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Community assembly across Subarctic landscapes

Exploring patterns of diversity

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Community assembly across Subarctic landscapes – Exploring patterns of diversity

Abstract

This thesis delves into the mechanisms driving community assembly, focusing on the impacts of environmental filtering and dispersal limitation on species richness and composition. I explore diversity patterns in vascular plants, soil fungi, and arthropods across two subarctic landscapes and at different spatial scales. As a background, I characterize the similarity in conditions between the two study areas and quantify patterns of alpha, beta and gamma diversity among the target taxa. I then relate these patterns to variation in microclimate, in productivity, and in the dispersal capacity of each taxon. In particular, I examine the influence of microclimatic conditions on species richness and abundance of arthropods and plants, and the similarity in taxon-specific responses to similar drivers. To test for an association between productivity and diversity, I examine alpha and beta diversity patterns of arthropods across productivity gradients at the local, landscape and regional scales, and test for scale-dependencies in the patterns observed. Finally, I assess how community dissimilarity varies among taxa across the landscape. Across the two subarctic regions, I found highly similar microclimatic conditions and productivity gradients. In both regions, species richness generally decreases with elevation and increases with soil temperature and moisture. The increase in arthropod richness along productivity gradients is consistent across scales, but plant richness shows weak relationships with arthropod richness. Higher species richness at lower elevations is attributable to species niche shapes, with a majority of "productivity-generalist" species covering the entire productivity gradient, and a minority of "productivity-specialist" species occurring exclusively at either low- or high-productivity sites – with the latter group being more specious. Higher species richness in high-productive areas did not translate into any greater dissimilarity in community composition. Moreover, highly dispersive species exhibit greater species turnover across the landscape compared to poorly dispersive species. Overall, my findings shed light on how abiotic factors, energy inputs, and dispersal capacity shape communities of plants, fungi and arthropods across subarctic landscapes, highlighting the complex interplay of factors in shaping community assembly.

Keywords: Community assembly, Subarctic, environmental filtering, dispersal.

Organismsamhällen i subarktiska landskap – en utforskning av mångfaldens mönster

Sammanfattning

I den här avhandlingen fördjupar jag mig i de mekanismer som formar organismsamhällen, med ett specifikt fokus på hur lokala miljöförhållanden och begränsningar i arternas spridningsförmåga påverkar den lokala artrikedomen och artsammansättningen. Specifikt utforskar jag rumsliga mönster i växternas, svamparnas och leddjurens mångfald över två subarktiska landskap, i olika rumsliga omfattningar. Först karakteriserar jag likheten i miljöförhållandena mellan de två studieområdena och kvantifierar mönster i alfa-, beta- och gammadiversitet bland växter, svampar och leddjur. Sedan relaterar jag dessa mönster till variation i mikroklimat, i produktivitet och i de olika artgruppernas spridningsförmåga. Speciellt undersöker jag inverkan av mikroklimat på arternas antal och utbredning, och hur olika artgrupper påverkas av miljön. Jag undersöker mönster i leddjurens alfa- och beta-diversitet över produktivitetsgradienter i lokal, landskaps- och regional skala. Slutligen bedömer jag hur mycket samhällen av olika organismgrupper skiljer sig mellan olika delar av landskapet. De två subarktiska regionerna uppvisar liknande förhållanden i fråga om mikroklimat och produktivitet. Inom de båda regionerna minskar artrikedomen med höjden över havet och ökar med markens temperatur och fuktighet. Leddjurens artrikedom tilltar med tilltagande produktivitet i olika skalor, men växternas artrikedom är vagt kopplad till leddjurens artrikedom. Högre artrikedom på lägre höjder återspeglar arternas ekologiska nischer: En majoritet av arterna är generalister i förhållande till produktivitet, och förekommer därmed över hela produktivitetsgradienten. En minoritet av arterna förekommer uteslutande på lokaler med antingen låg eller hög produktivitet – med fler arter i den senare gruppen. Högre artrikedom i högproduktiva områden återspeglar sig inte i större olikhet i lokalsamhällenas sammansättning. Artgrupper med högre spridningsförmåga uppvisar större artomsättning över landskapet än arter med lägre spridningsförmåga. Mina resultat belyser hur abiotiska faktorer, energitillförsel och spridningsförmåga formar samhällen av växter, svampar och leddjur över subarktiska landskap i samspel mellan olika faktorer.

Nyckelord: Samhällsstruktur, Subarktis, ekologiska nischer, spridningsförmåga.

Dedication

To my family. Papá, Mamá, Cris y Laura. Gracias por estar siempre ahí cuando se os necesita, especialmente los últimos 33 años.

El descubrimiento más importante es el de la ignorancia, pues nos permite seguir queriendo comprender el mundo que nos rodea.

The most profound discovery is that of ignorance, as it allows us to persist in our desire to comprehend the world around us.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Peña-Aguilera, P., Schmidt, N.M., Stewart, L., Parisy, B., van der Wal, R., Lindman, L., Vesterinen, E., Maclean, I.M., Kankaanpää, T., Wirta, H., and Roslin, T. (2023). Consistent imprints of elevation, soil temperature and moisture on plant and arthropod communities across two subarctic landscapes. *Insect Conservation and Diversity*. 16(5), 684-700. https://resjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/icad.12667

II. Peña-Aguilera, P., Schmidt, N.M., van der Wal, R., Maclean, I.M., and Roslin, T. Alpha diversity patterns are unmatched by beta diversity across productivity gradients of the Sub-Arctic (Manuscript).

III. Parisy, B., Peña-Aguilera, P., Stewart, L., Vesterinen, E., Wirta, H., and Roslin, T. Differential patterns in β-diversity among plants, microbes and insects: increased species sorting with increasing dispersal. (Submitted).

Paper I is open-access, under a Creative Commons Attribution 4.0 International License (CC BY-NC 4.0).

The contribution of Pablo de la Peña Aguilera to the papers included in this thesis was as follows:

I. Main Author. PPA conceived the idea together with TR. PPA planned, supervised and conducted the field work with help from TR, LS, BP, TK and HW. PPA analysed the data, interpreted the results and wrote the manuscript with inputs from TR.

II. Main Author. PPA conceived the idea with inputs from all co-authors. PPA planned, supervised and conducted the field work. PPA analysed the data with inputs from TR, interpreted the results and wrote the manuscript.

III. Main Author together with BP. PPA conceived the idea together with BP and TR. PPA planned, supervised and conducted the field work with help from BP, TR, LS, and HW. PPA analysed the data with inputs from BP and TR, interpreted the results and led the writing of the manuscript, jointly with BP.

During this doctorate, Pablo de la Peña Aguilera contributed to the following papers not included in the thesis:

I. Jiménez-Valverde, A., Rodríguez-Rey, M. & Peña-Aguilera, P. (2021). Climate data source matters in species distribution modelling: the case of the Iberian Peninsula. *Biodiversity Conservation* 30, 67–84. 10.1007/s10531-020-02075-6.

II. Ortuño, V. M., Arribas, O., Muñoz-Santiago, J., & Peña-Aguilera, P. (2021). A case of allopatric speciation in the Central System (Iberian Peninsula): Leistus elpis sp. nov., a sibling species of Leistus constrictus (Coleoptera, Carabidae). *Zootaxa*, 4995(3), 452-470. https://doi.org/10.11646/zootaxa.4995.3.3.

