]. However, these effects are not limited to vascular plants, and the often abundant non-vascular component of alpine vegetation such as mat-forming lichens and bryophytes can also impact soil microclimate. For example, bryophytes are known to insulate the soil and thereby influence permafrost thaw [4-6]. In addition, albedo, surface temperatures, and subsurface heat flux are differentially affected among lichen and bryophyte species in the field [7], which can subsequently affect ecological processes such as seedling recruitment [8]. Non-vascular vegetation is expect to decline in diversity and abundance under climate change scenarios [9].

Several traits may drive how mat-forming lichens can influence microclimate within the lichen, and in the soil directly below. First, the color of the lichen may determine how much shortwave radiation is reflected versus absorbed as heat. Many mat-forming lichens are yellowish white in color (caused by the secondary metabolite usnic acid [10]) and have a higher albedo, and thus cooler temperatures, than other darker-colored vegetation [11], but see [7]. Further, lichens are poikilohydric, which means they lack the specialized structures vascular plants have to maintain homeostasis, and their moisture content thus varies with environmental conditions. However, water holding capacity differs among lichen species, and lichens with thick thalli remain hydrated longer than those with thin, hair-like thalli [12, 13], although this may depend on the density at which lichens are clumped in mats [14]. As such, a high moisture content of the lichen mat is likely to dampen

temperature extremes due to high thermal conductivity and the high heat capacity of water [7, 15, 16].

The microclimate in mat-forming lichens may affect associated micro-arthropod communities in the lichen and in the soil below. In alpine and arctic ecosystems, Collembola and Oribatida are abundant and contribute to decomposition and nutrient cycling [17, 18], although their contribution may decrease with elevation [19]. While Collembola and Oribatida often show complex responses to environmental change, and their community composition often varies in space and with local vegetation [20], they tend to be negatively affected by drought [21-24]. Further, both Collembola and Oribatida are negatively affected by extreme climatic events such as mid-winter warmings and freeze-thaw cylces [25] and are relatively poorly adapted to cold summer temperatures [26]. These findings suggest that those mat-forming lichens that can provide a stable, moist environment may support the most abundant soil micro-arthropod communities.

In this study, we explore how monocultures of different mat-forming lichen species affect the abundance of Collembola and Oribatida. We use an experiment in Finse, southern Norway, where an earlier study [16] reported differential effects of mat-forming lichen species on soil microclimate. The lichen species differ in traits such as water holding capacity and mat density, and consequently how well they insulate the soil. We therefore hypothesize that the lichen species with the highest water holding capacity, and the lowest number of freeze-thaw cycles sustains the highest micro-arthropod abundance in the lichen itself and the associated soil. In addition, we expect that the relative number of micro-arthropods choosing lichens over soil will be highest in the favorable lichens.

Results

The monoculture gardens with different mat-forming lichen species sustained different levels of Collembola within the lichen but not in the soil below (Table 1 and Figure 1). As such, *Cladonia rangiferina/stygia* supported more Collembola than the other three lichen species, which had similar abundances (Table S1). Soil underneath the least favorable lichen species supported similar abundances of Collembola and Oribatida as bare soil plots. In addition, the abundance of Collembola in lichen increased with lichen water holding capacity (WHC) as did the ratio between Collembola abundance in lichen versus soil. Although Collembola abundances and ratios showed negative trends with the number of freeze-thaw cycles, these were not significant in our models (Figure 1 and Table 1). For Oribatida on the other hand, we found no significant differences in abundance in lichen, the soil below, or the ratio of mites in lichen versus soil between the different lichen monocultures. However, Oribatida in soil tended to be less abundant in *Flavocetraria nivalis* and *Cladonia rangiferina/stygia* than other lichen species (Figure 2). In contrast to Collembola, Oribatida abundance in lichen and soil showed no significant increase with WHC. However, the ratio of Oribatida in lichen versus soil was highest in lichens with high WHC. Further, Oribatida abundance did not respond to the number of freeze-thaw cycles (Table 1). The complete results of significant models are given in Table S2 for Collembola and Table S3 for Oribatida.

Discussion

Our results show that mat-forming lichens in alpine ecosystems can sustain high abundances of micro-arthropods, but that their abundance differs considerably among common lichen species. Soil underneath unfavorable lichens supports similar micro-arthropod abundance as bare soil. In line with our hypothesis, micro-arthropod abundance tends to be highest in those lichen species that hold a large amount of water and provide a stable environment with few temperature extremes, although Oribatida were less responsive than Collembola. Several alternative lichen traits not considered in this study may help explain the observed patterns. For example, lichen secondary compounds are known to repel herbivores, including arthropods [27, 28], possibly reducing food availability to fungal grazing Collembola and Oribatida. Further, lichen physiological traits and growth forms can impact invertebrate communities in epiphytic lichens [29]. As such, the lichen that supported the highest abundances in our study, *Cladonia rangiferina*/*stygia*, was also the most structurally complex lichen and may thus provide more space per dry mass for arthropods than the other lichens [30].

Our results show that mat-forming lichen species differ in the abundance of micro-arthropods they support, which suggests that the species composition of lichen mats can determine micro-arthropod abundance over the large areas they often cover in cold ecosystems. Although naturally occurring lichen mats can consist of monocultures like those created in our study, they often consist of mixtures of several species, possibly in combination with bryophytes and vascular plants. Such mixtures may provide a more heterogeneous habitat, and potentially support higher micro-arthropod abundances or diversity [31]. For example, Saitoh et al. 2014 [32] show that mixed substrates can affect micro-arthropod communities

indirectly by trophic effects, such as increased food availability or changes in predation pressure.

To conclude, environmental changes may alter the area lichen mats cover, or their species composition. As such, lichens are sensitive to increased competition from vascular plants [9], increases in snow cover [33], and trampling and grazing by reindeer [34]. Should these factors influence the abundance and composition of mat-forming lichen species, they can potentially also influence the micro-arthropod communities that lichen mats support, which could further translate into alterations in soil structure, nutrient cycling, and decomposition.

Figures

Figure 1

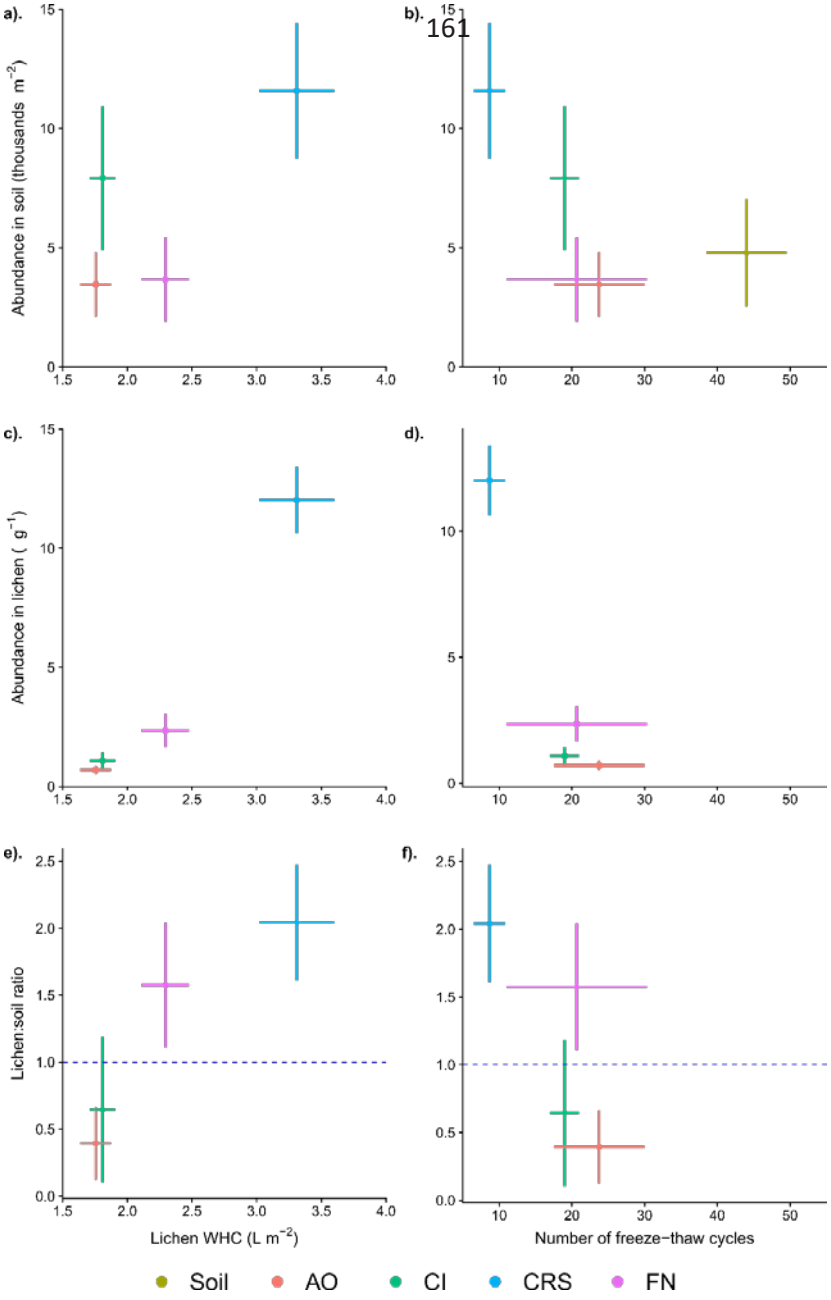
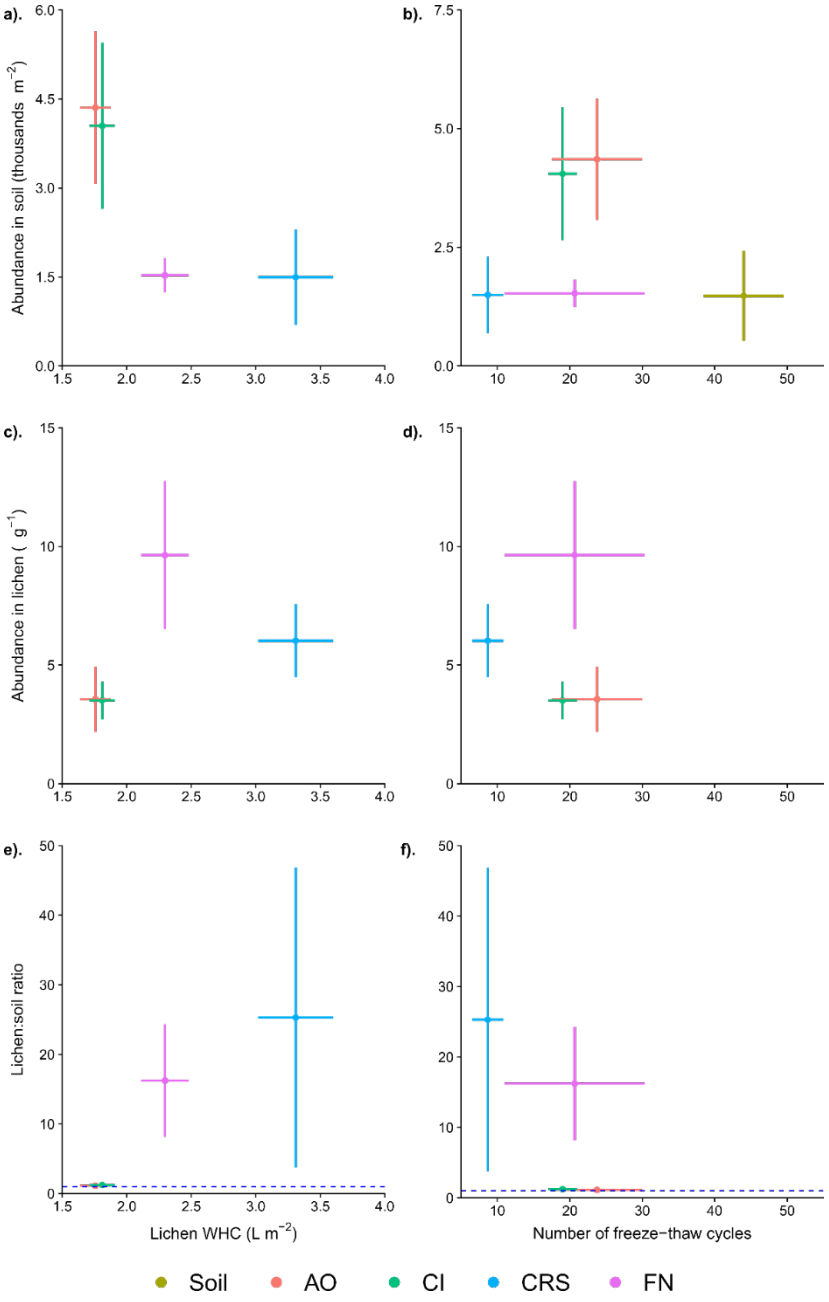


Figure 2


a).
b).
c).
d).
e).
f).
Abundance in soil (thousands m^{-2})
Abundance in lichen (g^{-1})
Lichen:soil ratio
Lichen WHC (L m^{-2})
Number of freeze−thaw cycles
Soil
AO
CI
CRS
FN

Methods

Study site and lichen garden establishment

This study was performed at an exposed alpine ridge at approximately 1400 m a.s.l. near Finse, southern Norway (60°35′ N, 7°35′ E) on metadacite bedrock. The site's vegetation mainly consists of mat-forming lichens such as *Alectoria ochroleuca* (Hoffm.) Massal., *Cetraria islandica* (L.) Ach., *Cladonia rangiferina* (L.) F. H. Wigg., and *Flavocetraria nivalis* (L.) Kärnefelt & Thell (nomenclature follows [35]). On 30 August, 2016, six blocks were established that each contained four 50 × 50 cm lichen "gardens" planted with the following monocultures: *A. ochroleuca*, *C. islandica, a*nd *F. nivalis.* Because *Cladonia rangiferina* and *Cladonia stygia* (Fr.) Ruoss grow intermixed, and have similar growth forms and secondary chemistry [35], they were combined into the fourth monoculture. As a reference, we also added a "garden" with 50 × 50 cm of bare soil in each block. To establish the garden plots, first all vegetation was removed, and then individual lichen thalli were transplanted into the plots from the immediate surroundings (c. 30 m radius). The plots were fenced with 10 cm high plastic insect netting (mesh size 2.5 mm) to keep the mats intact during high wind events. While transplanting, the lichens were cleaned from debris, but not defaunated. Because mat-forming lichens are not rooted in soil or otherwise attached to substratum, all lichens survived transplantation, except in one block that was destroyed by free-ranging sheep. This block was excluded from further analysis.

Micro-climatic variables and lichen traits

In each lichen garden, a soil moisture and temperature logger (ECH_2O 5TM) was placed 3 cm below the soil surface, and connected to Em50 data loggers (Decagon

189 Devices Inc., WA, USA). Measurements were taken and logged every 30 minutes
190 over the course of 14 months. From these measurements, the number of diurnal
191 freeze-thaw cycles during 15 October 2016 – 19 October 2017, was calculated as
192 described by Van Zuijlen et al. [16]. Further, for each lichen species, water holding
193 capacity (WHC) was calculated on a ⌀ 10 cm core from the particular lichen garden.
194 First, the lichens were air-dried and weighed, and subsequently hydrated by
195 incubating them in a sealed container lined with moistened paper for 30 minutes.
196 The lichens were then blotted dry and weighed again. WHC was expressed as water
197 content per lichen area, in L m^{-2} following Gauslaa [12].
198

199 ## Micro-arthropod extractions and identifications

200 After a period of 357 days (22 August, 2017), micro-arthropod samples were taken
201 from each lichen garden plot. A ⌀ 10 cm plastic ring with a metal serrated edge was
202 used to cut a core from the lichen mats, and, separately, the soil directly
203 underneath. The depth of the soil varied, but was never deeper than 5 cm. From
204 bare soil plots, only the soil was sampled. All samples were wrapped in plastic to
205 avoid desiccation, and transported to the lab in Ås, southeastern Norway where
206 extractions started no later than 24 hours after sampling. The cores were placed in
207 extraction apparatuses modified after Macfadyen [36] and as used by Hågvar and
208 Klanderud [37]. The temperature in the extractors was gradually increased from 30
209 °C to 65 °C over the course of four days and samples remained in the extractor at
210 65 °C until completely dry. Arthropods were extracted into a saturated solution of
211 NaCl in water. Collembola were identified following Hopkin [38] and Fjellberg [39],
212 Fjellberg [40]. Oribatida included the cohort Astigmatina. From this, we calculated
213 the abundance of Collembola and Oribatida in soil (thousands m^{-2}) and in lichen

(thousands m^{-2} and g^{-1} lichen dry weight). In addition, we calculated the ratio of Collembola and Oribatida abundance in lichen versus soil.

Statistical analyses

The size of the dataset in this study did not support complex modelling ambitions such as model selection procedures on models with all available climatic variables available from Van Zuijlen et al. 2019 [16], or random effect structures with random slopes. As such, to test how micro-arthropod abundance in soil, lichen, and their ratio responded to lichen treatment, lichen WHC, and the number of freeze-thaw cycles, we ran separate linear mixed effect models with the lme4-package [41] in R v. 3.5.2 (R Core Team, 2018) for each explanatory variable. In these models, experimental block was included as a random effect (random intercepts only). Data were log or square root transformed to satisfy assumptions of homogeneity of variance and heteroscedasticity of the residuals (see Table 1.). For each model, we tested the significance of the fixed effect by performing an F-test using Kenward-Roger approximation on the full model against an intercept-only model with the pbkrTest package [42]. In case the full model performed better than the null model, we estimated marginal means for the lichen treatments using the emmeans-package [43]. For some models, singular fits were triggered, and the random effect variance was estimated at or very near zero, likely due to the small number of random effect levels. One observation of seven individuals of severely damaged Collembola was removed from analysis.

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Acknowledgements

We wholeheartedly thank the Finse Alpine Research station for accommodation, and Erika Leslie for her hospitality. This work was supported by a grant from the Research Council of Norway (249902/F20) to JA.

Author contributions

Experiment was designed by JA, TB, and RR. Micro-arthropod identifications were done by SB. Fieldwork was performed by RR, KvZ, JA, and TB. Data analysis was performed by RR. All authors contributed to and agreed with the final version of this manuscript.

Competing interests

The authors of this paper have no conflicts of interest to report.

Data Availability

Data associated with this study will be deposited in the NMBU Open Research Database upon publication of the manuscript (http://dataverse.no/) at (DOI will be given upon acceptance of the manuscript).

Figure legends

Figure 1. The mean abundance ± SE of Collembola in the soil in thousands per square meter (a-b), in lichen per lichen dry weight (c-d), and the ratio between abundance in lichen:soil per square meter (e-f) against lichen water holding capacity (WHC) in liter per square meter (a, c, e) and the number of freeze-thaw cycles (b, d, f). AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina/stygia*, FN = *Flavocetraria nivalis*.

Figure 2. The mean abundance ± SE of Oribatida in the soil in thousands per square meter (a-b), in lichen per lichen dry weight (c-d), and the ratio between abundance in lichen:soil per square meter (e-f) against lichen water holding capacity (WHC) in liter per square meter (a, c, e) and the number of freeze-thaw cycles (b, d, f). AO = *Alectoria ochroleuca*, CI = *Cetraria islandica*, CRS = *Cladonia rangiferina*/*stygia*, FN = *Flavocetraria nivalis*.

380 # Tables

Table 1. Results from F-tests using Kenward-Roger approximations on a full model against an intercept-only model with the pbkrTest package. Lines printed in bold represent results significant to the p = 0.05 level.

Response variable	Explanatory variable	F-value	ndf, ddf	F-scaling	p-value
Collembola					
Abundance in lichen (by weight) * [1]	Lichen treatment	**38.407**	**3, 12**	**1**	**<0.001**
Abundance in soil (by surface) [1]		2.611	4, 15.082	0.999	0.077
Lichen:soil ratio (by surface)		2.699	3, 9.950	0.999	0.103
Abundance in lichen (by weight) * [2]	Lichen WHC	**27.476**	**1, 16.952**	**1**	**<0.001**
Abundance in soil (by surface) [1]		2.059	1, 14.474	1	0.173
Lichen:soil ratio (by surface) [1]		**7.271**	**1, 12.739**	**1**	**0.019**
Abundance in lichen (by weight) * [2]	Freeze-thaw cycles	1.900	1, 7.374	1	0.209
Abundance in soil (by surface) [2]		1.745	1, 14.869	1	0.207
Lichen:soil ratio (by surface) * ¤ [3]		<0.001	1, 6.490	1	0.984

Oribatida					
Abundance in lichen (by weight) [3]	Lichen treatment	1.655	3, 12.000	1	0.229
Abundance in soil (by surface) * [1]		1.652	4, 15.285	0.999	0.212
Lichen:soil ratio (by surface) * ¤ [3]		3.306	3, 10.698	0.999	0.062
Abundance in lichen (by weight) [3]	Lichen WHC	3.999	1, 15.518	1	0.063
Abundance in soil (by surface) * [2]		2.013	1, 15.378	1	0.176
Lichen:soil ratio (by surface) * [3]		**9.071**	**1, 14.326**	**1**	**0.009**
Abundance in lichen (by weight) * [3]	Freeze-thaw cycles	0.143	1, 9.999	1	0.713
Abundance in soil (by surface) * [1]		0.062	1, 14.570	1	0.807
Lichen:soil ratio (by surface) * [3]		0.135	1, 6.489	1	0.725

* singular fit ¤ suffers from heteroscedasticity of residuals [1] data sqrt(x) transformed [2] log(x + 1) transformed [3] log(x) transformed

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Supplements

Table S1. Emmean comparisons. Means and SEs are back transformed from the square root scale. For group comparisons, the Tukey method was used with alpha = 0.05. AO = *Alectoria ochroleuca,* CI = *Cetraria islandica,* FN = *Flavocetraria nivalis,* CRS = *Cladonia rangiferina / C. stygia*

Collembola	Lichen species	Emmean (sqrt)	SE	Df	Group
Abundance in lichen (by weight)	AO	0.651	0.318	16	1
	CI	0.846	0.363	16	1
	FN	2.180	0.583	16	1
	CRS	11.860	1.360	16	2

Table S2. Mixed effect model results of Collembola abundance (per lichen dry weight) in the different lichen treatments, abundance in lichen (per lichen dry weight) with water holding capacity (WHC), and abundance (per surface area) of Collembola in lichen:soil. Significance to the p = 0.05 level is printed in bold. AO = *Alectoria ochroleuca,* CI = *Cetraria islandica,* FN = *Flavocetraria nivalis,* CRS = *Cladonia rangiferina / C. stygia*

	Abundance in lichen [1]			Abundance in lichen [2]			Abundance in lichen:soil [1]		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.81	0.42 – 1.19	**0.001**	-0.93	-1.72 – -0.14	**0.033**	-0.10	-0.86 – 0.66	0.796
CI	0.11	-0.43 – 0.66	0.690						
CRS	2.64	2.09 – 3.18	**<0.001**						
FN	0.67	0.12 – 1.22	**0.029**						
WHC				0.94	0.61 – 1.26	**<0.001**	0.46	0.14 – 0.79	**0.015**
Random Effects									
σ^2	0.19			0.30			0.22		
τ_{00}	0.00_{block}			0.00_{block}			0.00_{block}		
ICC	0.00_{block}			0.00_{block}			0.01_{block}		
Observations	20			20			17		
Marginal R^2 / Conditional R^2	NA			NA			0.331 / 0.335		

[1] data was sqrt(x) transformed, [2] data was log(1+x) transformed

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Table S3. Mixed effect model results of Oribatida abundance (per surface area) in lichen:soil. Significance to the p = 0.05 level is printed in bold

	Abundance in lichen:soil [1]		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-2.12	-4.13 – -0.12	0.054
WHC	1.40	0.54 – 2.25	**0.006**
Random Effects			
σ^2	1.60		
$\tau_{00\ block}$	0.00		
ICC_{block}	0.00		
Observations	18		

[1] data was log(1+x) transformed

6

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Paper III

Synergistic effects of lichen mixtures on associated arthropods

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https://orcid.org/0000-0002-1580-6424

Pages: 29

Word count: 6722

Abstract

Whether primary producers grow in monocultures or in mixed-species assemblages determines biodiversity, and ecosystem functioning. However, the effect of mixing species often cannot reliably be predicted from the relative contributions of the individual species in the mixture. In this study, we use mat-forming lichens as natural microcosms to study the relation between mixed primary producers on abundance of higher trophic levels. We created patches of lichen mixtures of up to four different species and extracted Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae after incubation within lichen mats in the field. We hypothesized that mixing lichens would have synergistic effects on abundance of arthropods and that increasing the number of lichens in the mixtures would lead to stronger effects; that more dissimilar mixtures would lead to stronger synergistic effects; and that Collembola species richness would increase with the number of lichens in the mixture. Further, we explored to what extend water-holding capacity, and (for predators) prey abundance drive observed abundance patterns. We found synergistic effects on arthropod abundance in one third of the mixtures, but increasing the number of lichen species in mixtures did not increase the chance of synergistic effects. Further, we did not find consistent synergistic responses for particular mixtures, so we cannot conclude that mixtures that are more dissimilar yield stronger effects. In contrast to our hypothesis, increasing the number of lichens in a mixture, did not lead to higher species richness. The larger, more mobile macro-arthropods such as Pseudoscorpiones and Araneae were less dependent on lichen mixture *per se*, but more on water-holding capacity and prey abundance. Our findings show the importance of primary producer heterogeneity to the numerical abundance of associated arthropods, but that their biodiversity is not affected.

Key words: Collembola, Oribatida, habitat heterogeneity, habitat diversity, biodiversity, micro-arthropods, non-vascular plants

Introduction

Interactions between plants and invertebrates are key drivers of ecosystem functioning and community assembly processes (Bascompte and Jordano 2007, Ohgushi 2008, Biere and Bennett 2013, Poelman and Dicke 2018). The outcome of these interactions are partly influenced by vegetation composition, and whether species grow in monocultures or mixtures. For example, plant species richness affects the functional composition of arthropod communities in grasslands (Ebeling et al. 2018), and mixed-species forests provide higher levels of ecosystems services than single species stands do (Gamfeldt et al. 2013, Felton et al. 2016). As such, mixed-plant assemblages are important for both plant performance and key ecological processes (Cardinale et al. 2011).

The impact of mixed assemblages on biodiversity and ecological processes often cannot reliably be predicted from the relative contributions of the individual species in the mixture (i.e. simple additivity). Instead, many studies find non-additive, either synergistic (positive) or antagonistic (negative) effects. These non-additive effects of mixtures are mainly reported from studies on the decomposition (and flammability; Van Altena et al. 2012) of litter mixtures, where litter microclimate, morphology, quality, and the composition of the decomposer community are important drivers (Wardle et al. 1997, Gartner and Cardon 2004, Wardle et al. 2006, Ball et al. 2008, Chapman et al. 2013). Importantly, non-additive effects of species mixtures are not limited to dead organic matter, but also relevant

for mixtures of living organisms such as primary producers. In face of declining biodiversity, understanding non-additive effects of mixed assemblages is crucial to ecological conservation.

The majority of manipulative studies on mixtures of terrestrial primary producers focus on grassland systems (Spehn et al. 2005, Cardinale et al. 2011), but studies on trees and forests also exist. However, due to their large size and long life-cycles, forest systems are hard to manipulate and therefore entail obvious practical difficulties, although attempts have been made: e.g. Scherer-Lorenzen et al. (2007). As an alternative, miniature ecosystems or microcosms can be used to test ecological theories (Srivastava et al. 2004, Benton et al. 2007), but see (Carpenter 1996). For example, Åström and Bengtsson (2011) tested the effect of habitat destruction and fragmentation on small moss patches inhabited by micro-arthropods, and De Omena et al. (2017) investigated spiders living in bromeliads to quantify the cascading effect of predators on functioning of adjacent ecosystems. Using such miniature ecosystems may prove valuable in aiding our understanding of none-additive effects of mixed assemblages to biodiversity.

Mat forming lichens (Crittenden 2000) make excellent candidates as miniature ecosystems. They are a common appearance in boreal and alpine ecosystems where they cover extensive areas. They grow shrub-like thalli with complex 3D-structures analogous to shoots in vascular plants (Shorrocks et al. 1991) harbor many associated invertebrates such as Nematoda, Collembola, and Oribatida (Asplund and Wardle 2017). In contrast to vascular plants, lichens are unable to regulate their water content (i.e. they are poikilohydric) and considering that lichen species differ in their capacity to hold water (Gauslaa and Coxson 2011), they may

differ in their suitability as habitat to drought-sensitive invertebrates (Bokhorst et al. 2015). In addition to habitat, lichens are a food source to some micro-arthropods (Seyd and Seaward 1984, Reutimann and Scheidegger 1987, Meier et al. 2002, Bokhorst et al. 2007), but many micro-arthropod species may not feed on them or information on feeding preference is not available. Because mat-forming lichens are not attached to rock or rooted in the soil, and able to survive outside the field when dry, they can be moved, harvested, and manipulated without disturbance (e.g. Asplund et al., 2015).

In this study, we created lichen patches containing one, two, three or four different lichen species (i.e. 15 different mixes in total), and incubated these within natural lichen mats. From these patches, we then extracted Collembola, Oribatida, Mesostigmata, Pseudoscorpiones and Araneae. We used this experimental set-up to test the following hypotheses: (i) mixing lichen species results in synergistic effects on the abundance of associated Collembola, Oribatida, Mesostigmata, Pseudoscorpiones and Araneae, and these effects will increase with the number of lichen species in the mixture. (ii) non-additive effects will be greatest in mixtures resulting in the greatest habitat diversity, i.e. in mixtures of the most dissimilar species. As such, we consider mixtures between foliose (leaf-like) and fruticose (shrub-like) lichens more dissimilar than mixtures consisting of lichens of the same growth form. (iii) Collembola species richness will increase with the number of species richness in the mixture. Further, we explore whether differences in arthropod abundance can be explained by mixture identity alone, or if water holding capacity, or (for predators) prey abundance drive observed patterns. Here, we expect that the higher in the food chain, and the more generalist the diet, the less abundance will depend on lichen mixture directly. By testing these hypotheses,

we aim to advance our understanding of how primary producer diversity contributes to biodiversity and numerical abundance of higher trophic levels.

Methodology

Study site

This study was performed at the Kollåsen nature reserve (59° 45' N, 10° 56' E), in Akershus, Southeastern Norway at approximately 190 m a.s.l. The site is located on pre-Cambian gneiss bedrock and lies above the post-glacial loess deposits. It therefore has shallow, poor, organic soils that are limited to depressions in the landscape. *Pinus sylvestris* L. dominates the site with undergrowth of *Vaccinium myrtillus* L. and *Calluna vulgaris* (L.) Hull while dense lichen mats dominated by *Cladonia* species and *Cetraria islandica* (L.) Ach. cover the abundant rocky outcrops. The site has a humid continental/hemiboreal climate (Köppen classification *Dfb*). The nearest weather station, Ås NMBU (station ID 17850) at 14 km from the field site and at 92 m a.s.l., recorded an average temperature of 14.2 °C over the four month period June-September (by month: 14.5, 16.1, 14.6 and 11.6 °C) 2017 with 390.6 mm of precipitation (Norwegian Meteorological Institute – eKlima database).

Lichen collection and preparation of lichen patches

We collected *Cladonia arbuscula* (Wallr.) Flot., *Cladonia stellaris* (Opiz) Pouzar & Vezda, *Cladonia uncialis* (L.) Wigg., and *Cetraria islandica* (L.) Ach. approximately 1 km east-southeast of the experimental site, just outside the Kollåsen nature reserve (59°44' N, 10°57 E) in May 2017. These species are typical mat-forming lichens and common in our study area, Scandinavia and throughout the northern biome in general. The species differ in their morphological complexity. All four species have

upright, fruticose thalli but *Cetraria islandica* is foliose in growth, with large flattened lobes. In contrast, the *Cladonia* species are structurally more complex with dichotomic (branching in two's; *C. uncialis*), trichotomic (branching in three's; *C. arbuscula*) and tetrachotomic (branching in four's; *C. stellaris*) growth-forms. In addition, *Cladonia* thalli are hollow, and the insides should be readily accessible to micro-arthropods and provide additional habitat.

The collected lichens were identified to species, divided into mono-specific clumps of several thalli, and cleaned from litter and necromass (dead or senescent thallus parts) in the lab. At this stage, lichens were dried at room temperature and were moistened only when they needed to be handled. We then created patches of mono-specific or combinations of two, three, or four lichen species, i.e. 15 different combinations in total. Lichens were placed in a ⌀ 15 cm (176 cm^2) and 10 cm high ring made of nylon insect netting (mesh size 2.5 mm). The rings did not have bottoms to allow animals to move freely up and down into the soil. Lichens were divided over the rings by cover, i.e. in the multi-species patches each species covers 50 %, 33 %, or 25 % of the surface of the ring. Because some lichen species have a higher specific thallus mass, total biomass may differ among, but not so much within, lichen mixtures. The lichen patches were incubated within lichen mats in the field from June 21 to October 4, 2017. The experiment consisted of 10 blocks, spaced on average 83 meters apart. Each of the blocks contained one replicate of each lichen mixture, adding up to a total of 10 × 15 = 150 lichen patches used in the experiment.

Arthropod identifications

The lichen patches were collected from the field on October 4, 2017, 106 days after placement in the field, and transported to the lab in plastic bags to avoid desiccation. We consider the >100 day duration of this experiment sufficient for arthropods to recolonize the lichen patches and this is supported by results from Åström and Bengtsson (2011), who found ample recolonization of moss patches in a similar ecosystem after 70 days, although their patches were smaller (25 cm^2 versus 176 cm^2) than the ones used in our study. The lichen mixtures were transferred into ⌀ 10 cm diameter rings in extraction apparatuses modified after Macfadyen (1961) and used by Hågvar and Klanderud (2009). The temperature was gradually increased from 30 °C to 65 °C over the course of four days and samples remained in the extractor at 65 °C until completely dry (13 days for the first batch, 14 days for the second). Arthropods were extracted into saline water. In the first extraction batch, 76 samples were included, and the other lichen samples that were not immediately processed were stored at 6 °C in the dark until further processing (these batches were accounted for in statistical analyses). Lichen rings were placed in the extractors randomly, i.e. different lichen patches from different blocks were placed randomly in one of the extractors. Collembola were identified following Hopkin (2007) and Fjellberg (1998, 2007). Acari were grouped into Oribatida, Astigmatina, and Mesostigmata. Pseudoscorpiones and Araneae were also counted. After arthropod extractions, dry weights of each lichen ring were measured after removed of debris such as pine needles and cones (air dried, Mettler PE160, 160g x0.001g, Mettler Intrumente AG, Zürich).

Lichen water holding capacity

Because we consider the water holding capacity an important predictor of animal abundance, we measured the water holding capacity of each lichen patch after animal extractions. First, the lichen patches were saturated in tap water at room temperature for 15 minutes. Subsequently, lichen patches were placed in between two soil sieves (bottom one with 2 mm ⌀, top one with 5 mm ⌀) and forcefully shaken 10 times to remove access water. Some water will have remained on the lichen surfaces, but this "clinging water" we consider ecologically relevant. Lichen patches were then weighed (Mettler PE160) and subsequently dried for 96 hours in ventilated drying ovens at 70 °C. After drying, lichen patches were weighed again for dry weight (Sartorius ENTRIS323I - 1S). Water holding capacity was expressed as dry weight / wet weight*100.

Statistical analysis

To test our first and second hypothesis that mixing lichen species has synergistic effects on the abundance of arthropods and this effect is strongest in mixtures of the most dissimilar species, we calculated the expected abundance for each lichen mixture based on the abundances in the single-species mixtures. We then subtracted this expected abundance from the observed abundance to calculate the deviation from the expectation: a resulting value of zero would indicate no difference (i.e. a simple additive effect), a negative value would indicate a lower abundance than expected (antagonistic effect) and a positive value a higher abundance than expected (synergistic effect). Then, we ran mixed effects models on these observed-expected values, with lichen mixture as fixed effect and experimental block as random effect, and with the intercept set to zero; lmer(abundance ~ 0 + lichen mixture + (0 + 1|block), data = df) using the lme4-

package (Bates et al. 2014) in R v. 3.5.2 (R Core Team, 2018). In this case, removing the intercept is justified, as our interest was specifically to test whether the model estimates differ from zero. In addition, we ran similar models for the average for mixtures containing two, three and four species (regardless of the specific species included in the mixtures). Further, we ran an additional set of mixed-effect models to test how arthropod abundance and Collembola species richness responded to adding one, two, or three additional species to one of the lichen species. To test our third hypothesis that species richness will increase with an increasing diversity of lichens in the mixtures, we used similarly specified generalized mixed-effect models (Poisson family) to test how adding one, two, or three additional species to one of the lichen species affects species richness.