III. Schmidt, N.M., et al. (2023). Little directional change in the timing of Arctic spring phenology over the past 25 years. *Current Biology*, vol. 33, no 15, p. 3244-3249. e3. https://doi.org/10.1016/j.cub.2023.06.038.

IV. Wirta, H., Jones, M., Peña-Aguilera, P., Chacón-Duque, C., ... & Roslin, T. (2023). The role of seasonality in shaping the interactions of honeybees with other taxa. *Ecology and Evolution*, *13*(10). https://doi.org/10.1002/ece3.10580

V. Kemppinen, J, et al., (2024). Microclimate, an important part of ecology and biogeography. *Global Ecology and Geography* https://doi.org/10.1111/geb.13834.

VI. Niittynen, P., Salminen, H., Peña-Aguilera, P.,… & Kemppinen, J. A gridded microclimate dataset from a Sub-Arctic biodiversity hotspot in Finland. *bioRxiv* 2024.03.30.587419; doi: https://doi.org/10.1101/2024.03.30.587419. (*submitted*).

VII. Hartop, E., Lee, L., Srivathsan, A., Jones, M., Peña-Aguilera, P., Ovaskainen, O., Roslin, T., and Meier, R. A dive into the Terrestrial Deep-sea Trenches: Megabarcoding sheds light on the species richness, spatiotemporal distribution, and community composition of a dark taxon. (*submitted*).

Abbreviations

BIN	Barcode Index Number
BOLD	Barcode of Life Data
CO1	Cytochrome c oxidase I gene
GLMM	Generalized Linear Mixed Model
ITS2	Internal transcribed spacer 2
NDVI	Normalised Difference Vegetation Index
pSEM	Piecewise Structural Equation Modelling
SMTP	Swedish Malaise Trap Project
zOTU	Zero-radius Operational Taxonomic Unit

1. Introduction

Ever since the start of the field of ecology, a recurring question has captivated our collective curiosity: What shapes the distribution and diversity of species? While initially appearing straightforward, we soon recognize the impossibility of providing a general or globally applicable answer. In fact, nature is so complex that even when focusing on a specific group of species (e.g. arthropods) or on rather "simplified" systems (e.g. the Arctic), the initial question usually raise further questions rather than allowing for specific responses. As a result, the inherent complexity of nature compels us to formulate general concepts to elucidate patterns of diversity. To account for patterns in nature, several theoretical frameworks for community ecology have been developed, such as *niche theory* (Grinnell, 1917; Elton, 1927; Hutchinson, 1959; R. MacArthur & Levins, 1967; Chase & Leibold, 2003), *metacommunity theory* (Leibold et al., 2004; Holyoak et al., 2005), the *assembly rules framework* (Diamond, 1975; Zobel, 1997; Elith & Leathwick, 2009; Ovaskainen et al., 2017) and the *theory of ecological communities* (Vellend, 2010, 2016). These frameworks all aim to explain ecological communities and their diversity patterns. As stated by Ricklefs (2008) in his seminal work, "*Nonetheless, nature, including its diversity, does exhibit pattern, and it should be possible to understand the origin of that pattern*". To contribute to the validation and application of these frameworks, I have dedicated my thesis work to study patterns in the community diversity of vascular plants, soil fungi and arthropods across subarctic landscapes and how these are linked to spatial, environmental, energetic and dispersal factors.

1.1 Factors shaping community diversity

A community is defined by the set of species encountered at a given place at a given time (Begon & Townsend, 2021). To understand how ecological communities are formed and change over time, we need to examine the basic forces adding species to a site and preventing others from reaching it or persisting at this site. These mechanisms are collectively referred to as *fundamental* or *community assembly* processes.

Contemporary community ecology frameworks attribute the structure and dynamics of communities to a combination of speciation and migration processes (the so-called *phylogeographic assembly processes*) along with both stochastic (e.g. ecological drift) and deterministic (e.g. selection) processes (the so-called *ecological assembly processes*) (Zobel, 1997; Vellend, 2010; Chase & Myers, 2011; Ovaskainen & Abrego, 2020). Out of all species ever evolving in the world, only a subset will migrate and reach to a specific site, and from those, only some will be able to stablish at the site. This process is the result of two different stages: Firstly, the species must find the local abiotic conditions matching its niche. If there is a mismatch between the species niche and the local environmental conditions, the species will not survive, being filtered out from the local species pool – a phenomenon termed *environmental filtering*. Secondly, even if the species niche match the local conditions, species may still be excluded due to interactions with other species, such as competition, on a process known as *biotic filtering*. Additionally, during these steps, random events may play a significant role and modify community structure through a process termed *ecological drift*. In essence, according to Vellend (2016), the mechanisms shaping a community can thus be summarized into four basic processes: speciation, dispersal, selection, and drift. The same processes have also been referred to with slightly different terms in other frameworks (Figure 1).

However, it is well known that these processes come with differential imprints at different spatial scales (Wiens, 1989; Levin, 1992). When examining differences between communities from regional to local scales, processes like environmental and biotic filtering offer key insights into community structure. Conversely, at larger scales — i.e., when communities are compared between regions or at a global level — evolutionary forces and migratory limitations play a more significant role in shaping community structure (Chase & Leibold, 2003; Ricklefs, 2008). Therefore, when analysing differences at the global-to-regional scale, attention should be paid

to *phylogeographic assembly rules*, encompassing longer-term evolutionary and geological processes that influence species distribution. On the other hand, when studying community assembly processes from regional to local scales, the focus should primarily be on understanding *ecological assembly processes* at the local scale. This involves the assessment of how a series of filters, such as the environment, dispersal limitation or species interactions, act at the regional scale, distilling local communities from a wider species pool (Figure 1).

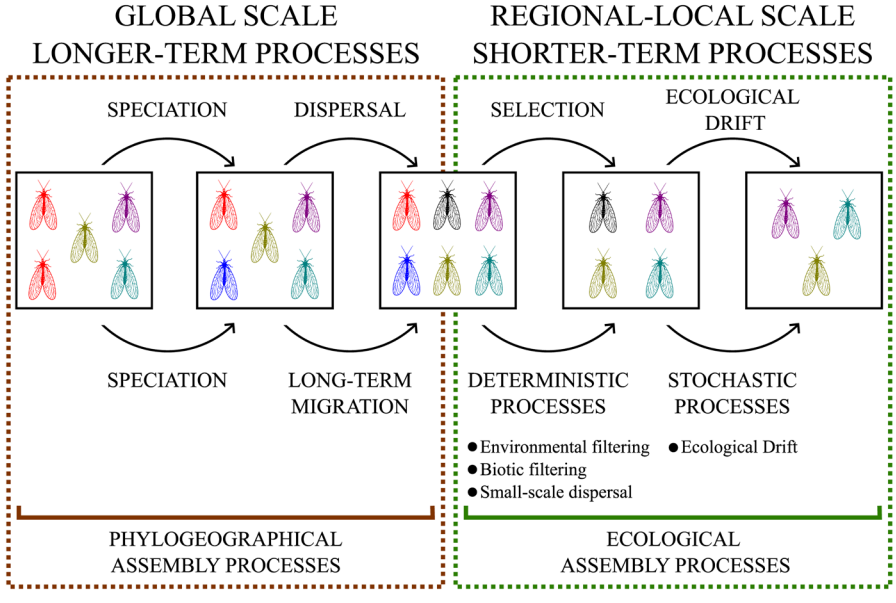

Figure 1. Schematic representation of community assembly processes. To illustrate convergence between different frameworks, I show terms used in the context of the *theory of ecological communities* (Vellend, 2016) on top of the squares, and terms used in the context of the *assembly rules framework* (Diamond, 1975) below the squares.