To explore whether the abundance of arthropods of low trophic levels are driven by lichen identity, but that arthropods at higher trophic levels would depend on prey abundance and water holding capacity of the lichen, we performed model selection on linear mixed-effect models with the lme4-package in R (Bates et al. 2014). In addition to lichen mixture, we considered water holding capacity and prey abundance as fixed effects. The Akaike information criterion (AIC) was used to evaluate models (see: Johnson and Omland 2004) and in case $\delta AIC < 2$, the simplest model was preferred. First, we selected for a random effects structure with REML in a full model that included lichen mixture, water holding capacity and for predatory Mesostigmata, Pseudoscorpiones and Araneae also prey abundance (prey = Collembola plus Oribatida) and their two-way interactions. Experimental block was selected as a relevant random effect for all arthropod groups, while extraction batch was selected out. However, as our data did not support (i.e. resulted in singular fits) complex random structures with both random slopes and

intercepts, we defined random intercepts only. Then, as fixed effects, we considered lichen mixture and lichen water holding capacity, and (for predatory animals) the total abundance of prey with ML. Because of limited interpretability, the three-way interaction between all potential fixed effects was not considered in these models. Yet, the most complex model did include three two-way interactions. To avoid issues with heteroscedasticity of the residuals and violation of normality, data for Collembola, Oribatida was log transformed; data for Mesostigmata, Pseudoscorpiones and Aranea was square root transformed. Due to scaling issues, water holding capacity was included in the models as a fraction, not percentage. In addition, we specifically tested for differences in water holding capacity between lichen mixtures with Kruskal-Wallis tests and pairwise Mann-Whitney U *post-hoc* tests.

Results

Lichen mixtures showed either additive (no difference between observed and expected) or synergistic effects on arthropod abundance, i.e. a higher abundance observed than expected (Figure 1 and Figure 2). Out of the eleven different multi-species mixtures, three show a synergistic effect for Collembola (au, aui, ausi), five for Oribatida (ui, si, aus, asi, ausi), and six for predatory Mesostigmata (as, us, ui, aui, usi, ausi) abundance. However, for Pseudoscorpiones and Araneae, only two mixtures show significant synergistic effects (aus and asi, and si and aus, respectively). The effect size, i.e. the model estimated observed - expected abundance as percentage of the observed abundance, was respectively 38.8 % and 59.7 % for Collembola in three and for species mixtures. For Oribatida the abundance was 28.9 %, 42.5 %, 56.2 % higher than expected for two, three, and

four species mixtures, while for Mesostigmata this was 61.6 %, 62.0 %, and 93.6 %. For Pseudoscorpiones, only three species mixtures differed significantly from expected values (70.2 %), while none were significant for Aranea. As such, we found synergistic effects in mixtures containing two, three, and four species, and in mixtures of different composition (Figure 1 and Figure 2). However, mixtures containing the most dissimilar species in terms of water-holding capacity and morphology (i.e. *Cetraria islandica* and *Cladonia stellaris*) did not consistently lead to stronger synergistic effects. In fact, synergistic effects also occurred in mixtures of species we considered relatively similar, for example in *Cladonia arbuscula* - *Cladonia stellaris* mixtures for Mesostigmata. Further, the averaged two-species mixtures show synergistic effects on Oribatida and Mesostigmata, three-species mixtures on all groups except Araneae, and four-species mixtures showed synergistic effects in Collembola, Oribatida and Mesostigmata.

Adding one or more lichen species to *Cetraria islandica* and *Cladonia uncialis* increased the abundance of Collembola (Figure 3). Similarly, abundance of Oribatida was increased when adding additional species to *C. islandica*, *C. uncialis*, and *Cladonia arbuscula*. The same effect was found for Mesostigmata when adding additional species to *C. islandica* and *C. uncialis*, but generally not for other predators i.e. Pseudoscorpiones and Araneae, although *Cladonia stellaris* showed a similar pattern for Pseudoscorpiones (Figure S1). No such patterns were found for Collembola species richness (Figure S2).

Model selection resulted in a best model for Collembola and for Oribatida abundance that only includes lichen mixture as fixed effect. Collembola abundance was lower for *Cladonia uncialis* compared to other species and mixes. Oribatida

were less abundant in *Cetraria islandica* and *Cladonia uncialis* than in other lichen species and mixtures. For Mesostigmata, the most complex model was considered the best, and included interactions between treatment and water holding capacity, treatment and total prey abundance, and water holding capacity and total prey abundance. For Pseudoscorpiones, the best model included both water holding capacity and total prey abundance. Pseudoscorpiones increased with increasing water holding capacity and were more abundant with increasing prey abundance. Araneae abundance was best modelled by total prey abundance only: the higher the prey abundance, the higher the abundance of spiders. The water holding capacity differed significantly between lichen mixtures (Kruskal-Wallis chi-squared = 101.38, df = 14, $P < 0.001$) and the single-species lichen patches showed strong differences: *Cetraria islandica* had the lowest water holding capacity while the more complex *Cladonia* species, most notable *C. arbuscula* and *C. stellaris*, had higher water holding capacities. Mixtures showed additive effects, with water holding capacities for mixtures similar to the mean of their components (Figure S3).

Discussion

In this study, we found both additive and synergistic effects of lichen mixtures on arthropod abundance. Synergistic effects on abundance were not present in each specific mixture, but were common for the average of mixtures consisting of two, three, and four lichen species, thus partly supporting our first hypothesis. Further, synergistic effects were more common in micro-arthropods such as Collembola, Oribatida, and Mesostigmata than in arthropods at higher trophic levels such as Pseudoscorpiones and Araneae. However, adding more species to the mixtures did not increase the strength of synergistic effects. In contrast to our second

hypothesis, we cannot conclude that mixtures that are more dissimilar show stronger synergistic responses. In contrast to our third hypothesis, we did not find any effect of lichen mixtures on Collembola species richness. Finally, we found that while the abundance of Collembola and Oribatida is well-predicted by lichen mixture alone, lichen water holding capacity and prey abundance become increasingly more important higher up the food chain, i.e. for Mesostigmata, Pseudoscorpiones, and Araneae.

Our results show that mixing lichens often has synergistic effects on arthropod abundance, although not in all specific cases. In addition, we found that increasing the number of species in the mixtures did not lead to stronger or more frequent synergistic effects. However, two-species mixtures for Collembola did not give synergistic effects, while three- and four-species mixtures did. As such, finding synergistic effects on Collembola abundance is more likely when more than two lichen species are mixed. Other studies on mixture effects such as those on litter mixtures and their decomposability often report idiosyncratic, unpredictable synergistic responses in a few of the treatments (e.g. Schädler and Brandl 2005). Our results contrast these unpredictable effects, as we found synergistic effects in one third of the mixtures in our experiment (in 18 out of 55 mixtures, across five arthropod groups), suggesting that synergistic effects are common.

While we predicted that mixtures containing more dissimilar lichen species would lead to stronger synergistic effects, we did not consistently find synergistic effects across all arthropod groups in mixtures containing the species we considered most dissimilar, i.e. *Cetraria islandica* and *Cladonia stellaris*. Possibly, these lichens provide less heterogeneity in habitat and resource availability than anticipated,

and/or the heterogeneity differentially affects arthropod groups. Lichen mixture heterogeneity may be further increased by introducing more contrasting lichen species, for example by including lichens that incorporate nitrogen-fixing cyanobacteria as symbionts (Henskens et al. 2012). As such, Bokhorst et al. (2015) report higher invertebrate abundance and diversity associated with nitrogen-fixing lichens, although this may also have been due to their often foliose growth form. Further supporting the idea that increasing habitat heterogeneity could increase abundance, are findings by Halaj et al. (2000) that increasing the density and complexity of pine branches and needles stimulates arthropod abundance, in particular that of Collembola. In addition, Saitoh et al. (2014) report that mixed substrate enhanced Collembola abundance, but that variation in the Collembola communities was partly related to root development and trophic interactions with other micro-arthropods.

In this study, we found differential effects of lichen mixtures on abundance of arthropods at different trophic levels, where arthropods at higher trophic levels were less tightly associated with lichen mixture identity. Specifically, for Collembola and Oribatida, who are mostly fungivorous (including lichens) or detrivorous and can thus be considered primary consumers in this system (Seyd and Seaward 1984, Hopkin 1997, Scheu and Maraun 2004), lichen species mixture was the best predictor for abundance. Mesostigmata, who feed on Collembola and Oribatida (Koehler 1997), are secondary consumers and their abundance was best modelled by lichen mixture, as well as other variables such as lichen water holding capacity, prey abundance, and their interactions. Pseudoscorpiones (Stol 2005, Eisenbeis and Wichard 2012) and Araneae feed on lower trophic levels, including smaller secondary consumers, and their abundance was driven by prey availability (here

defined as primary consumers) and for Pseudoscorpions also water holding capacity. These results suggest that, the further up the food chain, the more arthropods are disconnected from primary producers, possibly aided by their larger mobility (Uetz 1991).

Our results further suggest that arthropods abundance increases upon adding more lichen species to lichens that support low arthropod abundance, but that arthropod abundance does not increase when lichens are added to lichens that support high arthropod abundance. In other words, arthropod abundance is likely determined by lichen species identity more so than by mixture *per se*. Similar patterns were reported from studies on invertebrate communities in litter mixtures (Wardle et al. 2006), from arthropods in plant assemblages (Koricheva et al. 2000), and on the flammability of plant litter mixtures (Van Altena et al. 2012), where the most flammable species determined the rate and duration of the fire. However, other studies do show the importance of mixed habitats/substrate to micro-arthropods. For example, Hansen (2000) found that the abundance of Oribatid mites is higher and more stable through time in litters containing mixed species, and Andringa et al. (2019) found that invertebrate species richness is increased by mixing dead wood, both in terms of tree species and decomposition stage.

Our finding that Collembola species richness is unresponsive to habitat diversity, is supported by reports that many soil micro-arthropods such as Collembola and Oribatida are generalist feeders (Hopkin 1997, Scheu and Maraun 2004) and show little habitat specialization (Wehner et al. 2016). As such, micro-arthropods can successfully exploit microclimates and –habitats (Schneider et al. 2007), and their communities show high levels of functional redundancy (Setälä et al. 2005).

406 Whether or not micro-arthropod species richness responds to experimental
407 treatments therefore seems context dependent. For example, corridors connecting
408 moss patches may only benefit micro-arthropod richness under extreme
409 environmental conditions (Hoyle and Gilbert 2004), and the relation between local
410 species richness and regional species richness/composition in moss patches differs
411 between seasons (Starzomski et al. 2008). Although all samples in this study were
412 collected on the same day, it is likely that seasonal or even day-to-day variations in
413 climatic conditions may affect the arthropod communities mat-forming lichens
414 support, especially because lichens are unable to regulate their moisture content.
415
416 The findings from our miniature ecosystem study that mixtures of primary
417 producers, and thus increasing heterogeneity of habitat has positive and often
418 synergistic effects on abundance of higher trophic levels finds agreement with full-
419 scale studies. For example, farmland birds occur in higher abundance in more
420 diverse and mixed landscapes (Pickett and Siriwardena 2011). We did not find that
421 mixed species supported higher species richness, which contrasts the consensus
422 that more diverse habitats support higher biodiversity (Stein et al. 2014), but this
423 may be due to the generalist feeding and habitat selection particular to soil micro-
424 arthropods. Our findings stress the importance of habitat heterogeneity introduced
425 by mixed stands of primary producers, as human influences on natural ecosystems
426 will continue to increase (Palmer et al. 2004, Goudie 2018).
427

Acknowledgements

We thank Fylkesmannen Akershus for permitting us to work in the Kollåsen reserve (permit ref. no. 2017/17688-3 M-NA). This work was supported by a grant from the Research Council of Norway (249902/F20) to JA.

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Tables

Table 1.

Table. 1 Overview of lichen species and their characteristics

	Branching complexity	Chemistry
***Cladonia arbuscula* (Wallr.) Flot.**	Predominantly trichotomic, some tetrachotomic branching, anisotomic	(+)-Usnic acid, (+)-isousnic acid, fumarprotocetraric acid complex
***Cladonia stellaris* (Opiz) Pouzar & Vězda**	Predominantly tetrachotomic, some trichotomic or pentachotomic branching, isotomic	(–)-(Iso)usnic acid, perlatolic and pseudonorrangiformic acid
***Cladonia uncialis biuncialis* (Hoffm.) M. Choisy**	Predominantly dichotomic branching, anisotomic	(+)-Usnic acid, squamatic acid
***Cetraria islandica* Ach.**	Dichotomic branching, foliose	Fumarprotocetraric, lichesterinic and protolichesterinic acid

Thell et al. (2011), Ahti et al. (2013)

605 Table 2.

Table 2. Results of mixed-effect model selection based on AIC for arthropod abundance. All models included experimental block as random effect. Data was transformed to improve normality of residuals and avoid heteroscedasticity. To calculate p-values, type III Analysis of Variance Table was performed with Kenward-Roger's method. The marginal R^2 describes the variance explained by the fixed effects only, while the conditional R^2 also incorporates variation explained by the random effect. The number of observations = 144. [a]: Data were log transformed, and [b]: data were square root transformed.

Abundance of	Fixed effects selected in model	F-value	P-value	Marginal R^2	Conditional R^2
Collembola [a]	Lichen mixture	4.221	**<0.001**	0.233	0.497
Oribatida [a]	Lichen mixture	5.491	**<0.001**	0.273	0.545
Mesostigmata [b]	Treatment	3.048	**<0.001**	0.700	0.746
	WHC	2.897	0.092		
	Prey abundance	1.508	0.222		
	Treatment : WHC	2.614	**0.003**		
	Treatment : prey abundance	2.283	**0.010**		
	WHC : prey abundance	2.655	0.107		
Pseudoscorpiones [b]	WHC	8.112	**0.005**	0.122	0.125
	Prey abundance	12.386	**<0.001**		
Araneae [b]	Prey abundance	18.118	**<0.001**	0.121	0.232

606

Figure captions

Figure 1. Model estimates +/- 95% CIs for observed – expected abundance per gram dry weight lichen for (a) Collembola and (b) Oribatida. A positive value indicates that abundances in a mixture are higher than expected by the mean of the components (i.e. a synergistic non-additive effect). The emmeans package (Lenth et al. 2017) was used to compare effect size of treatments within in each micro-arthropod group among each other, but none of these differences were significant (Tukey method with alpha = 0.05). Asterisks denote significant differences of the model fit from zero ('*'p = 0.05, '**' p= 0.001, '***' p < 0.001). Percentages denote the model estimated observed – expected abundance per gram lichen dry weight, expressed as percentage of the observed abundance per gram lichen dry weight. a = *Cladonia arbuscula*, i = *Cetraria islandica*, s = *Cladonia stellaris*, u = *Cladonia uncialis*.

Figure 2. Model estimates +/- 95% CIs for observed – expected abundance per gram dry weight lichen for (a) Mesostigmata, (b) Pseudoscorpiones, and (c) Araneae. A positive value indicates that abundances in a mixture are higher than expected by the mean of the components (i.e. a non-additive effect). The emmeans package (Lenth et al. 2017) was used to compare effect size of treatments within in each micro-arthropod group among each other, but none of these differences were significant (Tukey method with alpha = 0.05). Asterisks denote significant differences of the model fit from zero ('*'p = 0.05, '**' p= 0.001, '***' p < 0.001). Percentages denote the model estimated observed – expected abundance per gram lichen dry weight, expressed as percentage of the observed abundance per gram lichen dry weight. a = *Cladonia arbuscula*, i = *Cetraria islandica*, s = *Cladonia stellaris*, u = *Cladonia uncialis*.

Figure 3. The abundance of Collembola (a through d), Oribatida (e through h), Mesostigmata (I through l) for each lichen species in monoculture and in mixture with one, two, or three additional lichen species. *Cetraria islandica Cladonia uncialis*, and for Oribatida also *Cladonia arbuscula* associated arthropod abundance increases when additional lichen species are added, while arthropod abundance does not increase if lichen species are added to *Cladonia stellaris*. We ran mixed-effect models that included experimental block as random effect and letter coding results from comparisons by the emmeans-package in R (Tukey method with alpha = 0.05). In these models, data were log-transformed for Collembola in all three *Cladonia* species and for Oribatida in *C. islandica*, *C. uncialis*, and *C. arbuscula*.