Determining what comprises a set of relevant environmental conditions for each community is clearly a moot point. Among a potentially endless set of environmental factors (such as temperature, soil moisture, pH, carbon, nitrogen, and phosphorus content, elevation, aspect, snow depth, or snow melt date, to name just a few) some have received more attention than others. For ectothermic organisms – such as arthropods – which rely on external energy throughout their life cycle, accounting for energy availability and

plant productivity is essential. Conversely, soil properties like pH, carbon, nitrogen, and phosphorus contents may be more significant to heterotrophic organisms such as fungi. In the case of vascular plants, the combination of the above-mentioned factors is key to assess their diversity patterns. Therefore, any characterization of environmental conditions should be tailored to the focal organism, with a focus on specific abiotic factors justified by their potential impact on the studied group.

In this thesis, my focus will be on understanding the mechanisms that shape communities of arthropods, vascular plants, and soil fungi across various spatial scales, including the local, landscape, and regional levels. As mentioned earlier, the key processes influencing diversity patterns at these scales include environmental and biotic filtering, as well as dispersal limitation, which becomes increasingly significant from local to regional scales. Given the challenges associated with quantifying interactions in natural ecosystems, particularly for taxa spanning multiple levels, I will prioritize the roles of dispersal and environmental filtering forces, while relegating biotic interactions to a secondary role. Moreover, my research will be centred on the processes that contribute to current diversity and community structure, leaving evolutionary, phylogeographic, and historical imprints beyond the scope of this thesis.

1.2 Community diversity measurements

In principle, the dimensionality of an ecological community is as high as the number of species it contains. Thus, to comprehend "the community emerging as the result of assembly processes", we must define useful and informative summary metrics. Undoubtedly, the most extensively studied community properties are the diversity and abundance of species in the community. In this context, we can differentiate between alpha, beta or gamma diversity. Gamma diversity describe the overall number of species inhabiting a specific geographic area, alpha diversity describes the number of species inhabiting any single location within that geographic area, and beta diversity describes variation in species composition between locations within that area. These three components of diversity are clearly interrelated, as beta diversity was originally defined as the ratio between gamma and mean alpha diversities ($\beta = \gamma / \alpha$, *sensu* Whittaker (1972)). In this sense, the overall number of species in a geographic area will be equal to the mean

alpha diversity in the same area only if all species are present at all locations (Baselga, 2012), resulting in full similarity in species composition between sites. However, this is never the case in nature, as there is always *some* variation in species richness and composition between localities. Such variation in species richness and species composition can be further partitioned into two different contributions: spatial turnover and nestedness. Turnover refers to the replacement of some species by others from one location to another, while nestedness refers to the difference in species richness between two locations where the species of the less species-rich site are a subset of the richer one (Figure 2; Baselga (2012)). This differentiation between turnover and nestedness is key to assess the mechanisms shaping community assembly, since the two components will inform us about the relative contribution of the antithetic processes of species loss (nestedness) and species replacement (spatial turnover) (Baselga, 2010).

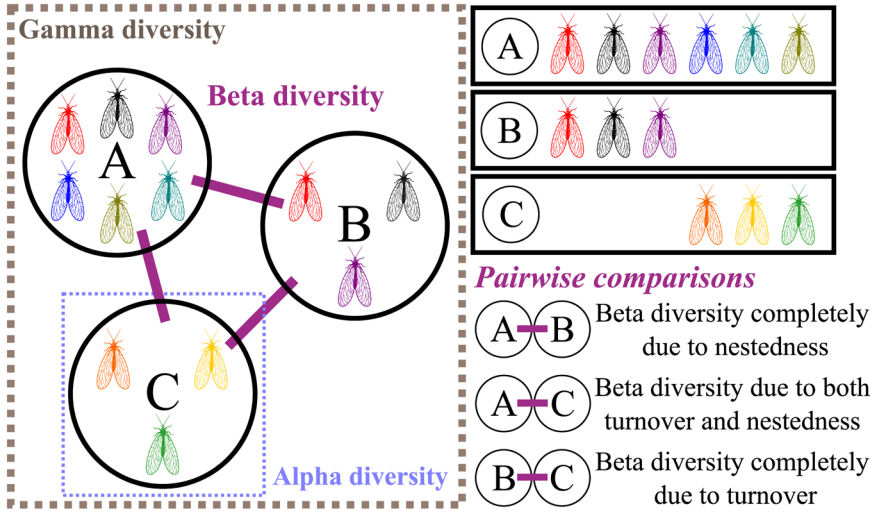

Figure 2. Schematic representation of the diversity metrics used in this thesis: Gamma, Beta and Alpha diversity. Circles labelled with A, B and C represent different sites. Within each site, species are represented by differently coloured insects. On the right side of the figure, I illustrate contrasting scenarios for the relative contribution of turnover (species replacement) vs. nestedness (difference in species richness between sites), as based on comparisons between communities at sites A, B and C.

Nestedness is often associated with extinction–colonization dynamics while spatial turnover typically reflects species sorting by the environment or dispersal processes, particularly at large-scales (Dobrovolski et al., 2012). However, at the local and regional scales, one component of beta diversity may prevail over the other (turnover or nestedness), despite similar underlying processes (e.g. environmental filtering and dispersal capacity). Notably, a dominance of the species replacement component (turnover) paired with minimal differences in species richness (nestedness) suggests that the local species pool is constrained by resource availability or niche partitioning. This pattern has been usually linked with communities at lower latitudes, often related with tighter species packing and expanded niche space (Cao et al., 2021). Conversely, a preponderance of the nestedness-resultant component imply that the species pool is not yet saturated, as evidenced by a large variation in species richness between sites, thus allowing for additional species. This tendency is typically observed in communities at higher latitudes, often linked with the effect of past glaciation events (Baselga, 2010; Dobrovolski et al., 2012). Therefore, confounding these terms, or relying solely on overall beta diversity, will likely bias our interpretations of the true processes behind community dissimilarity and variation in species composition among locations.

Overall, analysing patterns in alpha, beta, and gamma diversity provides insights into the mechanisms driving community assembly. In this thesis, I anticipate that these diversity metrics will be influenced in distinct ways by environmental filtering, productivity gradients, and the impact of dispersal, with the specific effects varying depending on the characteristics of the organism group.

1.3 Diversity patterns in the Subarctic realm

As a study region, I selected the subarctic biome. These high-latitude ecosystems are characterized by a particularly pronounced energy limitation, distinct vegetation transitioning between mountain birch forests and barren tundra, and highly variable spatiotemporal abiotic conditions (Figure 3). Such characteristics create diverse mosaics of environmental conditions across the landscapes, likely exerting significant influence on the distribution and abundance of the species inhabiting them.