Figures

Figure 1

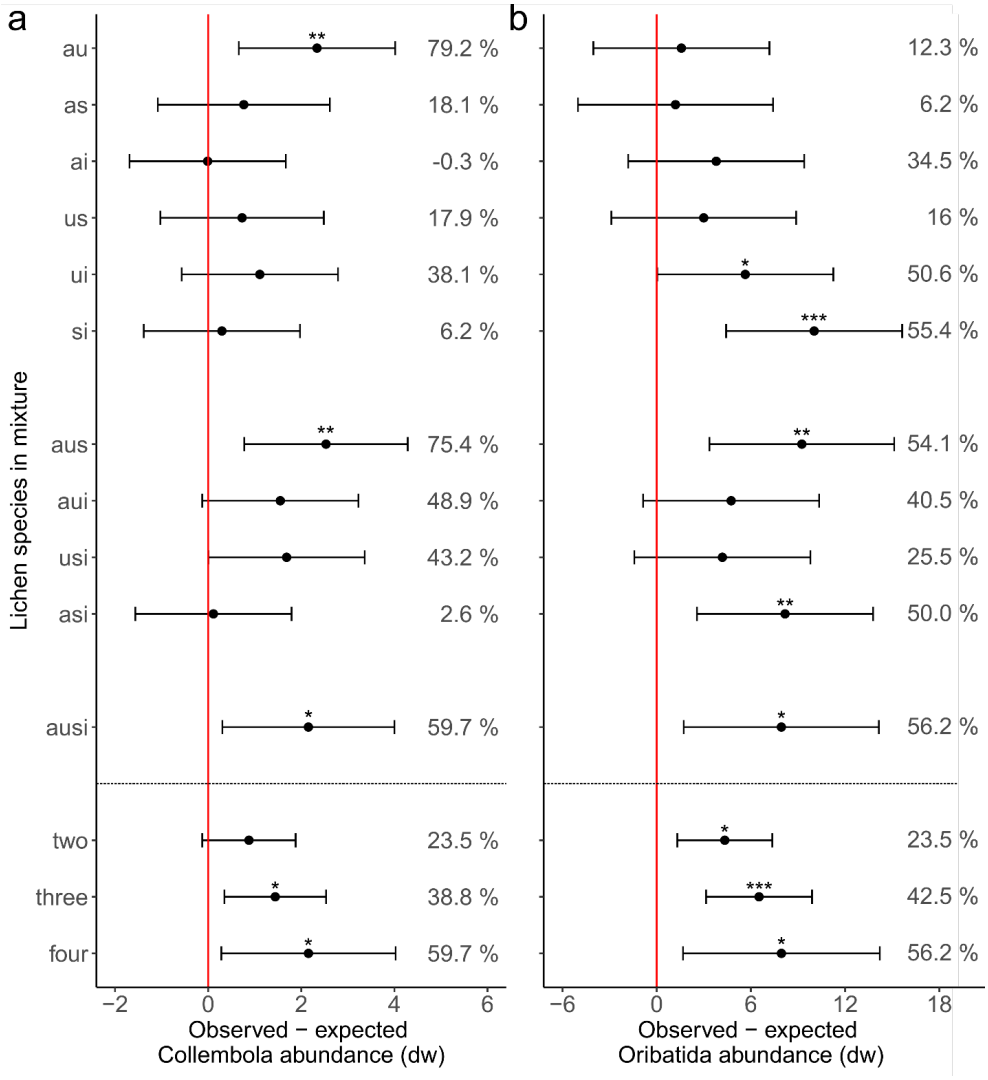
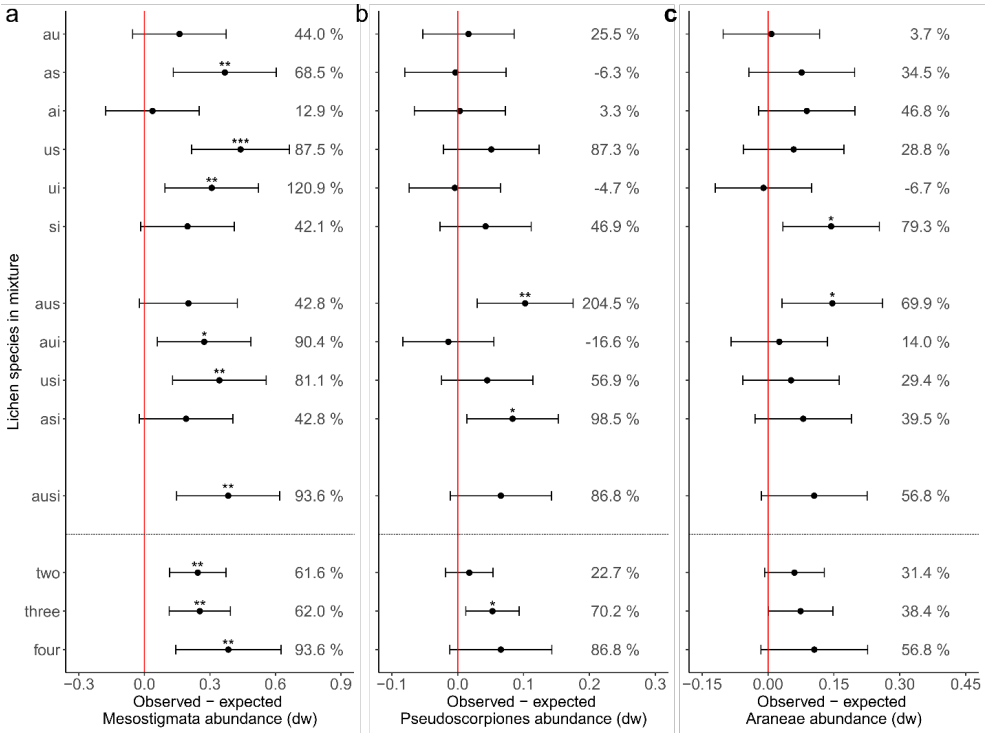


Figure 2


a
b
c
Lichen species in mixture
au
as
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si
aus
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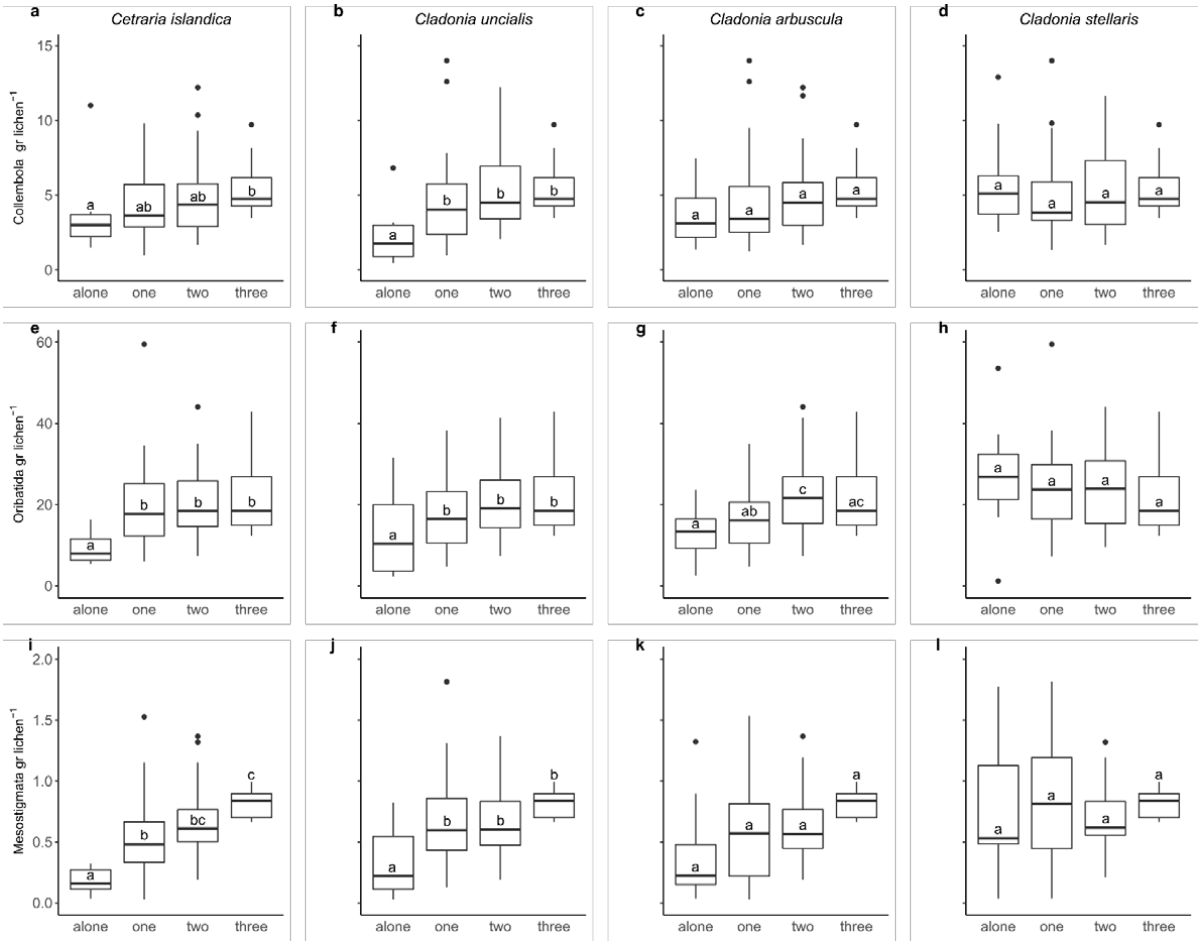
usi
asi
ausi
two
three
four
44.0 %
68.5 %
12.9 %
87.5 %
120.9 %
42.1 %
42.8 %
90.4 %
81.1 %
42.8 %
93.6 %
61.6 %
62.0 %
93.6 %
25.5 %
-6.3 %
3.7 %
34.5 %
46.8 %
28.8 %
-6.7 %
79.3 %
69.9 %
14.0 %
29.4 %
39.5 %
56.8 %
31.4 %
38.4 %
56.8 %
204.5 %
-16.6 %
56.9 %
98.5 %
86.8 %
22.7 %
70.2 %
86.8 %
−0.3
0.0
0.3
0.6
0.9
−0.1
0.0
0.1
0.2
0.3
−0.15
0.00
0.15
0.30
0.45
Observed − expected
Mesostigmata abundance (dw)
Observed − expected
Pseudoscorpiones abundance (dw)
Observed − expected
Araneae abundance (dw)

643 Figure 3



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Author contributions

The study was designed by JA, TB, and RR. Fieldwork was performed by RR, TB, and JA. Animals were identified by SB. Statistics were done by RR. All co-authors contributed to manuscript revisions and agree with the final version of this manuscript.

Competing interests

The authors of this paper have no conflicts of interest to report.

Data Availability

Data associated with this study will be deposited in the NMBU Open Research Database upon publication of the manuscript (http://dataverse.no/) at (DOI will be given upon acceptance of the manuscript).

Supplements

Figure S1

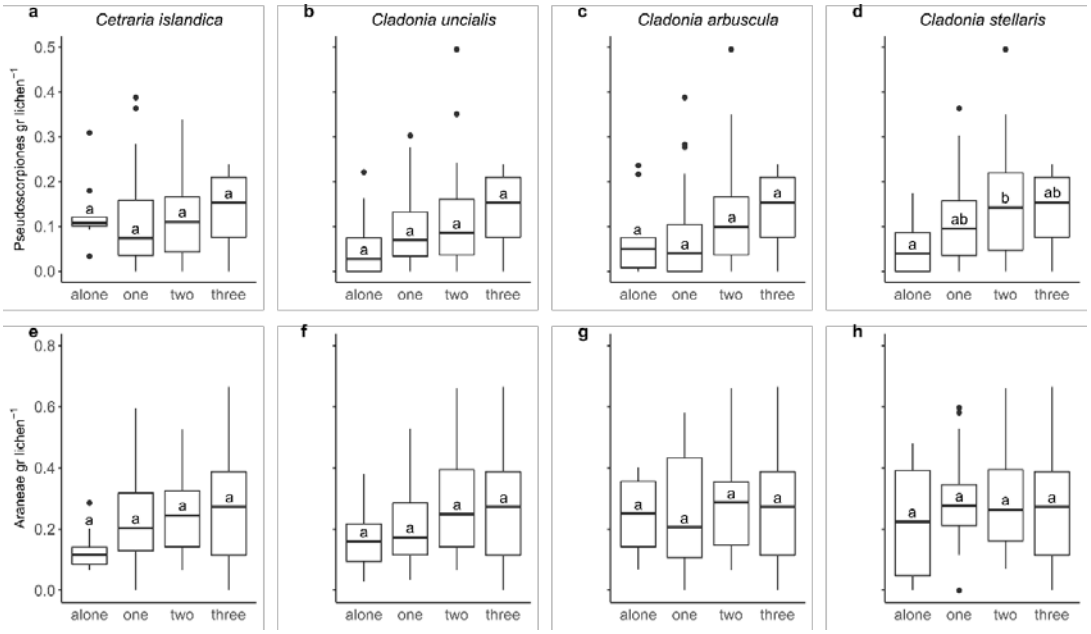

Figure S1. The abundance of Pseudoscorpiones (a through d) and Araneae (e through h) for each lichen species in monoculture and in mixture with one, two, or three additional lichen species. Only for *C. stellaris* did adding lichen species to the mix result in higher abundance of Pseudoscorpiones. We ran mixed-effect models that included experimental block as random effect and letter coding results from comparisons by the emmeans-package in R (Tukey method with alpha = 0.05). In these models, data were square root-transformed for all Pseudoscorpiones and for *C. islandica* and *C. arbuscula* in Araneae.

Figure S2

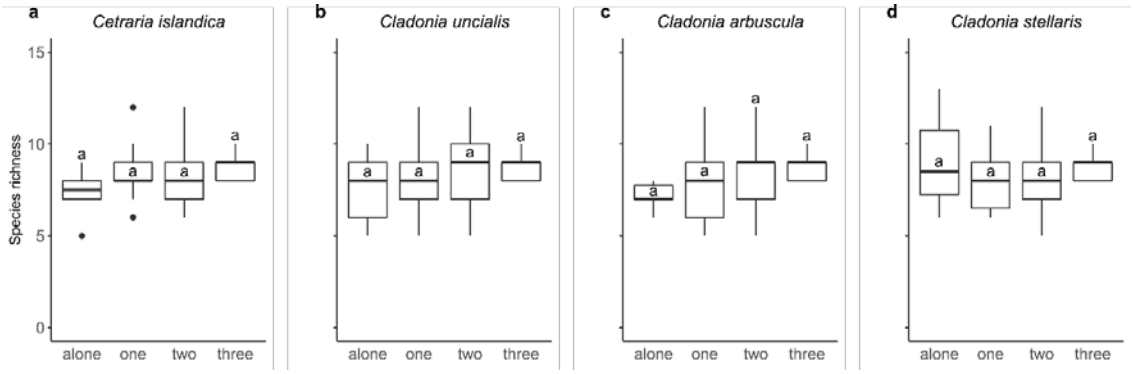

Figure S1. The species richness of Collembola for each lichen species in monoculture and in mixture with one, two, or three additional lichen species. In none of the cases did adding lichen species to the mix result in higher species richness. We ran generalized mixed-effect models (family = Poisson) that included experimental block as random effect and letter coding results from comparisons by the emmeans-package in R (Tukey method with alpha = 0.05).

Figure S3

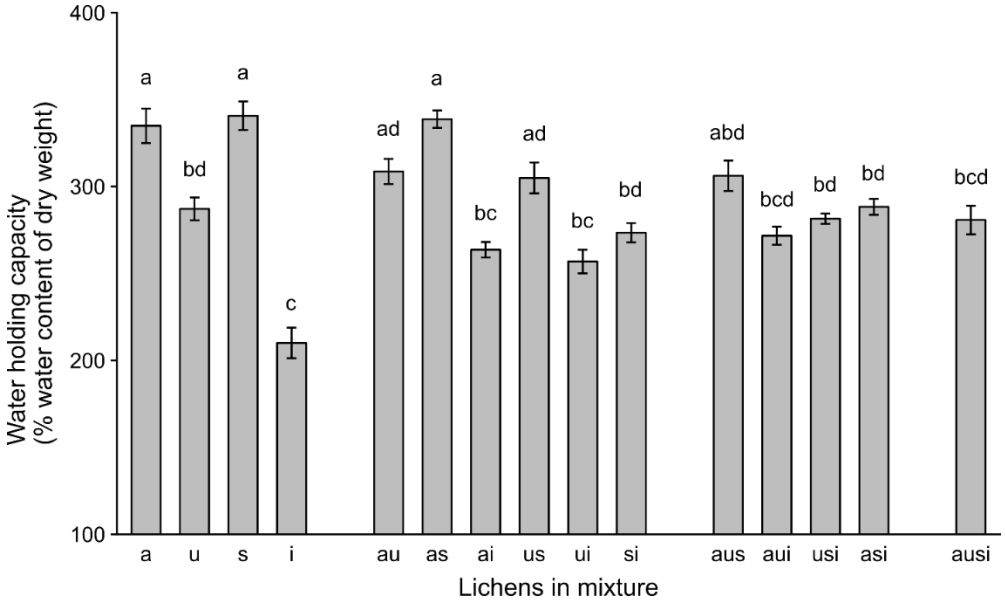

Figure S3. Water holding capacity (% water content of dry weight) for different lichen mixtures +/- SE. Letter coding denotes which groups differ significantly from each other (at the p = 0.05 level) after Kruskal-Wallis analysis with *post-hoc* pairwise Mann–Whitney U-tests. The least complex lichen, *Cetraria islandica* (i) has the lowest water holding capacity, while the other lichens (u: *Cladonia uncialis*, a: *C. arbuscula*, s: *C. stellaris*) have a higher structural complexity and water holding capacity. The effect of mixing lichens is in most cases additive, i.e. the mean water holding capacity of lichen mixtures generally falls between the mean values of their components. For example, the water holding capacity of the *Cladonia arbuscula-uncialis* (au) mixture falls between those of *C. arbuscula* and *C. uncialis*.

Paper IV

Article type: Articles

Recovery of soil micro-arthropod communities after cessation of experimental environmental change

Running head: Micro-arthropod recovery

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Abstract

Changes in environmental conditions can alter species abundance and community composition and thereby the functioning of ecosystems. However, it is often unknown to what extend these changes are permanent or if ecosystems can recover when environmental conditions return to their original levels. In this study, we assess the recovery of alpine soil micro-arthropod communities from changes due to warming and nutrient addition treatments in terms of abundance, species richness, and species composition. We resampled an experimental site in Finse, southern Norway for Collembola and Acari nine years after cessation of warming and nutrient addition treatments. During the recovery period, the vegetation only partly recovered, but mammalian grazing increased the recovery rate. We hypothesized that micro-arthropod recovery follows recovery of the vegetation and would therefore be limited. Also, we expected large-bodied, generalist Collembola with short life-cycles to be most adaptive to environmental changes and thus most responsive and best able to recover. Our results show complete recovery of Collembola and Mesostigmata in terms of abundance. However, we found persistent changes in community composition of Collembola and Oribatida, arguing against recovery. The generalist *Folsomia quadrioculata* was the

most responsive Collembola species and although its abundance recovered, it remained dominant in Collembola communities after cessation of the treatments. Grazing affected community composition of both Collembola and Oribatida but we did not find grazing to speed up recovery of soil micro-arthropods as it does for vegetation. We therefore conclude that micro-arthropods can recover quickly from environmental manipulation in terms of overall abundance, but that effects on individual species and therefore species composition may be long-lasting and less predictable.

Key words: Acari, alpine ecology, Collembola, community responses, ecological resilience, ecosystem recovery, experimental warming, herbivory, Oribatida, nutrient addition.