At present, these areas are experiencing rapid environmental change. Over recent decades, the Arctic and high-latitude regions have been warming at rates 3-4 times faster than any other biome on Earth (Rantanen et al., 2022). Following shifts in climatic conditions, we may also anticipate shifts in community composition, species richness, and abundances (Post et al., 2009; Pecl et al., 2017; Warren et al., 2018; Kankaanpää et al., 2020; Antão et al., 2022). Of particular interest are the responses of vascular plants, fungi and arthropods. These organisms are ecologically interconnected, forming the primary trophic foundation of many ecosystems. Since these communities rely on external temperatures for their metabolism and have different dispersal abilities, their distribution is highly susceptible to changes in environmental conditions – with knock-on effects on species interactions and community structure (Schmidt et al., 2017).

Figure 3. Subarctic landscapes show a steep/rapid transition between mountain birch forests and open tundra. Photo: Tristan Ubaldi.

There is already evidence of ongoing distributional changes, with highly dispersive species like shrubs shifting towards higher latitudes and elevations in response to changing climatic conditions (Wilson & Nilsson, 2009; Hallinger et al., 2010; Myers-Smith & Hik, 2018; Mamantov et al., 2021). These shifts not only mark initial changes, but will also result in further dispersal of different organisms across the landscapes, as the location of favourable microhabitats in terms of soil conditions and food availability are currently shifting (Kemppinen et al., 2021b).

2. Outline of the study

This thesis comprises three papers investigating spatial patterns in community characteristics (species richness and abundance; **Paper I**) and assembly processes (community dissimilarity; **Papers II & III**) of different taxa (flying and ground-dwelling arthropods; **Papers I, II & III**, vascular plants; **Papers I & III** and soil fungi; **Paper III**). To account for these patterns, I invoke microclimate (**Paper I**), plant productivity (**Paper II**) and dispersal capacity (**Papers II & III**) across different spatial scales (local; **Papers I, II & III**, landscape; **Paper II** and regional; **Papers I, II & III**).

In **paper I**, I start by exploring the similarities in both microclimatic conditions and species pools between two subarctic regions. I then investigate how elevation, snow depth and their indirect effects (as mediated through soil temperature and soil moisture) shape the species richness and abundances of arthropods and vascular plants. Finally, I examine the relationship between arthropod and plant richness, asking whether plant richness may be used as a proxy for arthropod richness. The questions asked were explicitly these: Do these communities respond to the same microclimatic drivers, despite their use of different parts of the environment? Are the imprints of these drivers consistent across study sites and years? Can I predict richness patterns in arthropods based on richness patterns in plants?

In **paper II**, I explore how alpha and beta diversity patterns are formed across productivity gradients. Specifically, I search for mechanisms creating higher arthropod richness in areas of higher productivity (Figure 10), and whether this pattern also translates into higher community dissimilarity among the most productive parts of the landscape (Figure 4).

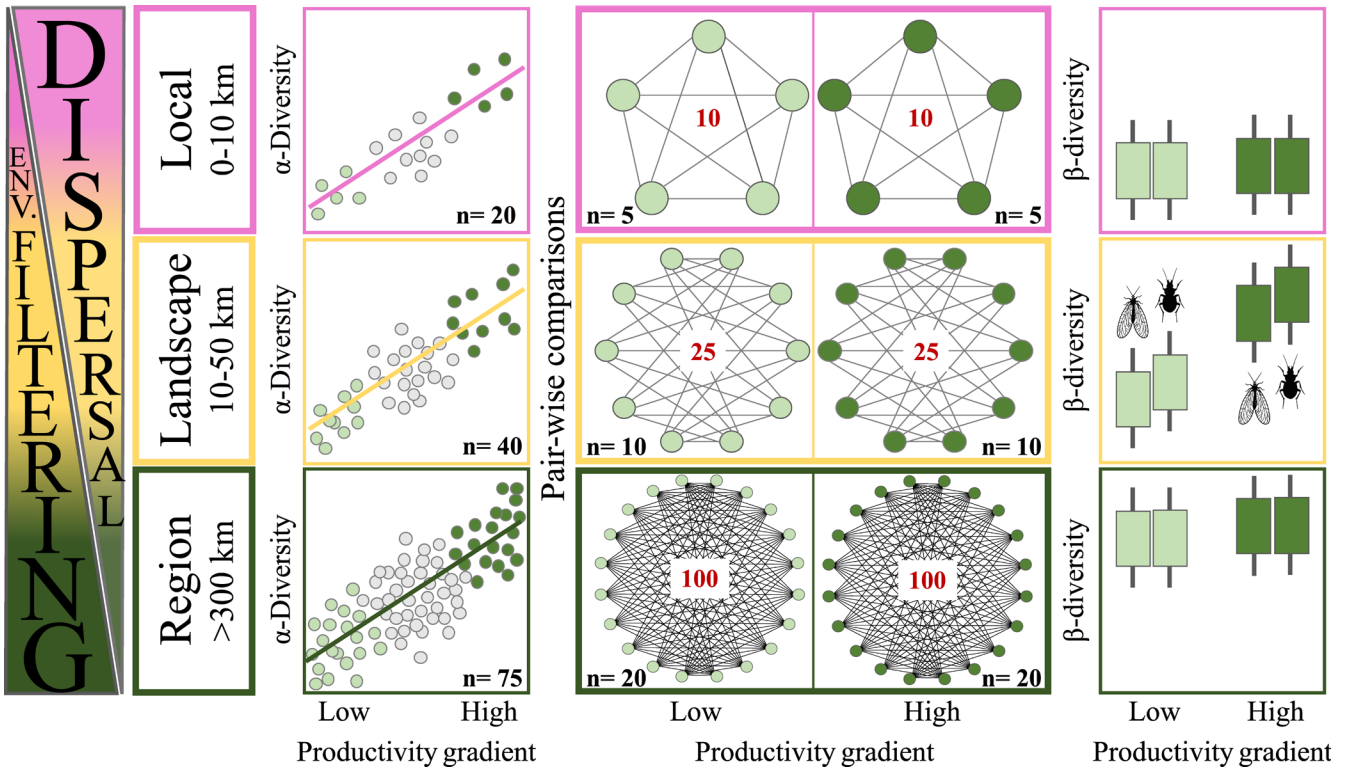

Figure 4. Conceptual setting of **paper II** and *a priori* hypotheses tested. For a detailed legend see Chapter II, page 9.

I then compare patterns across different spatial scales, hypothesizing that the biggest imprints will appear at intermediate extents (i.e., at the landscape level), as an outcome of the combined effects of both environmental filtering and dispersal limitation (Figure 4, see beta diversity panel for the landscape scale in yellow).

In **paper III**, I assess how beta diversity patterns of different taxa are formed across landscapes. Since communities of vascular plants, soil fungi, ground-dwelling and flying arthropods differ in their dispersal capacity, I expected to see distinct patterns of turnover among these groups. Since I collected all taxa at the very same sampling sites, I assumed that the environmental distance matrix between sampling sites was the same across taxa, regardless of the factors involved in shaping the distribution of each taxon. Drawing on differences in dispersal capacity between groups, I predicted higher turnover in space from locally-dispersing flying and ground-dwelling arthropod communities (weak dispersers) through wind-dispersed vascular plants (intermediate dispersers) to fungi dispersed by air-borne spores (strong dispersers) (Figure 5).

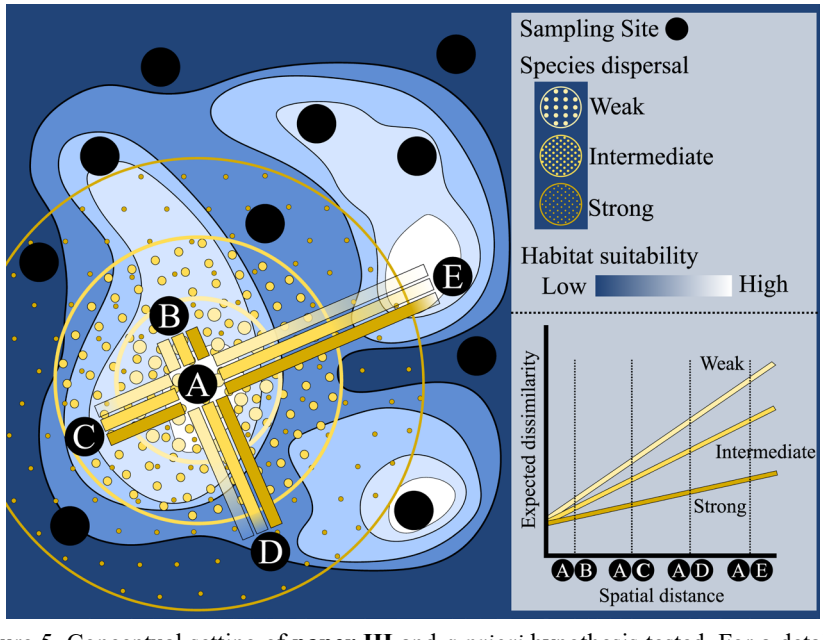

Figure 5. Conceptual setting of **paper III** and *a priori* hypothesis tested. For a detailed legend see Chapter III, page 3

3. Methods

3.1 Study sites

In my thesis, all data was collected from two study sites: Kilpisjärvi and the Varanger Peninsula (Figure 6). These landscapes are representative of the sub-arctic biome. While they share similar characteristics regarding microclimatic conditions, topography or vegetation, they comprise distinct features in terms of elevation and in the extent of the region studied.

3.1.1 (Dis) similar features between study sites

Kilpisjärvi, located in north-western Finland (69°03´N, 20°51´E) and the Varanger Peninsula, in north-eastern Norway (70°31'N, 29°05'E), are characterized by mountainous tundra landscapes featuring heterogeneous topographical gradients and strong microclimatic contrasts in space and time. Although there is a great variation in microclimatic conditions within each region, soil temperature, soil moisture and snow deposition are similar between the two study areas (**Paper I**). In both areas, mountain birch (*Betula pubescens*) forest dominates the vegetation from the lowest elevations to the tree line, while dwarf shrubs such as *Empetrum nigrum*, *Betula nana*, *Juniperus communis* and *Vaccinum spp*. dominate the alpine heaths above the tree line. Indeed, about half of the local vascular plant species surveyed in this thesis are present in both study sites (**Paper I & III**).

Kilpisjärvi and Varanger differ in two main features: the elevation range and the extent of the study area. The Kilpisjärvi region ranges over higher absolute elevations than does the region of Varanger. Absolute elevations around Kilpisjärvi rise from a high plateau located around Lake Kilpisjärvi (473 m a.s.l.) and reach the mount Saana (1029 m a.s.l.). In the Varanger region, due to its proximity to the Barents Sea, elevations start closer to the

sea level and reach approximately 620 m a.s.l. in the inner part of the peninsula. Despite these differences in absolute elevation, both regions feature a similar range of elevational difference (~450 m) and the same series of vegetation zones, from birch forest to open tundra.

The other differing feature between the two study areas is their spatial extent. The Kilpisjärvi study area covers an area of approximately 14 km^2 while the Varanger study area covers a bigger extent of approximately 425 km^2. This difference allowed me to assess the scale-dependency of community assembly processes in **Paper II**. Here, I used a subset of sampling sites in Varanger to match the spatial extent of the study area in Kilpisjärvi, thus defining a "local" scale. I then examined the larger Varanger area as the "landscape" scale, and finally used comparisons between the Kilpisjärvi and Varanger study areas to address patterns at the "regional" scale (Figure 4 and 6).

Overall, the elevational ranges and spatial scales here defined allowed me to study how microclimate shapes species richness across these two regions (**Paper I**), whether species richness and community dissimilarity increase along productivity gradients (**Paper II**), whether such patterns are scale dependent (**Paper II**) and how the dispersal capacity of different taxa shape their distributional patterns across local landscapes (**Paper III**). Figure 7 shows a summary of diversity metrics, taxa, explanatory variables, scales and dispersal assumptions used for each paper.

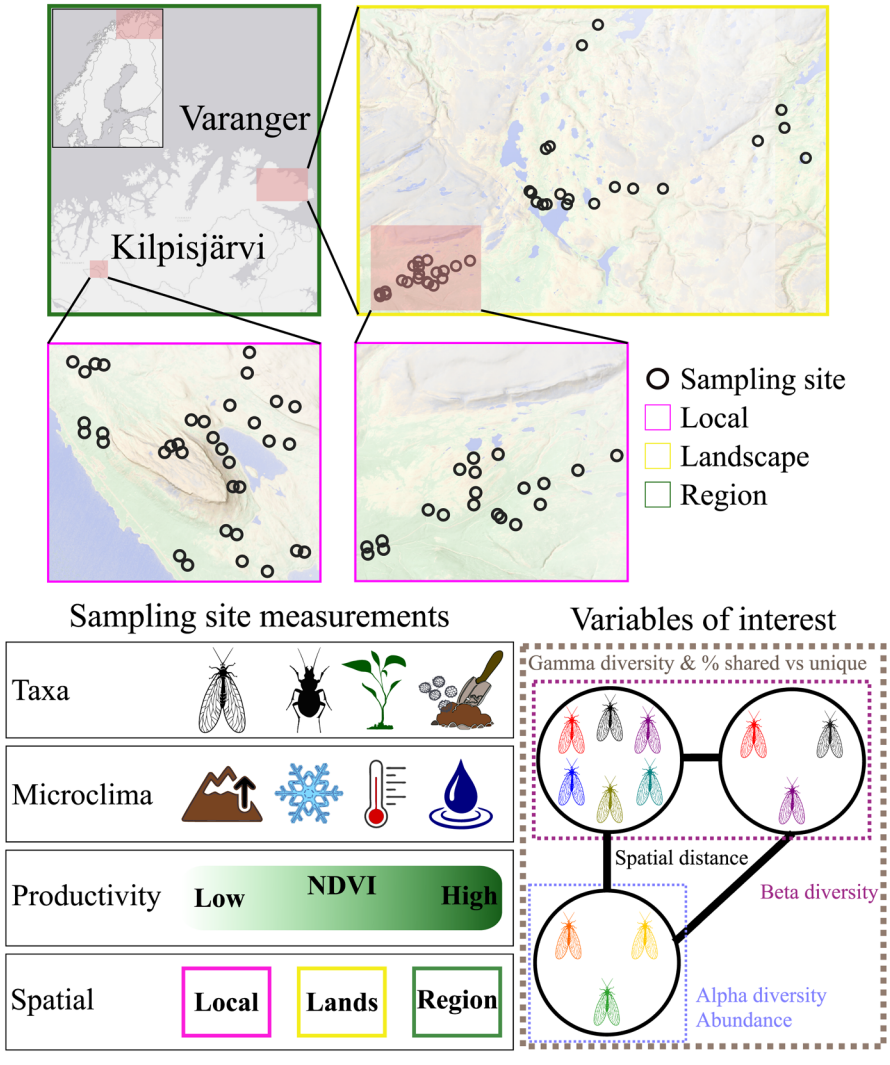

Figure 6. Maps showing the location of the two study areas within the subarctic biome: Kilpisjärvi (north-western Finnish Lapland; bottom-left map; location within Fennoscandia indicated by smallest red square in top-left inset map) and Varanger Peninsula (north-eastern Norway; bottom- and top-right maps; location within Fennoscandia indicated by biggest red square in top-left inset map). Within these landscapes, the location of individual sampling sites (n=35 in Kilpisjärvi and n=40 in Varanger) are shown by black circles. In the bottom-part of the figure, I identify the measurements made and the metrics calculated.