Introduction

Changes in environmental conditions can push ecosystems into alternative states that differ in species composition, species abundance, and ecological functioning (May 1977, Scheffer et al. 2001, van de Koppel et al. 2001, Beisner et al. 2003, Suding et al. 2004). These environmental changes can be either gradual (e.g. increased nitrogen deposition rates) or episodic (e.g. drought events), but both can have legacy effects long after environmental

58 conditions have returned to their original state (Bengtsson 2002, Seneviratne
59 and Ciais 2017, Bowman et al. 2018, De Boeck et al. 2018). Identifying and
60 predicting when and how ecosystems shift from one alternative state to
61 another, and whether they are able to recover, is difficult (Schröder et al.
62 2005, Scheffer et al. 2009, Bestelmeyer et al. 2011) but important to
63 ecosystem conservation (Suding and Hobbs 2009) and to define a safe
64 operating space for ecosystems (Scheffer et al. 2015).
65
66 Over the last decades, ecosystems at high latitude and altitude have
67 experienced a significant temperature increase (e.g. Isaksen et al. 2016, Rizzi
68 et al. 2017) and this trend will likely continue in the future (Stocker 2014).
69 Simultaneously, nitrogen availability may increase due to increased
70 mineralization rates (Nadelhoffer et al. 1991, Hobbie 1996, Rustad et al.
71 2001, Aerts et al. 2006) and increased atmospheric nitrogen deposition related
72 to increased precipitation (Hole and Engardt 2008) and human practices such
73 as agriculture (Vitousek et al. 1997). Observational and experimental studies
74 show that arctic and alpine ecosystems respond to these changes by a shift
75 towards shrub and graminoid dominance at the expense of lichens and
76 bryophytes (Cornelissen et al. 2001, Sturm et al. 2001, Klanderud and Totland

2005, Parmesan 2006, Elmendorf et al. 2012, Elmendorf et al. 2015). Although climate and nutrient conditions abruptly change after cessation of experimental manipulation (Boxman et al. 1998, Limpens and Heijmans 2008, O'Sullivan et al. 2011), changes in the composition and functioning of the ecosystem may persist much longer (Strengbom et al. 2001, Olsen and Klanderud 2014, Street et al. 2015). However, grazing by large herbivores has been found to mitigate the effects of climate warming on vegetation (Post and Pedersen 2008, Olofsson et al. 2009), and to increase the ability of the vegetation to recover from climate-induced changes in species composition (Olsen and Klanderud 2014).

Most studies on the responses of arctic and alpine ecosystems to experimental environmental change, as well as their capability to recover, have focused on vegetation (e.g. Strengbom et al. 2001, O'Sullivan et al. 2011, Olsen and Klanderud 2014, Street et al. 2015, De Boeck et al. 2018). Yet, aboveground vegetation is intricately linked to belowground processes and communities (Wardle et al. 2004). In arctic and alpine ecosystems, where soil macrofauna (e.g. earthworms) is often absent, micro-arthropods such as Collembola (springtails) and Acari (mites) together with the microbial community, play

96 an important role in ecological processes such as decomposition (Wallwork
97 1970, Seastedt 1984, Hopkin 1997, Rusek 1998, Bradford et al. 2017). The
98 responses of micro-arthropods to experimental manipulation are complex
99 (Coyle et al. 2017) because micro-arthropod communities are linked to
100 vegetation (Coulson et al. 2003, Mitchell et al. 2016, Mitchell et al. 2017), to
101 food availability (many soil micro-arthropods are fungivorous or
102 bacterivorous species), and to microclimatic conditions (Coulson et al. 1996,
103 Hodkinson et al. 1998, Sjursen et al. 2005). On the species level, responses
104 of micro-arthropods are likely to be trait-dependent. For example, Makkonen
105 et al. (2011) found drought tolerant, large bodied, surface living Collembola
106 to be most tolerant to experimental warming treatments, and Bokhorst et al.
107 (2012) found small bodied fauna to be more sensitive to winter climate
108 change than large bodied.
109
110 In this study, we assess the recovery of micro-arthropod (i.e. Collembola and
111 Acari) communities in an alpine ecosystem in southern Norway nine years
112 after the end of a seven year nutrient addition and warming experiment
113 (Klanderud and Totland 2005). In this system, Hågvar and Klanderud (2009)
114 found distinct responses of micro-arthropod communities to nutrient addition

with and without warming. Additionally, Olsen and Klanderud (2014) reported incomplete recovery of the vegetation five years after cessation of the treatments, but found that herbivore grazing increased recovery compared to when herbivores were fenced out. We used this experiment to test the hypothesis that micro-arthropod communities follow the same recovery pattern as the vegetation. Specifically, we do not expect full recovery, but increased recovery rates with herbivory. In addition, we expect that large bodied, drought resistant Collembola that live on top of the soil will be faster to recover - as they are better adapted to variable environmental conditions - than species living deeper within the soil. We assess recovery in terms of abundance, species richness, and species composition, by comparing plots that received environmental manipulation to control plots. The results of this study will help us understand to what extent common and important micro-arthropods can recover from environmentally induced changes in alpine ecosystems.

Materials and methods

Study system

This study was performed at the southwest-exposed slope of Mt. Sanddalsnuten in Southern Norway (60° 36' 55" N, 7° 31' 8" E) at

approximately 1500 m a.s.l. The site has calcareous phyllite bedrock and is dominated by *Dryas octopetala* heath (see Klanderud and Totland 2004) for detailed site description and vegetation species lists). The mean monthly summer temperature (June – August) at the nearest meteorological station (Finse; located 2.5 km from the plots, at 1210 m a.s.l) is +6.3 °C with an average monthly precipitation of 89 mm over 1969-1990 (Aune 1993, Førland 1993). In the month of sampling for this study (June 2016), the average temperature was +6.1 °C and 67.6 mm of precipitation (Norwegian Meteorological Institute, eklima database). The area is moderately grazed by domestic sheep and wild reindeer (*Rangifer tarandus* Linneus, 1758). Lemming (*Lemmus lemmus* Linneus, 1758) populations in Finse peaked in 2014, while other rodent species showed low abundances throughout the entire duration of the study (Framstad 2017).

In July 2000, ten blocks of four 1 × 1 m plots were randomly established in the *Dryas* heath (Klanderud and Totland 2005). Within each block, plots received one of four treatments: warming by open top chambers (OTCs), nutrient addition (slow-released NPK fertilizer: 10 g N, 2 g P and 8 g K per m^2 at the start of each growing season), nutrient addition combined with

153 warming, and control (no treatment). Within each plot, two permanent 60 ×
154 30 cm vegetation-sampling subplots were established, separated by a 10 cm
155 wide row. In these subplots, vegetation was recorded in 2000 and 2003 to
156 assess vegetation responses to the treatments (Klanderud and Totland 2005,
157 Klanderud 2008). In 2004, Hågvar and Klanderud (2009) sampled soil micro-
158 arthropods in the row between the subplots. The environmental treatments
159 were discontinued in 2007, after seven years of treatment. In the same year,
160 herbivore fences designed to exclude all mammalian herbivores were
161 randomly erected around half the plots within each block, while ensuring that
162 each treatment had the same number of fenced and unfenced plots overall (see
163 Olsen and Klanderud 2014 for more details). Vegetation was again recorded
164 in 2007 and 2012 to assess vegetation recovery under different grazing
165 regimes (Olsen and Klanderud 2014). The herbivory treatment continued
166 until the sampling for this study in June 2016. Figure 1 illustrates the study
167 and plot design in more detail.
168
169 *Arthropod sampling and identification*
170 We sampled micro-arthropods on June 28, 2016 by extracting eight soil cores
171 from each plot (10 cm^2 surface area, 3 cm deep) which included the vegetation

172 and litter on top of the soil. The soils at this site are approximately 5 – 15 cm
173 deep. Our methodology followed Hågvar and Klanderud (2009), but to avoid
174 sampling from disturbed soil (by the sampling in 2004), we took four soil
175 cores from within each vegetation subplot, approximately 20 cm from the
176 original sampling locations (see Figure 1c). Micro-arthropods were then
177 extracted onto water saturated with benzoic acid with the same high-gradient
178 apparatuses modified after Macfadyen (1961) as used in 2004. Extractions
179 lasted for 10 days with a gradual increase in temperature from 30 to 70 °C
180 during the first five days. After extraction, the animals were transferred into
181 containers with 70% ethanol. Collembola and Acari were sorted under a
182 binocular stereomicroscope and identified under a phase-contrast microscope
183 (Leica DM2500). The identification of Collembola followed Fjellberg
184 (1998), Bretfeld (1999), Potapov (2001), and Dunger and Schlitt (2011).
185 Within Acari, Oribatida were identified to species following Weigmann
186 (2006). The order Oribatida presently also includes the cohort Astigmatina
187 (after Krantz and Walter 2009) which were grouped separately and not
188 identified to species level. Other, non-Oribatid, Acari were grouped into
189 Prostigmata and Mesostigmata (including Gamasina and Uropodina). For
190 analyses, species were grouped in accordance with the study with the lowest

taxonomic detail (i.e. this one or Hågvar and Klanderud 2009). See Table S1 for Collembola and Table S2 for Acari identifications, abbreviations and groupings.

Eco-morphological groups

Collembola were grouped into eco-morphological groups that describe their vertical distribution in the soil: epi-edaphic species live above the surface of the soil, hemi-edaphics live near the soil surface, and eu-edaphic species live in deeper layers of the soil. Classifications were based on Hopkin (1997) and the personal database of Prof. dr. Matty Berg (unpublished, but see Makkonen et al. 2011). "*Isotoma* sp." and "Other Symphypleona" could contain species belonging to more than one eco-morphological group and were therefore excluded from statistical analysis on eco-morphological groups (see Table S1).

Statistical analyses

We examined the effects of environmental treatment, sampling year, and herbivory on Collembola and Acari abundance and species richness with linear mixed-effect models using the lmerTest-package (Kuznetsova et al.

2015), lme4-package (Bates et al. 2014), and output via the sjPlot-package (Lüdecke 2016) in R version 3.4.2 (R Development Core Team, 2017). In these models, environmental treatment (levels: warming, nutrient addition, both warming and nutrient addition, and control) and a combined variable of year and herbivory treatment (year+herbivory, levels: 2004: herbivory, 2016: herbivory, 2016: no herbivory) were included as fixed factors and block (numbered 1 through 10) as random factor. To meet assumptions of normality of the residuals, and heteroscedasticity, abundance data were natural log transformed. For species richness, generalized mixed effects models from the Poisson family (log link) were used. Due to very low abundances, the epi-edaphic Collembola dataset only allowed for a binomial model on absence or presence in treatments, and Astigmatina were not analyzed separately. To test for *a priori* differences in abundance for all Collembola and Acari groups between herbivory treatments, we performed separate mixed-model analysis on the 2004 data with environmental treatment and herbivory treatment (future herbivory, no future herbivory) as fixed factors, and block as random effect. To test whether treatment effects remained in 2016 and whether controls differed between years, we performed Tukey pairwise comparisons with the emmeans package (Lenth et al. 2017) for all treatments versus the

control, for both grazed and ungrazed plots. We consider the abundance of soil-microarthropods to be recovered when there are no differences between the plots that received environmental treatment and the controls.

To examine how the species composition of Collembola and Oribatida in the treatment plots changed over time, we used unconstrained and constrained multivariate ordination techniques. First, we used global non-metric multidimensional scaling (GNMDS) to examine the trajectory of the Collembola and Oribatida species composition of the different environmental treatments from 2004 to 2016. The GNMDS was run as specified in Olsen and Klanderud (2014). Because no sampling prior to the start of the treatments was performed, we interpret a shift towards the species composition of control plots as indication of recovery (Figure S1). Second, to test for treatment effects on species composition in 2004 and 2016, we used redundancy analysis (RDA). In this analysis, environmental treatment and herbivore treatment, as well as their interactions, were used as explanatory variables, and block was used as a conditioning variable. To assess variable significances, we used Monte Carlo permutation tests with 999 permutations. Then, to visualize the relative effects of treatments over time and the response

of species of different edaphic groups (for Collembola), we used principal response curves (PRC). The environmental treatment with and without grazing exclosure and year were used as explanatory variables in the construction of the PRCs.

Results

Abundance and species richness

Four years of nutrient addition and nutrient addition combined with warming led to an increase in the abundance of Collembola in 2004 (Table 1, Figure 2, and see Hågvar and Klanderud 2009). However, there were no differences in Collembola abundance between the environmental treatments and controls in 2016 (Table S3), which satisfies our interpretation of recovery in terms of abundance. Nine years after cessation of the environmental treatments (i.e. in 2016), overall Collembola abundance was reduced compared to 2004, but only significantly so in ungrazed plots ($p < 0.001$). The decrease in Collembola abundance was strongest for the nutrient addition with warming treatments that were grazed ($p = 0.05$). Although Collembola were also less abundant in the ungrazed control plots in 2016 compared to 2004 (Table S3) this effect was small compared to the responses in the plots that received

environmental treatment, supporting the validity of the responses of Collembola abundance to nutrient addition and warming treatments.

The responses of Collembola to, and recovery from, nutrient addition and warming treatments were mainly driven by the abundance of hemi-edaphic species (Table 1 and Figure 2c). Eu-edaphic Collembola also responded to nutrient addition ($p = 0.014$). However, their tendency to decrease (i.e. recover) in abundance after cessation of treatments was not significant to the $p = 0.05$ level (grazed: $p = 0.090$, ungrazed: $p = 0.070$). Hemi-edaphic Collembola were more abundant *a priori* in grazed than ungrazed plots (est. = 1.06, std. error = 0.34, df = 31.92, $t = 3.079$, $p = 0.004$, Figure S2), but despite that, reductions in abundance were generally stronger in ungrazed plots (Table 1). We found no effects of environmental treatment, year, or herbivory on the species richness of Collembola communities (Table S4).

The abundance of all Acari, as well as the subgroups Oribatida, and Prostigmata was not affected by environmental treatments (Table 2). This means there is no recovery, or lagged response to environmental treatments for these groups. The abundance of Acari overall ($p = 0.001$, Table 2 and

285 Figure S3) and in the controls (Table S3) was lower in 2016 compared to
286 2004, suggesting some inter-annual variability in Acari abundance. The
287 abundance of the subgroup Mesostigmata however, responded positively to
288 nutrient addition alone and in combination with warming, and recovered after
289 cessation of the treatments (Table 2, Figure S3d, Table S3). We found no
290 effect of environmental treatment or herbivory on Oribatida species richness
291 (Table S5). Generally, responses in grazed and ungrazed plots were in similar
292 directions, indicating that the treatments and/or the sampling year had greater
293 effects than herbivory.
294
295 *Community composition and recovery*
296 The Collembola species composition was strongly affected by treatments
297 with nutrient addition, as shown by a clear separation in ordination space from
298 warming treatments and controls (Figure 3a). This was driven by a shift in
299 dominance structure in favor of certain Collembola species, most notably the
300 two hemi-edaphic species *Folsomia quadrioculata* and *Parisotoma notabilis*
301 (Figure S4, and see Hågvar and Klanderud 2009). During the recovery period,
302 from 2004 to 2016, species composition in all environmental treatments and
303 the controls was displaced along GNMDS axis 1 and to some extend along

304 GNMDS axis 2. In general, Collembola composition converged to one point
305 in ordination space, regardless of herbivory treatment. However, control plots
306 remained separated in ordination space from those that received treatments
307 with nutrient addition, indicating incomplete recovery. For all environmental
308 treatments except warming, displacement in ordination space was larger for
309 ungrazed plots. For Oribatida, the only Acari group identified to species in
310 this study, species compositions were tightly clustered in ordination space in
311 2004, except for ungrazed nutrient addition and grazed nutrient addition with
312 warming treatments (Figure 3b). After the recovery period (i.e. in 2016), all
313 environmental treatments show similar amounts of displacement along
314 GNMDS axis 1, and to some extent along axis 2. In contrast to Collembola,
315 Oribatida species composition of the different environmental treatments
316 diverged into ordination space, suggesting lack of recovery.
317
318 In accordance with the GNMDS plot, the RDA-analysis showed that the
319 species composition of Collembola communities was significantly affected
320 by all environmental treatments in 2004 (Table 3), but most strongly by
321 treatments with nutrient addition, and that this was mainly driven by the hemi-
322 edaphic *F. quadrioculata* and *P. notabilis* (Figure 4a). In 2016, the effect of

treatments with nutrient addition on the Collembola community remained, but was less pronounced than in 2004, suggesting partial recovery. In 2016, species composition differed significantly between grazed and ungrazed plots overall and differed for grazed and ungrazed plots within the nutrient addition treatment. This suggests that grazing affects the Collembola community composition. For Oribatida, the RDA showed that community composition was significantly affected by nutrient addition in 2004, which was reduced to non-significant in 2016 (i.e. recovery). While there was no notable effect of warming in 2004, there was in 2016 (Table 3, Figure 4b). Similar to Collembola, Oribatida community composition differed between grazed and ungrazed plots, specifically in nutrient addition treatments, suggesting that grazing also affects Oribatida communities.

Discussion

The aim of this study was to assess the recovery of micro-arthropod (Collembola and Acari) communities nine years after cessation of different environmental manipulation treatments. We hypothesized that micro-arthropod recovery would keep pace with the partial recovery of the vegetation (Olsen and Klanderud 2014). However, we found recovery only

342 for some aspects of the soil micro-arthropod community. On the one hand,
343 we found full recovery in terms of abundance for Collembola and
344 Mesostigmata, the only Acari group that initially responded to environmental
345 treatments. On the other hand, for species composition, we found persisting
346 differences between the treatments nine years after cessation, and thus no
347 clear sign of recovery. The effect of herbivores on recovery in terms of
348 abundance were minor. However, both Collembola and Oribatida
349 communities differed in their species composition in grazed and ungrazed
350 plots. Hemi-edaphic Collembola that live near the soil-surface interface, in
351 particular *Folsomia quadrioculata*, were most responsive to environmental
352 treatments and remained dominant in Collembola communities after the
353 recovery period.
354
355 Although the vegetation in our alpine system had not completely recovered
356 from nutrient addition treatments by 2016 (personal observation, Olsen and
357 Klanderud 2014), we propose several mechanisms that may have contributed
358 to the observed recovery of Collembola abundance. First, nutrient addition
359 may have had a direct, stimulatory effect on the microbial and fungal
360 community, which is an important part of the micro-arthropod diet (Mack et

al. 2004, Nemergut et al. 2008, A'Bear et al. 2014). If this effect was reduced shortly after cessation of the treatments, there may not have been sufficient food available to sustain high Collembola abundances. However, the effects of nitrogen addition are reported to be long-lasting and recovery is often incomplete (Street et al. 2015, Bowman et al. 2018), so the availability of food to fungivorous micro-arthropods would have to be tested directly. Second, an increase in the abundance of predators could have lowered Collembola abundance. For example, we found predatory Mesostigmata to increase in parallel with Collembola and, together with other predators such as Lycosidae (Lawrence and Wise 2000, Wise 2004), they may have suppressed Collembola populations (Koehler 1997, Koehler 1999, Schneider and Maraun 2009). It is likely that Mesostigmata recovered in our study as their prey (Collembola) abundance recovered to pre-treatment levels. Further, epi- and hemi-edaphic Collembola are considered to be opportunistic, requiring higher food quality, and having higher fecundity and mobility, but also mortality (Petersen 2002), than eu-edaphic species and Oribatida. These life-history strategies can explain why hemi-edaphic Collembola were most responsive to our treatments as well as why their abundance recovered quickly when conditions became less favorable. Finally, our plots are

surrounded by a matrix of untreated terrain, which could have aided recovery in a source-sink like system (Bengtsson 2002). For example, in a microcosm experiment, Shackelford et al. (2018) showed that isolated micro-arthropod communities recover at slower rates from a disturbance than those connected to other, disturbed or undisturbed, communities. It is therefore possible that, should the entire alpine landscape be affected by changes in environmental conditions, recovery will be slower than was observed in our experimental study. Such scaling up from experimental plot to landscape scale remains one of the major challenges in ecology (Levin 1992, Dunne et al. 2004, Jackson and Fahrig 2015).

While we found that Collembola and Mesostigmatid mites recovered in terms of abundance, we found that differences in Collembola species composition for nutrient addition and nutrient addition with warming treatments compared to the controls remained throughout the nine-year recovery period. In contrast, the composition of the Oribatid mite community only responded to nutrient addition and fully recovered nine years after cessation of the treatment. However, Oribatida did respond to warming treatment after sampling in 2004 or during the recovery period, suggesting that Oribatida

399 communities may take a long time to respond and thus adapt to environmental
400 change. Similar responses, i.e. a fast recovery of abundance but slower
401 responses in terms of species composition, were found for Collembola and
402 Oribatida communities recovering from experimental summer drought in a
403 boreal forest (Lindberg and Bengtsson 2005).
404
405 The changes in Collembola community composition in our study were mostly
406 driven by *Folsomia quadrioculata,* which dominated communities that
407 received nutrient addition, and remained dominant after the nine-year
408 recovery period, although its abundance did decrease. *Folsomia*
409 *quadrioculata* is a common, generalist species that can be found in many
410 different habitats from forests at mid-latitudes to the high Arctic (Somme and
411 Birkemoe 1999, Sengupta et al. 2016), and is able to colonize glacial
412 forelands approximately 50 years after glacial retreat (Hågvar 2010). In alpine
413 ecosystems in Norway, *F. quadrioculata* has one generation per year
414 compared to species such as *F. brevicauda*, which has a longer, two year life
415 cycle (Fjellberg 1975). *Folsomia brevicauda* was only abundant in the
416 controls and the warming treatments in our study. Its opportunistic life-

417 history strategy could make *F. quadrioculata* highly adaptive to short-term
418 environmental changes.
419
420 Grazing by herbivores can affect the structure and composition, competitive
421 interactions, and chemistry of arctic and alpine vegetation, although its impact
422 is often time and place dependent (Bernes et al. 2015, Barrio et al. 2016 and
423 references therein). In addition, herbivory can act as a buffer against the
424 effects of climatic change (e.g. Olofsson et al. 2009) and can increase the rate
425 of recovery after environmental manipulations are ceased (Olsen and
426 Klanderud 2014, Kaarlejärvi et al. 2015). We therefore hypothesized that the
427 increased vegetation recovery of grazed plots in our experiment (Olsen and
428 Klanderud 2014) would translate into increased recovery rates of micro-
429 arthropods. However, our results do not fully support this hypothesis as we
430 generally found stronger reductions (i.e. recovery) in Collembola abundances
431 in ungrazed versus grazed plots. Further, herbivory affected the species
432 composition of both Collembola and Oribatida communities and we found
433 different species compositions in grazed versus ungrazed nutrient addition
434 treatments for both Collembola and Oribatida. Nevertheless, it is difficult to
435 interpret these differences as evidence for increased or decreased recovery

because all plots, including controls, showed changes in species composition between the sampled years. These changes may be due to the high spatial heterogeneity in alpine soils (Opedal et al. 2015), or temporal (year-to-year) variation in community composition (Somme and Birkemoe 1999, Coulson et al. 2003, Ims et al. 2004, Alatalo et al. 2017). Alternatively, they can be explained by background warming or changes in other climatic variables, such as date of snow melt (see Høye and Forchhammer 2008), during the twelve years between sampling.

Our results show that soil micro-arthropods are responsive to environmental treatments in terms of abundance and species composition, and that recovery from these responses is only partial when treatments are ceased. An important next step is to understand how persistent changes in micro-arthropod decomposer communities translate into the functional composition of the decomposer community (Handa et al. 2014) and thereby ecosystem processes such as decomposition, nutrient cycling, and ecosystem respiration.

Author contributions

The study was designed by J.A., J.M.A., and K.K. Field work was performed by R.E.R., J.A., K.K., and T.B.. P.L and N.R. identified micro-arthropods. Statistical analyses were performed by R.E.R. and S.L.O. All co-authors contributed to manuscript revisions, and agree with the final version.

Acknowledgements

This study was funded by Carl Tryggers stiftelse för vetenskaplig forskning through a grant to J.M.A. and a grant from the Research Council of Norway (249902) to J.A. We thank Sigmund Hågvar for sharing his original data, comments and feedback, Hans Cornelissen and Stef Bokhorst for useful discussions, and Matty Berg for sharing data from his personal Collembola database. Mari Steinert, Ross Wetherbee, Mahdieh Tourani, and Richard Bischof were of great help for discussions on the statistical analyses. We thank the Finse Alpine Research Center and Erika Leslie for hospitality during fieldwork and Kristel van Zuijlen assisted with sampling in the field.

Data accessibility

Data associated with this manuscript are deposited in the Dataverse Network Norway (https://dataverse.no/) at (DOI will be given upon acceptance of the manuscript).

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773 Tables

774 *Table 1.*

Table 1. Model parameter estimates from linear mixed-effect and binomial models examining the effects of treatment (control (C), warming (W), nutrient addition (N), nutrient addition + warming (NW)), the three year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory) and their interactions on Collembola abundance. Data for all, hemi-, and eu-edaphic Collembola were natural log transformed. The odds of presence of epi-edaphic Collembola was tested for treatments only. Model estimates from mixed-effect models are shown on the log or square root scale. P-values were computed via Kenward-Roger approximation and significant results ($p < 0.05$) are printed in bold.

	Collembola (log)				**Epi-edaphic Collembola (binomial)**			**Hemi-edaphic Collembola (log)**				**Eu-edaphic Collembola (log)**			
Predictors	*Estimates*	*CI*	*p*	*df*	*Odds Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*df*	*Estimates*	*CI*	*p*	*df*
(Intercept)	3.39	3.12 – 3.67	**<0.001**	66.00	3.00	1.16 – 9.22	**0.033**	2.79	2.44 – 3.14	**<0.001**	67.00	2.28	1.85 – 2.71	**<0.001**	51.00
N	1.42	1.05 – 1.80	**<0.001**	59.00	1.89	0.40 – 10.50	0.433	1.71	1.22 – 2.20	**<0.001**	59.00	0.83	0.29 – 1.37	**0.014**	59.00

NW	1.34	0.97 – 1.72	**<0.001**	59.00	1.00	0.23 – 4.30	1.000	1.64	1.15 – 2.13	**<0.001**	59.00	0.27	-0.27 – 0.81	0.412	59.00
W	0.03	-0.34 – 0.41	0.880	59.00	1.89	0.40 – 10.50	0.433	-0.36	-0.85 – 0.13	0.227	59.00	0.35	-0.19 – 0.89	0.287	59.00
2016 no herbivory	-1.10	-1.57 – -0.64	**<0.001**	63.00				-1.13	-1.74 – -0.52	**0.003**	63.00	-1.15	-1.82 – -0.47	**0.007**	62.00
2016 herbivory	-0.39	-0.86 – 0.07	0.170	63.00				-0.48	-1.09 – 0.12	0.195	63.00	-0.71	-1.38 – -0.03	0.090	62.00
N : 2016 no herbivory	-0.66	-1.32 – -0.01	0.102	61.00				-0.86	-1.71 – -0.00	0.103	61.00	-0.24	-1.18 – 0.70	0.671	60.00
NW : 2016 no herbivory	-0.73	-1.40 – -0.06	0.076	65.00				-1.12	-1.98 – -0.25	**0.038**	65.00	0.70	-0.26 – 1.67	0.236	63.00
W : 2016 no herbivory	0.69	0.02 – 1.36	0.095	66.00				1.28	0.41 – 2.15	**0.018**	66.00	0.21	-0.76 – 1.19	0.719	64.00
N : 2016 herbivory	-0.76	-1.42 – -0.11	0.060	61.00				-0.54	-1.40 – 0.31	0.298	61.00	-1.05	-1.99 – -0.11	0.070	60.00
NW : 2016 herbivory	-0.81	-1.48 – -0.14	**0.050**	65.00				-0.70	-1.56 – 0.17	0.191	65.00	0.09	-0.88 – 1.06	0.879	63.00

W : 2016 herbivory	-0.06	- 0.73 – 0.61	0.886	66.00		0.58	-0.29 – 1.45	0.278	66.00	-0.39	-1.37 – 0.59	0.513	64.00

Random Effects

σ^2	0.26		0.44	0.53
τ_{00}	0.02 $_{Block}$		0.02 $_{Block}$	0.15 $_{Block}$
ICC	0.06 $_{Block}$		0.04 $_{Block}$	0.22 $_{Block}$
Observations	80	80	80	80
Marginal R^2 / Conditional R^2	0.679 / 0.698	0.016 / 0.025	0.643 / 0.657	0.335 / 0.483

775

Table 2. Model parameter estimates from linear mixed-effect and binomial models examining the effects of treatment (control (C), warming (W), nutrient addition (N), nutrient addition + warming (NW)), the three year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory) and their interactions on Acari abundance. Data were natural log transformed and model estimates are shown on the log scale. P-values were computed via Kenward-Roger approximation and significant results ($p < 0.05$) are printed in bold.

	Acari (log)				**Oribatida (log)**				**Prostigmata (log)**				**Mesostigmata (log)**			
Predictors	*Estimates*	*CI*	*p*	*df*	*Estimates*	*CI*	*p*	*df*	*Estimates*	*CI*	*p*	*df*	*Estimates*	*CI*	*p*	*df*
(Intercept)	3.67	3.39 – 3.95	**<0.001**	65.00	2.66	2.27 – 3.04	**<0.001**	41.00	3.08	2.75 – 3.42	**<0.001**	65.00	0.81	0.45 – 1.18	**0.001**	41.00
N	0.38	0.01 – 0.75	0.100	59.00	0.10	-0.35 – 0.55	0.711	59.00	0.37	-0.08 – 0.82	0.178	59.00	1.05	0.62 – 1.47	**<0.001**	59.00

NW	0.29	-0.08 – 0.67	0.201	59.00	0.00	-0.45 – 0.45	0.991	59.00	0.31	-0.15 – 0.76	0.270	59.00	0.98	0.55 – 1.40	**<0.001**	59.00
W	0.18	-0.19 – 0.56	0.429	59.00	-0.00	-0.45 – 0.45	0.998	59.00	0.30	-0.15 – 0.75	0.279	59.00	-0.14	-0.56 – 0.29	0.602	59.00
2016 no herbivory	-1.34	-1.81 – -0.88	**<0.001**	63.00	-0.96	-1.53 – -0.39	**0.007**	61.00	-2.15	-2.71 – -1.59	**<0.001**	63.00	-0.84	-1.38 – -0.31	**0.012**	61.00
2016 herbivory	-1.56	-2.03 – -1.10	**<0.001**	63.00	-1.15	-1.71 – -0.58	**0.001**	61.00	-2.44	-3.01 – -1.88	**<0.001**	63.00	-0.77	-1.30 – -0.23	**0.022**	61.00
N : 2016 no herbivory	0.51	-0.14 – 1.16	0.206	60.00	0.29	-0.49 – 1.08	0.540	60.00	1.30	0.51 – 2.09	**0.008**	60.00	-0.35	-1.09 – 0.39	0.443	60.00
NW : 2016 no herbivory	-0.38	-1.04 – 0.29	0.357	65.00	-0.59	-1.40 – 0.23	0.239	62.00	0.18	-0.63 – 0.98	0.718	65.00	-1.08	-1.84 – -0.31	**0.025**	62.00
W : 2016 no herbivory	0.27	-0.40 – 0.94	0.509	65.00	0.49	-0.33 – 1.31	0.328	63.00	0.29	-0.52 – 1.09	0.563	65.00	0.49	-0.28 – 1.27	0.299	63.00

N : 2016 herbivory	-0.45	-1.10 – 0.20	0.263	60.00	-0.65	-1.44 – 0.13	0.177	60.00	-0.09	-0.88 – 0.69	0.846	60.00	-0.74	-1.48 – -0.00	0.105	60.00
NW : 2016 herbivory	-0.22	-0.88 – 0.45	0.593	65.00	-0.34	-1.16 – 0.47	0.493	62.00	0.26	-0.54 – 1.06	0.596	65.00	-0.64	-1.41 – 0.13	0.174	62.00
W : 2016 herbivory	0.39	-0.28 – 1.06	0.346	65.00	0.45	-0.37 – 1.27	0.371	63.00	0.76	-0.04 – 1.57	0.125	65.00	0.11	-0.67 – 0.88	0.821	63.00
Random Effects																
σ^2	0.26				0.37				0.38				0.33			
τ_{00}	0.03 $_{Block}$				0.17 $_{Block}$				0.04 $_{Block}$				0.15 $_{Block}$			
ICC	0.09 $_{Block}$				0.32 $_{Block}$				0.09 $_{Block}$				0.32 $_{Block}$			
Observations	80				80				80				80			
Marginal R^2 / Conditional R^2	0.681 / 0.710				0.424 / 0.607				0.736 / 0.760				0.494 / 0.654			

778 *Table 3*

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780

Table 3. *F* and *P*-values (significance levels: **P* < 0.05, ***P* < 0.01, ****P* < 0.001) of RDA analysis testing the effects of nutrient addition (N), warming (W), and warming combined with nutrient addition (NW) and herbivore exclosures (E) on species composition of the Collembola and mite communities at Finse, Norway, in 2004 and 2016. Significant effects at *P*<0.05 are printed in bold.

	Collembola		**Oribatida**	
Treatment	**2004**	**2016**	**2004**	**2016**
N	**6.03 ****	**3.79 ***	**3.42***	1.39
NW	**10.66 *****	**4.70 ***	1.60	0.30
W	**3.96 ***	0.62	0.54	**4.40***
E	0.50	**5.25 ***	0.24	**3.48***
N×E	0.94	**3.21 ***	0.84	**3.95***
NW×E	1.49	0.57	0.74	0.69
W×E	0.14	0.83	0.45	1.02

Figure captions

Figure 1.

Figure 1. a) A timeline of the experiment at Finse and measurements taken. Leaf symbols indicate years of vegetation recording (2000, 2003, 2007, and 2012), mite symbols indicate arthropod sampling (2004 and 2016). From 2000 to 2007, plots received environmental treatments (nutrient addition and/or warming by open top chambers, OTCs). In 2007, treatments were ceased and herbivore fences were erected around half of the plots until sampling for this study in 2016. b) Each block contains four plots that each received an environmental treatment. In 2007, two plots of each block were randomly selected to be fenced, ensuring that, overall, an equal number of plots for each treatments was fenced or left unfenced. In total, the study contained 10 blocks and 40 plots. c) Soil micro-arthropods were sampled in between the two 60 × 30 cm vegetation subplots (open circles) in 2004 and from the middle of each vegetation subplot in 2016 (closed circles).

Figure 2.

Figure 2. Mean abundance (in thousands m^{-2}) for a) all Collembola, b) epi-edaphic Collembola, c) hemi-edaphic Collembola, and d) eu-edaphic

Collembola per treatment (control, nutrient addition, warming, and nutrient addition + warming) per sampled year in Finse, southern Norway. Data are shown on the non-transformed scale but error bars indicate exponentiated 95% confidence intervals calculated on natural log transformed data (but on square root data for epi-edaphic Collembola).

Figure 3.

Figure 3. GNMDS ordination of the trajectory of mean Collembola a) and Oribatida b) community composition from 2004 (start of arrow) to 2016 (end of arrow) in control, warming, nutrient addition, and warming combined with nutrient addition treatments with herbivores present (solid line) and herbivores excluded (dashed line) in an alpine heath at Finse, Norway. Species names are shown only for the 12 most common Collembola and 13 most common Oribatida species, the remaining species are shown as open circles. Collembola species names and circles are colored according to edaphic group but some species were grouped and therefore not assigned to a specific edaphic group (no group). A few species names were slightly adjusted to avoid overlap. For species abbreviations, see Table S1 and Table S2.

819

820 *Figure 4.*

821 Figure 4. PRC ordination of a) mean Collembola and b) mean Oribatida
822 community composition in 2004 and 2016 in control, warming, nutrient
823 addition, and warming combined with nutrient addition treatments with
824 herbivores present (solid line) and herbivores excluded (dashed line) in an
825 alpine heath at Finse, Norway. The horizontal grey line represents control
826 plots with herbivores present, to which all other treatments are compared.
827 Species names are shown only for the eight most common Collembola, and
828 six most common Oribatida species. Collembola species names are colored
829 according to their eco-morphological group (epi-edaphic, hemi-edaphic, eu-
830 edaphic). For species abbreviations, see Table S1 and Table S2.