3.1.2 Sampling design and characterization of taxa

In the study areas of Kilpisjärvi and Varanger, I implemented a stratified random sampling design to capture variation in microclimatic conditions and productivity within each landscape. Within each region, I maximized the coverage of both elevational and geographical distances between sampling sites. In total, I sampled 75 sites, of which 35 were located in Kilpisjärvi and 40 in Varanger. At each sampling site, I characterized each of the taxa studied in this thesis: arthropods (differentiating between flying and ground-dwelling groups), vascular plants and soil fungi. In addition, I monitored microclimatic conditions, measured snow depth in winter, calculated productivity in summer and noted the elevation of each sampling site. Below I will briefly explain how.

At each sampling site, I characterized arthropod communities by collecting flying arthropods with Malaise traps and ground-dwelling arthropods with two pitfall traps. I characterized soil fungi communities by obtaining two soil cores around a pre-selected set of individual plant species. I characterized plant communities by surveying all vascular plant species present within an area of 100 m^2 around each sampling site. Arthropod communities were sampled weekly during the summers of 2020 and 2021, while fungal communities and vascular plants were sampled only once in the summer of 2020 and 2022, respectively. From these samples, I scored the main feature of interest, i.e. taxon-specific presence across the landscapes.

To characterize microclimatic variation at each sampling site, I placed a logger to record the soil moisture and soil temperature every 15 minutes between 2020 and 2024. Moreover, I measured the average snow depth by taking four measurements around each sampling site. I then calculated the vegetation productivity (using the Normalized Difference Vegetation Index; NDVI) between 2017 and 2023 by using satellite images for July and August (coinciding with the vegetation peak). Lastly, I noted the elevation of each sampling site and calculated pairwise geographical distances between all site-pairs (Figure 6).

3.2 A DNA-based approach

In my thesis, I based the species identification of arthropods and soil fungi on DNA metabarcoding. A detailed description of the laboratory workflow can be found in each paper. In brief, arthropods and fungi were identified

using the CO1 and ITS2 regions, respectively. Sequences were aggregated to the level of zero-radius operational taxonomic units (ZOTUs; Edgar 2010), which were then assigned a taxonomy by matching with the database BOLD (Ratnasingham & Hebert, 2007) for arthropods and to UNITE for fungi (Nilsson et al., 2019). As proxies of arthropod species, we used Barcode Index Numbers (BINs; Ratnasingham & Hebert (2013)), which closely match morphologically identified species, especially among arthropods (Ratnasingham & Hebert, 2013). As proxies of fungi species, we used ZOTUs assigned to both genus and species level.

During the sampling in 2020 and 2021, I collected a total of 1959 samples of flying arthropods, 1594 samples of ground-dwelling arthropods, and 55 samples of soil fungi. These samples yielded 992 million sequence reads for flying arthropods, 434 million reads for ground-dwelling arthropods, and 9 million reads for soil fungi. Of these, 85% and 84% were attributed to specific species within flying and ground-dwelling arthropods, respectively, while 36% were assigned to species within soil fungi. When these sequences were aggregated to the level of ZOTUs, I obtained 51197, 72870, and 4715 ZOTUs for flying arthropods, ground-dwelling arthropods, and soil fungi, respectively. Within these ZOTUs, 73%, 70%, and 25% were assigned to species level for flying arthropods, ground-dwelling arthropods, and soil fungi, respectively.

To secure commensurability among data, all DNA samples were collected and processed by uniform methods. Consequently, I can assume that: a) an equal sampling effort was invested in generating each sample, and b) the impact of any biases introduced by the molecular workflow remain consistent across all samples.

As any other method, molecular approaches are not exempt of caveats. Distinguishing genuine biological information within the sequences from surrounding noise can pose significant challenges. Nonetheless, the volume of samples and individuals collected could never be identified by any other method. In **paper I**, I mentioned the Swedish Malaise Trap Project (SMTP; Karlsson et al., (2020)). This project deployed 73 Malaise traps to gather material, which was subsequently sent to over 300 expert taxonomists for identification (Karlsson et al., 2020). Over the past 19 years, only about 2% of this material has been processed and identified so far, highlighting the inherent impracticality of traditional methods to identify substantial amounts of species within a reasonable time frame.

3.3 Diversity metrics and analytical approach

Based on the community datasets obtained by both molecular (for arthropods and fungi) and inventory (for vascular plants) approaches, I generated the relevant community diversity metrics.

In **papers I** and **III**, I calculated gamma diversity as the overall taxon-specific richness for both Kilpisjärvi and Varanger. I then determined the proportion of unique vs shared species across these regions. In **papers I** and **II**, I calculated each taxon-specific alpha diversity as the sum of unique species found at each sampling site. Additionally, for **paper I**, I assessed arthropod abundance by summing all flying arthropod sample weights (g). In **papers II** and **III**, I characterized overall community dissimilarity between sampling sites using taxon-specific Jaccard community dissimilarity (beta diversity: β_{jac}). Following the approach proposed by Baselga (2010), I then partitioned overall beta diversity into the components of turnover (i.e. species replacement; β_{jtu}) and nestedness resultant-dissimilarity (defined as the dissimilarity not explained by species turnover, i.e. differences in species richness between sampling sites; β_{jne}). For details regarding the specific taxa subjected to these diversity measurements, see figure 7.

To explain variation in the diversity metrics defined above, I used a series of taxon-relevant metrics (see *1.1. Factors shaping community diversity*): In **paper I**, I used site-specific metrics including elevation, snow depth, soil temperature and soil moisture to understand how environmental filtering may shape species richness and abundance. In addition, I tested whether the species richness of vascular plants may offer a meaningful proxy for arthropod richness. In **paper II**, I used site-specific productivity (NDVI values) to explain patterns in arthropod richness. To address community dissimilarity patterns at each extreme of the productivity gradient, I classified each sampling site as being characterised by either low or high productivity based on its NDVI value. To subsequently assess how community dissimilarity patterns at both ends of the productivity gradient might change with spatial scale, I defined three separate scales (the local, landscape and regional scales; Figure. 4 and 6) and categorized each sampling site accordingly to each scale. In **paper III**, I used Euclidean distances between each pair of sampling sites to assess how community dissimilarity patterns of different taxa are formed across landscapes (Figure 5).