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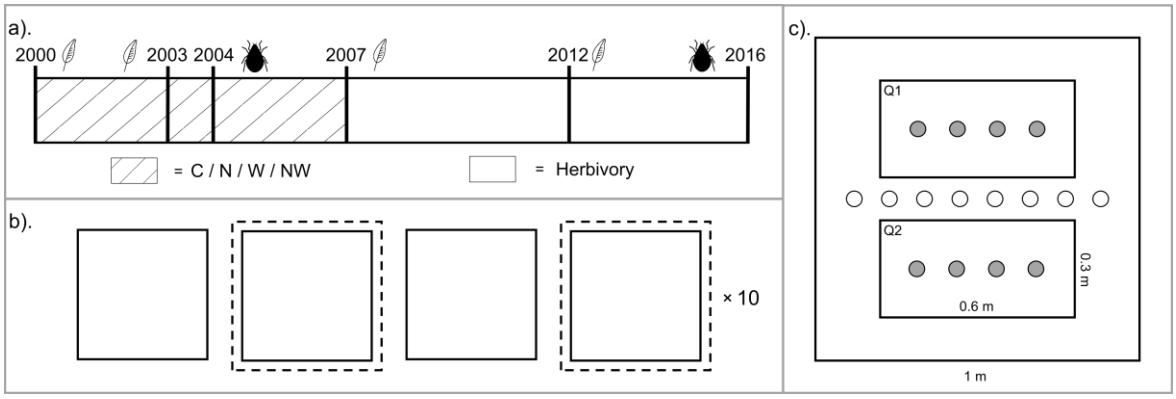
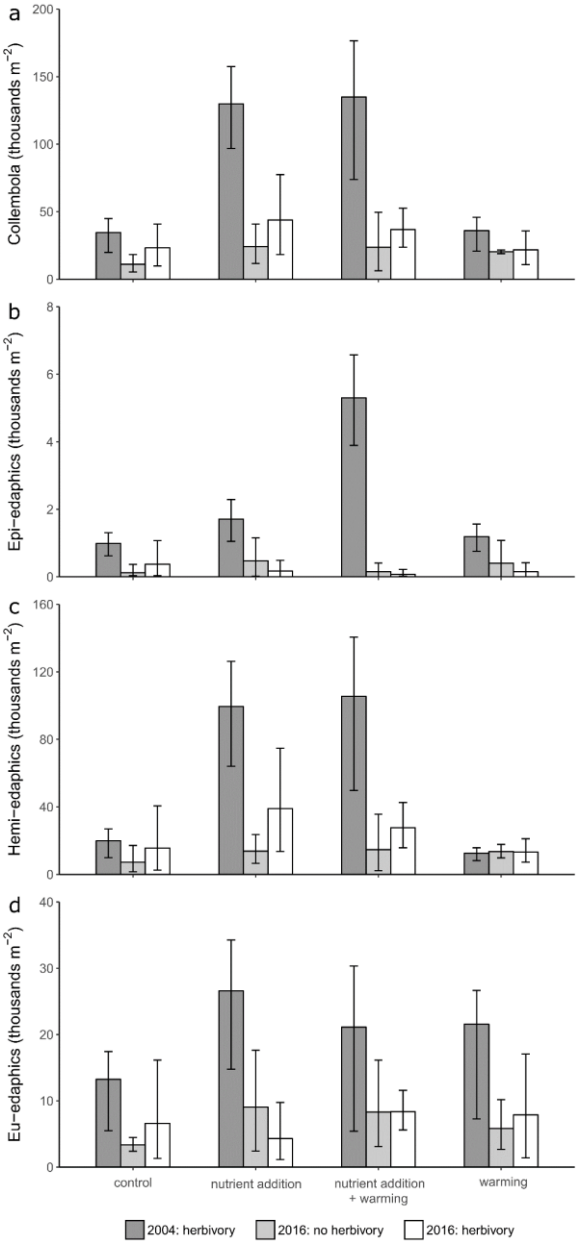
Figures

Figure 1



837 *Figure 2*



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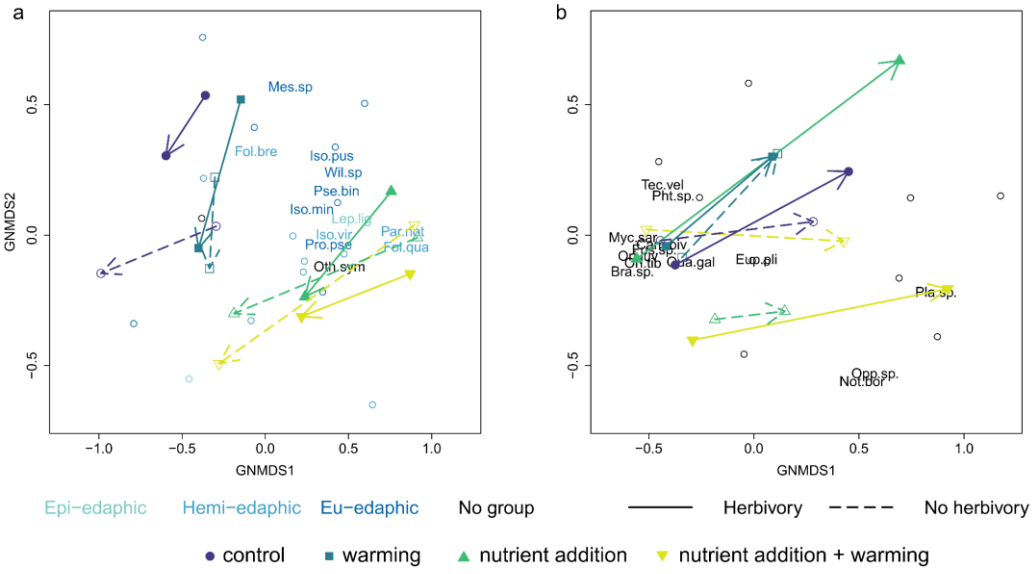
840 *Figure 3*



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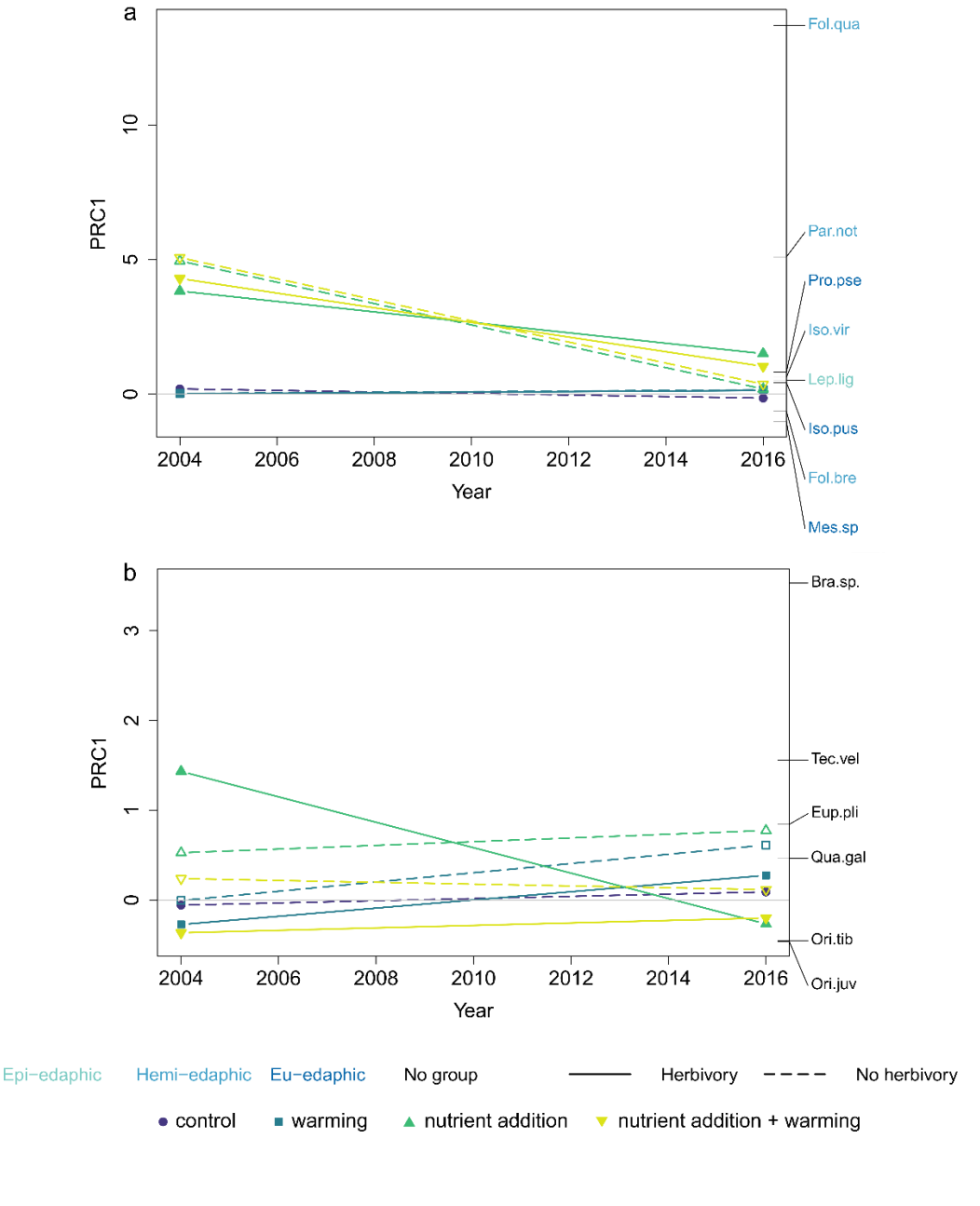
843 *Figure 4*



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Supplementary Figures

Figure S1

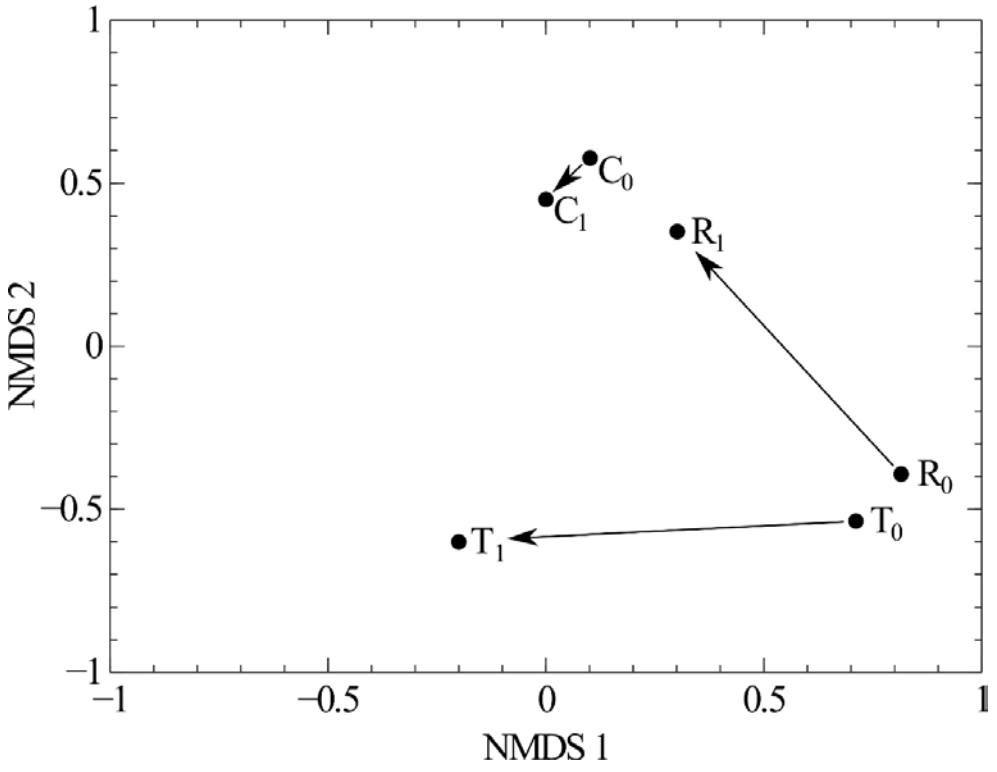


Figure S1. Conceptual diagram of NMDS results. Each community was sampled twice: first, after a certain period of receiving treatment (time = 0) and second, after a period following cessation of treatments (time = 1). The

control community (C) has not received any treatment and its species composition has therefore changed very little between the two sampling years (C_0 very close to C_1 in ordination space). In contrast, the Treatment community (T) has responded strongly to the treatment (T_0 is far from C_0) and shows no sign of recovery (T_1 far from C_1) even though its species composition has changed from time = 0 to time = 1 (as indicated by the arrow). The recovering community (R) initially responded to treatment (R_0 far from C_0), but shows recovery (R_1 close to C_1).

Figure S2

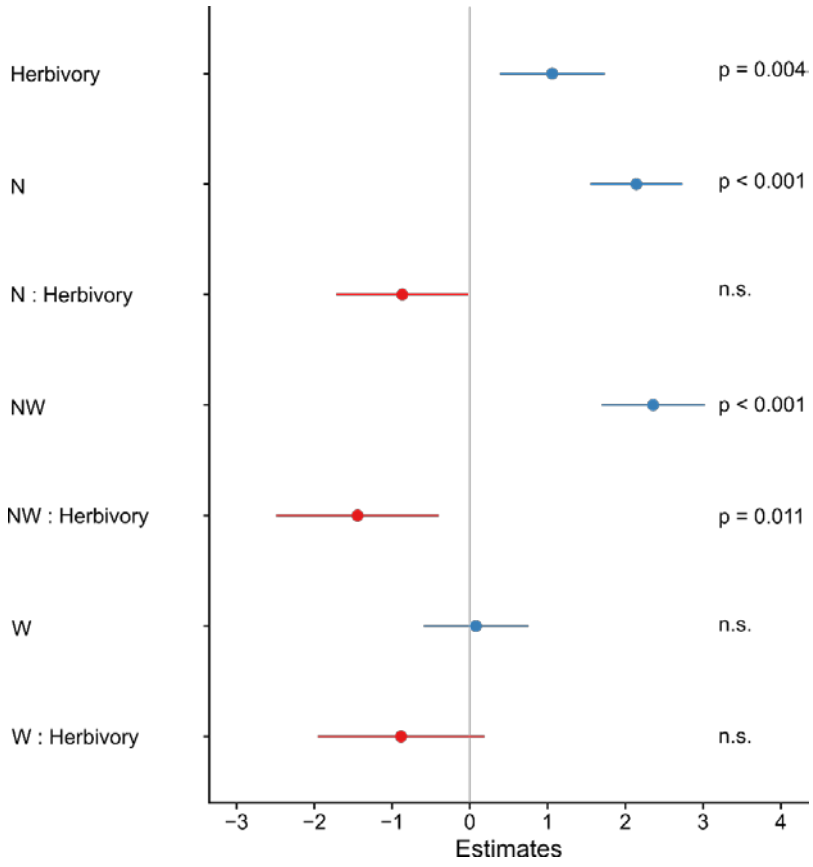
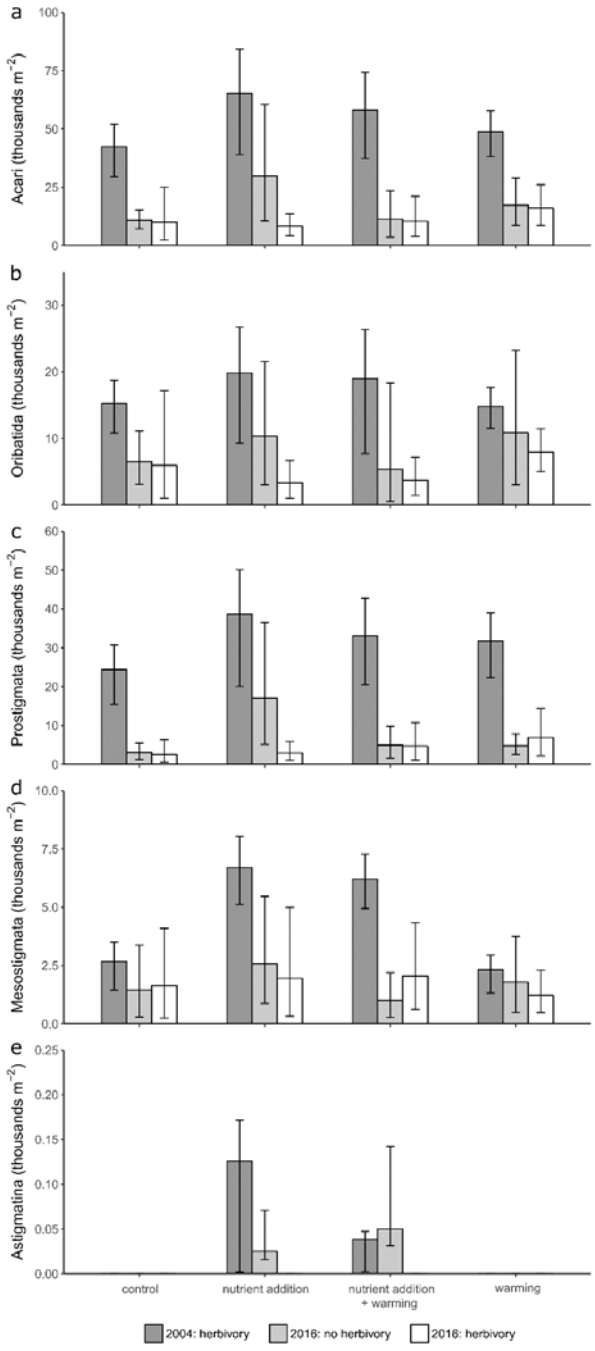


Figure S2. Mixed effect model (log(abundance) ~ treatment*herbivory + (1 | block)) estimates +/- standard error and p-values for hemi-edaphic Collembola after four years of environmental manipulation (blue = positive estimates, red = negative estimates). Plots that would receive grazing from 2007 onwards, had a higher abundance of hemi-edaphic Collembola, and responded less strongly to treatment.