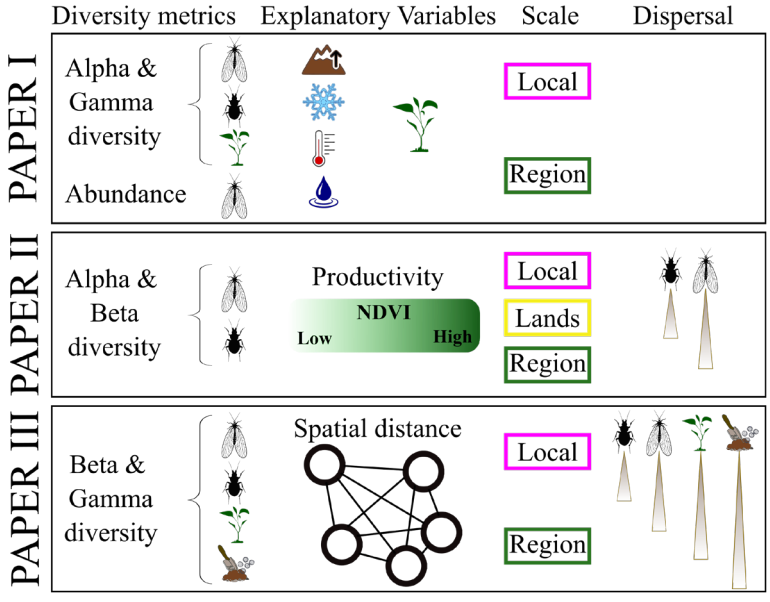

Figure 7. Summary of the diversity metrics, explanatory variables, scales assessed and dispersal assumptions used in each of the papers included in this thesis. In this context, ground-dwelling arthropods are assumed to have the lowest dispersal capacity due to their limited mobility while fungi are expected to have the highest dispersal capacity due to their microscopic wind-dispersed spores.

As my analytical approach, in **paper I**, I employed piecewise structural equation modelling (pSEM) to evaluate the effects of elevation and snow depth (and their indirect effects mediated through soil moisture and temperature) on species richness and abundance of arthropods and vascular plants. I then used regression analyses (GLMMs; generalized linear mixed models) to assess the relationship between arthropod and plant richness. In **paper II**, I also used regression analyses (GLMMs) to model community dissimilarity as a function of productivity and scale as well as of their interaction. To assess differences between low and high productivity sites across scales, I made *post-hoc* pairwise comparisons using marginal means with Tukey`s adjustments. Similarly, in **paper III**, I used regression analyses (GLMMs) to examine gradients of community dissimilarity against pairwise spatial distance matrices for each taxa across regions. Since paired values are non-independent of each other, I used custom-built permutation tests to establish the statistical significance of patterns.

4. Results and Discussion

In this section, I provide an overview of the main findings of my study on the spatial diversity patterns and community assembly processes of fungi, vascular plants and arthropods across subarctic landscapes. Besides, I also discuss the general implications of these results and future steps needed to understand community assembly processes.

4.1 Similar species pools, microclimatic conditions and productivity gradients across study regions

I found that the species pools of Kilpisjärvi and Varanger are relatively similar in terms of species richness. While Kilpisjärvi had an overall diversity of 1891 flying-arthropods, 1291 ground-dwelling arthropods, 127 vascular plants and 973 fungi species, Varanger had an overall diversity of 1955 flying-arthropods, 1273 ground-dwelling arthropods, 103 vascular plants and 743 fungi species. Across each taxon, **approximately half of the species were shared between Kilpisjärvi and Varanger, while a quarter was unique to each region** (**Papers I & III**). Even though I used a higher number of traps in Kilpisjärvi than in Varanger (35 vs 40, respectively), I found a higher diversity in Kilpisjärvi for all taxa except for flying arthropods (Figure 8).

Indeed, the Kilpisjärvi region is considered one of the biodiversity hot-spots within the Scandic Mountains. Many rare plant species are found on the slopes of the mount Saana due to its calcareous properties and the high-alpine conditions (Kauhanen, 2013). Given a substantial difference in species composition between Kilpisjärvi and Varanger, my key interest was in whether the environmental filtering, productivity and dispersal limitation still exert comparable imprints across regions.

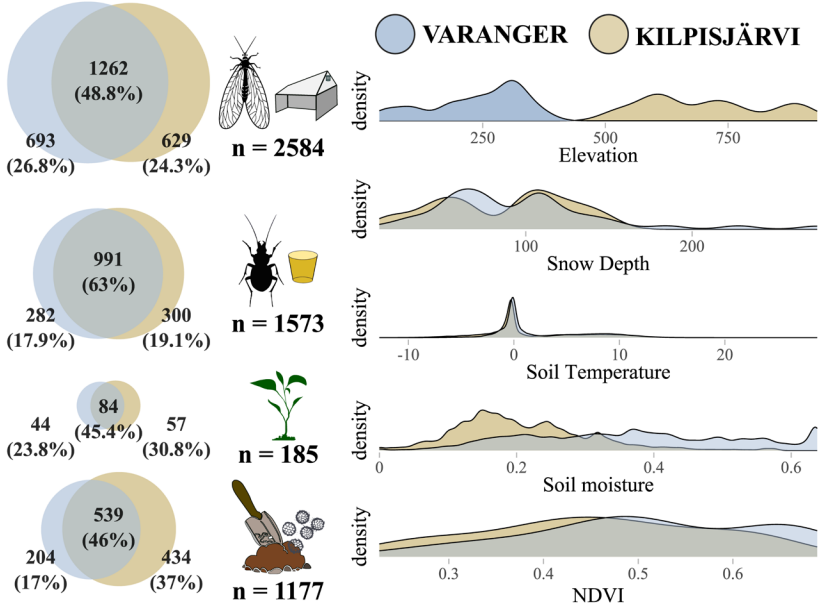

Figure 8. Comparisons between Kilpisjärvi and Varanger in terms of species pools and measured variables. On the left, Venn diagrams depict the overall number of identified species for each taxon (*n*), alongside the *shared* vs *unique* species for each study region. On the right, density plots show the elevation range, microclimatic conditions, and productivity values for each study region.

Regarding microclimatic conditions and productivity gradients, I found **closely similar ranges of variation in soil temperature, soil moisture, snow depth and productivity (NDVI) across sampling sites in Kilpisjärvi and Varanger** (Figure 8, **Papers I & II**). This indicates successful coverage of local conditions by my sampling design. As mentioned earlier, there is a difference in elevation between these regions, implying that the occurrence of almost identical microclimatic conditions and productivity values between Kilpisjärvi and Varanger is shifted 450 m in absolute elevation. The soil moisture and productivity ranges were also similar, with Varanger being slightly more humid and productive. Within each study area, I found **large variation in microclimatic conditions among sampling sites, reflecting into large variation in local species pools** (**Paper I** and see section below). I attributed such variation in soil moisture, soil temperature and snow depth to the heterogeneity of the landscapes in terms of elevation, topography and vegetation cover.