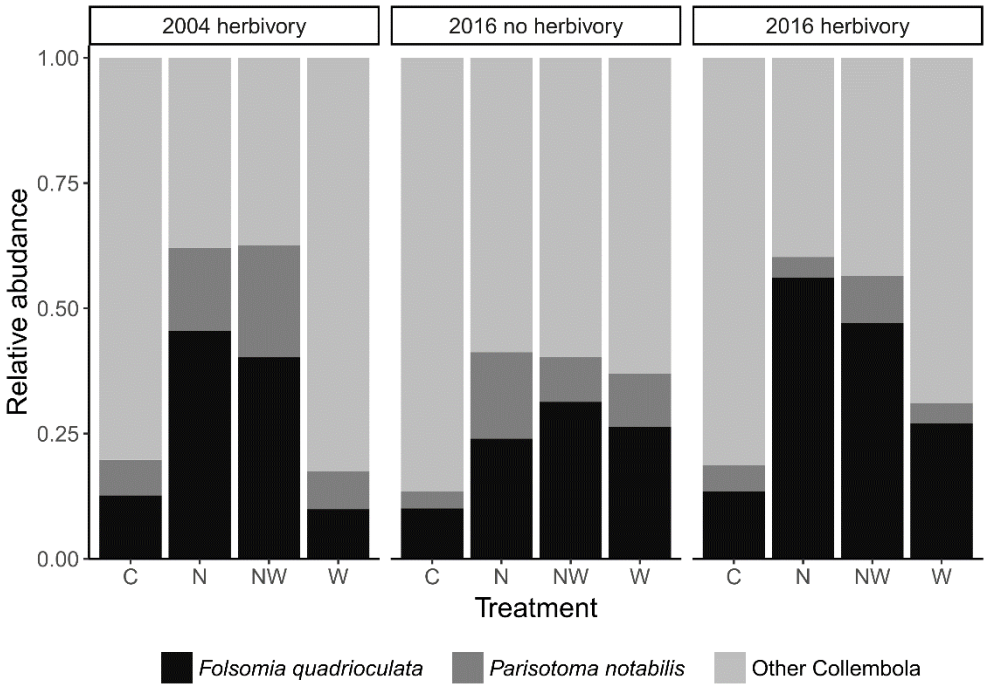

a
Acari (thousands m^{-2})
100
75
50
25
0
b
Oribatida (thousands m^{-2})
30
20
10
0
c
Prostigmata (thousands m^{-2})
60
50
40
30
20
10
0
d
Mesostigmata (thousands m^{-2})
10.0
7.5
5.0
2.5
0.0
e
Astigmatina (thousands m^{-2})
0.25
0.20
0.15
0.10
0.05
0.00
control
nutrient addition
nutrient addition + warming
warming
2004: herbivory
2016: no herbivory
2016: herbivory

27

Figure S3

Figure S3. Mean abundance (in thousands m^{-2}) of a) all Acari, b) Oribatida, c) Prostigmata, d) Mesostigmata, and e) Astigmatina per treatment (control, nutrient addition, warming, and nutrient addition + warming) per sampled year and herbivory treatment in Finse, southern Norway. Data are shown on the non-transformed scale and error bars indicate exponentiated 95% confidence intervals calculated on natural log transformed data, but for Astigmatina on root transformed data.

38 *Figure S4*



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41 Figure S4. Dominance structure of Collembola communities under different
42 environmental treatments (control (C), nutrient addition (N), warming (W),
43 and nutrient addition + warming (NW)) after three years of manipulation
44 (2004) and nine years after cessation of the treatments (2016). *Folsomia*
45 *quadrioculata* and *Parisotoma notabilis* were the most abundant and
46 responsive Collembola species. During the recovery period (2007 - 2016) half
47 the plots were fenced to exclude herbivores while the other half was grazed

Supplementary tables

Table S1

Table S1. The Collembola species identified in this study. Groupings were made according to the study with the lowest taxonomic detail (this study (2016) or Hågvar and Klanderud 2009 (2004)). Species or groups with no equivalent in the other study were unique to that year. Species were divided into eco-morphological groups: epi-edaphic, hemi-adaphic, eu-edaphic. "*Isotoma* sp." and "Other Symphypleona" contain species belonging to several eco-morpholigical groups, and were therefore not assigned one.

2004	**2016**	**Abbreviation**	**Eco-morphological group**
Ceratophysella scotica	*Ceratophysella scotica* Carpenter & Evans, 1899	Cer.sco	Hemi
Isotoma olivacea	*Desoria olivacea* (Tullberg, 1871)	Des.oli	Hemi

Isotoma tolya	*Desoria tolya* Fjellberg, 2007	Des.tol	Hemi
Folsomia brevicauda	*Folsomia brevicauda* Agrell, 1939	Fol.bre	Hemi
Folsomia diplophthalma (Axelson, 1902)	-	Fol.dip	Eu
Folsomia dovrensis	*Folsomia dovrensis* Fjellberg, 1976	Fol.dov	Eu
-	*Folsomia palearctica* Potapov & Babebnko, 2000	Fol.pal	Hemi
Folsomia quadrioculata	*Folsomia quadrioculata* (Tullberg, 1871)	Fol.qua	Hemi
Friesea truncata	*Friesea truncata* Cassagnau, 1958	Fri.tru	Hemi
Isotomiella minor	*Isotomiella minor* (Schaffer, 1896)	Iso.min	Eu
Isotoma sp.	*Isotoma* sp.	Iso.sp.	n.a.
Isotoma viridis	*Isotoma viridis* Bourlet, 1839	Iso.vir	Hemi
Isotomodella pusilla	*Isotomodella pusilla* Martynova, 1967	Iso.pus	Eu
Lepidocyrtus lignorum	*Lepidocyrtus lignorum* (Fabricius, 1775)	Lep.lig	Epi
Megalothorax minimus	*Megalothorax minimus* Willem, 1900	Meg.min	Eu
Mesaphorura sp.	*Mesaphorura critica* Ellis, 1976	Mes.cri	Eu
Mesaphorura sp.	*Mesaphorura sylvatica* (Rusek, 1971)	Mes.syl	Eu
Micranurida forsslundi	*Micranurida forsslundi* Gisin, 1949	Mic.for	Eu

Micranurida pygmaea	*Micranurida pygmaea* Börner, 1901	Mic.pyg	Eu
Isotoma ekmani	*Parisotoma ekmani* (Fjellberg, 1977)	Par.ekm	Eu
Isotoma notabilis	*Parisotoma notabilis* (Schäffer, 1896)	Par.not	Hemi
Protaphorura pseudovanderdrifti	*Protaphorura pseudovanderdrifti* (Gisin, 1957)	Pro.pse	Eu
Pseudanurophorus binoculatus	*Pseudanurophorus binoculatus* Kseneman, 1934	Pse.bin	Eu
Other Symphypleona	*Sminthurinus aureus* (Lubbock, 1836)	Smi.aur	n.a. / Epi
Other Symphypleona	*Deuterosminthurus* cf. *sulphureus* (Koch, 1840)	Deu.sul	n.a / Epi
Other Symphypleona	*Arrhopalites* sp. juveniles	Arr.juv	n.a. / Eu
Other Symphypleona	*Bourletiella* sp.	Bou.sp.	n.a. / Epi
Tetracanthella brachyura	*Tetracanthella brachyuran* Bagnall, 1949	Tet.bra	Hemi
Tetracanthella wahlgreni	*Tetracanthella wahlgreni* Linnaniemi, 1907	Tet.wah	Hemi
-	*Tullbergia simplex* Gisin, 1958	Tul.sim	Eu
Willemia sp.	*Willemia* cf. *intermedia* Mills, 1934	Wil.int	Eu
Willemia sp.	*Willemia denisi* Mills, 1932	Wil.den	Eu
Willemia sp.	*Willemia scandinavica* Stach, 1949	Wil.sca	Eu
Neanura muscorum (Templeton, 1835)	-	Nea.mus	Epi

Table S2. The Acari groups and species in this study. Groupings were made according to the study with the lowest taxonomic detail. Species or groups with no equivalent in the other study were unique to that year. For analysis of species abundance and richness, juveniles and adults were combined for each species/group.

2004	**2016**	**Abbreviation**
	Oribatida	
Belba sp.	*Belba compta* (Kulczynski, 1902)	Bel.com
Brachychthoniidae	*Liochthonius dilutus* Moritz, 1976	Lio.dil
Brachychthoniidae	*Liochthonius lapponicus* (Trägårdh, 1910)	Lio.lap
Brachychthoniidae	*Liochthonius sellnicki* (Thor, 1930)	Lio.sel

Brachychthoniidae	*Brachychochthonius immaculatus* Forsslund, 1942	Bra.imm
Brachychthoniidae	*Brachychochthonius* sp. juveniles	Bra.juv
Brachychthoniidae	*Liochthonius* sp. juveniles	Lio.juv
Camisia sp. adults	*Camisia biverrucata* (Koch, 1839)	Cam.biv
Camisia sp. adults	*Camisia horrida* (Hermann, 1804)	Cam.hor
Camisia sp. juveniles	*Camisia* sp. juveniles	Cam.juv
Carabodes sp.	-	Car.sp.
-	*Ceratozetes gracilis* (Michael, 1884)	Cer.gra
-	*Edwardzetes edwardsi* (Nicolet, 1855)	Edw.edw
-	*Epidamaeus bituberculatus* (Kulczynski, 1902)	Epi.bit
Eupelops sp. adults	*Eupelops plicatus* (Koch, 1835)	Eup.pli
Eupelops sp. juveniles	*Eupelops* sp. juveniles	Eup.juv
Fuscozetes sp.	*Fuscozetes* sp.	Fus.sp.
-	*Kunstidamaeus nidicola* (Willmann, 1936)	Kun.nid
-	*Metabelba parapulverosa* Moritz, 1966	Met.par
Mycobates sp.	*Mycobates sarekensis* Trägårdh, 1910	Myc.sar

Nothrus borussicus	*Nothrus borussicus* Sellnick, 1928	Not.bor
Oppia sp. / Oppiidae	*Oppiella (Oppiella) beskidyensis* (Niemi & Skubala, 1993)	Opp.bes
Oppia sp. / Oppiidae	*Oppiella* (*Moritzoppia*) *escotata* (Subias & Rodriguez, 1986)	Opp.esc
Oppia sp. / Oppiidae	*Oppiella* (*Moritzoppia*) *neerlandica* (Oudemans, 1900)	Opp.nee
Oppia sp. / Oppiidae	*Oppiella* (*Rhinoppia*) *subpectinata* (Oudemans, 1900)	Opp.sub
Oribatula tibialis	*Oribatula tibialis* (Nicolet, 1855)	Ori.tib
Oromurcia sp.	*Oromurcia* sp.	Oro.sp.
Phtiracarus sp. / box mite	*Phtiracarus* sp. / box mite	Pht.sp.
Plathynotrus sp.	*Platynothrus peltifer* (Koch, 1839)	Pla.sp
Plathynotrus sp.	*Platynothrus thori* (Berlese, 1904)	Pla.sp
-	*Punctoribates punctum* (Koch, 1839)	Pun.pun
Quadroppia sp.	*Quadroppia galaica* Mínguez, Ruiz & Subías, 1985	Qua.gal
Suctobelba sp.	*Suctobelba trigona* (Michael, 1888)	Suc.tri
Suctobelba sp.	*Suctobelbella acutidens* (Forsslund, 1941)	Suc.acu

Suctobelba sp.	*Suctobelbella* cf. *sarekensis* (Forsslund, 1941)	Suc.sar
Tectocepheus velatus adults	*Tectocepheus velatus sarekensis* Trägårdh, 1910	Tec.sar
Tectocepheus velatus adults	*Tectocepheus velatus velatus* (Michael, 1880)	Tec.vel
Tectocepheus velatus juveniles	*Tectocepheus* sp. juveniles	Tec.juv
	Astigmatina	
Astigmata	Oribatida / Astigmatina	
Schwiebea	Oribatida / Astigmatina	
	Prostigmata	
Prostigmata	Prostigmata	
Scutacaridae	Prostigmata	
Actinedida	Prostigmata	
	Mesostigmata	
Gamasina adults	Mesostigmata / Gamasina	
Gamasina juveniles	Mesostigmata / Gamasina	

Zerconidae adults	Mesostigmata / Gamasina
Zerconidae juveniles	Mesostigmata / Gamasina
Uropodina	Mesostigmata / Uropodina
Mesostigmata total (Undetermined Mesostigmata + Gamasidae + Zerconidae + Uropodina)	Mesostigmata total (Mesostigmata / Gamasina + Mesostigmata / Uropodina)

Table S3. Results of post-hoc pairwise comparisons between the abundance of all Collembola and Mesostigmata in the treatments (C, N, NW, W) within the year 2016 and between control plots in 2004 and 2016 for abundance of all Collembola and all Acari. Tests were performed on the natural log scale. P-value were adjustment by the Tukey method and significant results ($p < 0.05$) are printed in bold.

Contrast	Ratio	SE	df	t-ratio	p-value
Collembola abundance by treatment in 2016					
C2016: no herbivory – N2016: no herbivory	0.4670973	0.15227290	61.17	-2.335	0.4642
C2016: no herbivory – NW2016: no herbivory	0.5415428	0.18120487	66.93	-1.833	0.7940
C2016: no herbivory – W2016: no herbivory	0.4846853	0.16351790	67.61	-2.147	0.5923

C2016: herbivory – N2016: herbivory	0.5170866	0.16856932	61.17	-2.023	0.6763
C2016: herbivory – NW2016: herbivory	0.5869077	0.19638434	66.93	-1.593	0.9057
C2016: herbivory – W2016: herbivory	1.0240836	0.34549429	67.61	0.071	1.0000
Collembola abundance in Controls, 2004 vs 2016					
C2004: herbivory – C2016: no herbivory	3.0188898	0.85740925	63.02	3.890	**0.0120**
C2004: herbivory – C2016: herbivory	1.4832759	0.42127224	63.02	1.388	0.9617
Mesostigmata abundance by treatment in 2016					
C2016: no herbivory – N2016: no herbivory	0.4982311	0.18432783	59.74	-1.883	0.7645
C2016: no herbivory – NW2016: no herbivory	1.1000524	0.42849290	63.44	0.245	1.0000

C2016: no herbivory – W2016: no herbivory	0.6992589	0.27530790	63.89	-0.909	0.9988
C2016: herbivory – N2016: herbivory	0.7389494	0.27338507	59.74	-0.818	0.9995
C2016: herbivory – NW2016: herbivory	0.7137152	0.27800663	63.44	-0.866	0.9992
C2016: herbivory – W2016: herbivory	1.0288161	0.40505913	63.89	0.072	1.0000
Acari abundance in Controls, 2004 vs 2016					
C2004: herbivory – C2016: no herbivory	3.8274934	1.0848984	62.68	4.735	**0.0007**
C2004: herbivory – C2016: herbivory	4.7766627	1.3539393	62.68	5.517	**<0.0001**

55 *Table S4*

56

Table S4. Model parameter estimates (exponentiated) from generalized linear mixed-effect (Poisson family, log link) and binomial models examining the effects of treatment (control (C), warming (W), nutrient addition (N), nutrient addition + warming (NW)), the three year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory) and their interactions on Collembola species richness. P-values were computed based on Wald statistics and significant results ($p < 0.05$) are printed in bold.

	All Collembola			**Epi-edaphic Collembola**			**Hemi-edaphic Collembola**			**Eu-edaphic Collembola**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	14.20	12.05 – 16.74	**<0.001**	3.00	1.16 – 9.22	**0.033**	5.80	4.48 – 7.50	**<0.001**	6.60	5.19 – 8.40	**<0.001**

N	1.12	0.89 – 1.40	0.327	1.89	0.40 – 10.50	0.433	1.10	0.77 – 1.57	0.587	1.14	0.82 – 1.58	0.449
NW	1.04	0.82 – 1.30	0.769	1.00	0.23 – 4.30	1.000	1.10	0.77 – 1.57	0.587	0.95	0.68 – 1.35	0.792
W	1.06	0.84 – 1.33	0.640	1.89	0.40 – 10.50	0.433	1.00	0.69 – 1.44	1.000	1.02	0.72 – 1.43	0.931
2016 no herbivory	0.89	0.66 – 1.19	0.430				1.03	0.67 – 1.61	0.880	0.79	0.50 – 1.24	0.303
2016 herbivory	1.00	0.75 – 1.33	1.000				1.24	0.82 – 1.88	0.308	0.79	0.50 – 1.24	0.303
N : 2016 no herbivory	1.05	0.70 – 1.57	0.817				1.03	0.56 – 1.88	0.931	1.05	0.57 – 1.95	0.879
NW : 2016 no herbivory	1.09	0.72 – 1.64	0.685				1.00	0.54 – 1.83	0.992	1.25	0.67 – 2.33	0.486
W : 2016 no herbivory	0.99	0.66 – 1.50	0.969				1.10	0.60 – 2.03	0.761	0.87	0.45 – 1.68	0.681
N : 2016 herbivory	0.79	0.53 – 1.19	0.264				0.73	0.40 – 1.34	0.308	0.88	0.47 – 1.66	0.694

NW : 2016 herbivory	1.09	0.73 – 1.61	0.673		0.98	0.55 – 1.75	0.950	1.45	0.79 – 2.67	0.233
W : 2016 herbivory	0.88	0.59 – 1.32	0.537		0.92	0.50 – 1.66	0.775	0.99	0.52 – 1.87	0.963
Random Effects										
σ^2	1.00				1.00			1.00		
τ_{00}	0.00 $_{Block}$				0.00 $_{Block}$			0.00 $_{Block}$		
ICC	0.00 $_{Block}$				0.00 $_{Block}$			0.00 $_{Block}$		
Observations	80		80		80			80		
Cox & Snell's R^2 / Nagelkerke's R^2	NA		0.016 / 0.025		NA			NA		

58
59 *Table S5*

Table S5. Model parameter estimates (exponentiated) from generalized linear mixed-effect (Poisson family, log link) and binomial models examining the effects of treatment (control (C), warming (W), nutrient addition (N), nutrient addition + warming (NW)), year and herbivory treatments (year 2004: herbivory, year 2016: no herbivory, and year 2016: herbivory) and their interactions on Oribatida species richness. P-values were computed based on Wald statistics and significant results ($p < 0.05$) are printed in bold.

	Oribatida species richness		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	8.90	7.23 – 10.96	**<0.001**
N	0.81	0.59 – 1.10	0.181
NW	0.80	0.58 – 1.09	0.156
W	0.92	0.68 – 1.24	0.593
2016 no herbivory	0.85	0.58 – 1.25	0.415
2016 herbivory	0.79	0.53 – 1.16	0.229
N : 2016 no herbivory	1.01	0.57 – 1.78	0.977
NW : 2016 no herbivory	0.66	0.35 – 1.23	0.192

W : 2016 no herbivory	1.03	0.60 – 1.77	0.920
N : 2016 herbivory	1.02	0.57 – 1.83	0.936
NW : 2016 herbivory	0.82	0.45 – 1.52	0.534
W : 2016 herbivory	1.02	0.58 – 1.80	0.936

Random Effects

σ^2	1.00
$\tau_{00\ Block}$	0.00
ICC $_{Block}$	0.00
Observations	80

ISBN: 978-82-575-1631-4
ISSN: 1894-6402

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