4.2 Microclimate shape the species richness of plants and arthropods and the abundance of arthropods

Local communities are the result of both deterministic and stochastic processes acting on the regional species pools. Environmental filtering can exert huge effects determining the distribution and abundance of species across the landscape. In this context, I found that the richness of flying arthropods, ground-dwelling arthropods and vascular plants is largely affected by the same microclimatic drivers. **Local species richness generally decreased with elevation, and increased with soil temperature and soil moisture** (**Paper I**). The decrease in species richness with elevation is a well-known phenomenon. A wealth of papers have found the same pattern across multiple ecosystems and taxa (McCain & Grytnes (2010) and references therein) – although the opposite pattern has also occasionally been reported (Sanders et al., 2003; Grytnes et al., 2006). To account for a decrease of species with elevation, the factors of climate, nutrient limitation, species-area relationships or biotic interactions have been variously invoked (McCain & Grytnes, 2010). Within this perspective, elevation has typically been used as a proxy for variation in other latent factors. In fact, although variation in elevation emerged as the strongest predictor for both species richness and abundance, only part of its effects were mediated through local soil temperature and moisture. This finding points to further, unmeasured factors explaining species richness along elevational gradients.

When examining the direct effects of soil moisture and temperature, I generally found an **increase in species richness across all taxa with increasing soil temperature and soil moisture**. Regarding the specific imprints of soil temperature, I had hypothesised that ground-dwelling arthropod communities and plant communities would be most strongly influenced by soil temperature, due to their proximity to the ground. Contrarily to my expectations, I found that soil temperature had a more consistent impact on the richness of flying arthropods than on the other taxa. This pattern emerged despite the fact that flying arthropods occupy an environmental stratum (air) whose conditions may be partly decoupled from conditions at the soil surface. This finding may stem from the fact that flying arthropods possess a high dispersal capacity, allowing them to effectively select locally favourable conditions. Across the study areas of Kilpisjärvi and Varanger, warmer soils were usually found in areas dominated by mountain birch forest (unpublished results), a contrast which persisted across seasons.

This difference is contrary to what has been found by other studies, where woody plant cover has been shown to cool soil temperatures via shading effects (Blok et al., 2010; Lantz et al., 2013; Myers-Smith & Hik, 2013; Kemppinen et al., 2021a). These areas are also characterized by a higher plant productivity, harbouring higher species richness, especially for flying arthropods (see **Paper II**). This leads to a higher aggregation of species in more-productive areas, which are simultaneously characterized by warmer soil conditions.

Higher soil moisture seemed to always promote the richness of ground-dwelling insects and plants. While soil moisture is a well-known key factor for the development of different ground-dwelling species (Danks, 2004), its effects on flying arthropods may be less evident since flying arthropods tend to use highly different habitats and substrates as larvae. As a matter of fact, most of these flying arthropods have aquatic larval phases or overwinter in especially moist habitats (Danks, 2004). However, their distribution as adults, as explained before, might be totally or partly decoupled from their habitats as larvae, and therefore poorly reflecting the measured soil moisture conditions. Higher soil moisture also positively affected plant richness, which is a recurrent pattern reported across landscapes (Moeslund et al., 2013; Deng et al., 2016; Mathur & Sundaramoorthy, 2016; Jordan et al., 2020). Lastly, I did not find snow depth as a key modulator of either plants or arthropod species richness, although snow modulates air-to-soil conditions which in turn affect species distributions and community composition (Niittynen & Luoto, 2018; Roos et al., 2022). Shortly, this is probably the effect of some limitations in my study which I further discuss in **paper I**.

In summary, species richness varied by almost an order of magnitude across the landscapes of Varanger and Kilpisjärvi. This variation was mostly explained by different environmental conditions among which elevation imposed the strongest imprints.

4.3 Plant richness is not a good proxy for arthropod richness, but plant productivity is

Several authors have proposed that patterns of plant species richness could be adopted as efficient proxies for patterns of arthropod species richness (Lewinsohn & Roslin, 2008; Basset et al., 2012). In **paper I**, I found

no support for this approach in the studied groups, since **vascular plant richness showed no relationship with ground dwelling arthropod richness and only a slightly positive relationship with flying arthropod richness** (Figure 9). In the case of ground-dwelling arthropods, this result may be explained by the dominance of predatory taxa. Ground-dwelling arthropods do tend to rely on vegetation *structure*, as vegetation provides the necessary hunting ground and microclimatic conditions for many predatory species (Brose et al., 2003; Jiménez-Valverde & Lobo, 2007; Bowden & Buddle, 2010). However, the direct impact of plant *diversity* on these communities is likely less pronounced. In further evidence of the predominant role of vegetation *structure*, in **paper II** I discovered an **increasing number of arthropod species, both flying and ground-dwelling, along the productivity gradients of Kilpisjärvi and Varanger** (Figure 9). More productive areas across these landscapes coincide with the presence of mountain birch (*Betula pubescens*) forest. The denser and more complex vegetation structure of these areas appears to support larger species pools, a phenomenon often linked with increased resource availability and habitat complexity (Leigh, 1965; R. H. MacArthur, 1965; Waide et al., 1999; Gillman & Wright, 2006; Cusens et al., 2012).

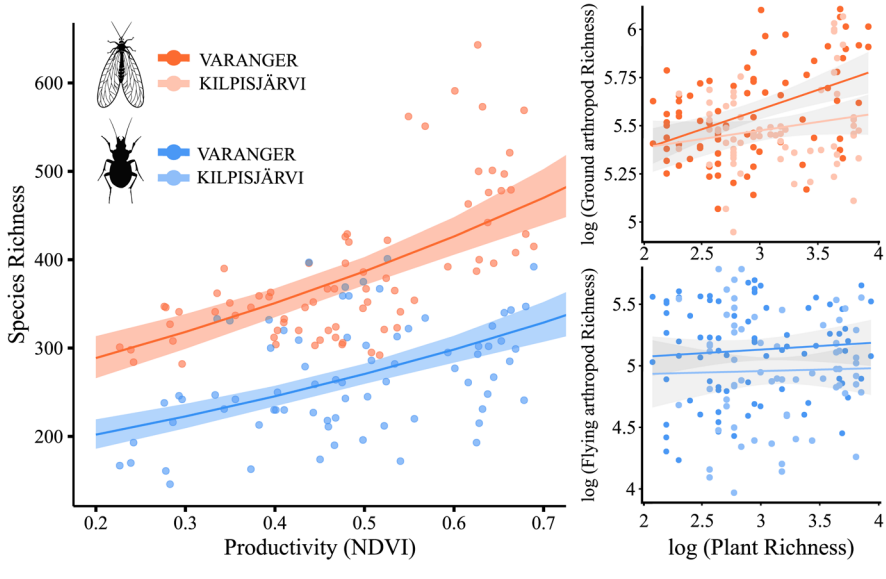

Figure 9. On the left side, species richness of arthropods across the productivity gradient. On the right side, species richness of each arthropod group against plant richness.

For the flying arthropod community, the relationship between productivity and species richness was even more pronounced. These taxa are likely to include a higher proportion of truly herbivorous taxa which are also dependent on vegetation structure. Moreover, **the relationship between productivity and arthropod richness remained constant across scales** (local, landscape and region), **highlighting the consistency of the mechanisms shaping species richness across landscapes (Paper II)**.

4.4 Arthropod community dissimilarity does not increase with productivity but does so with spatial scale

The effects of environmental filtering and dispersal rates are two of the main factors shaping community composition from the regional to the local scale. In **paper II**, I showed how **species richness increased towards highly productive areas regardless of the scale assessed**. In response to the increase of species at more productive areas, classical niche theory (R. H. MacArthur, 1965; R. MacArthur & Levins, 1967) predicts three potential outcomes at these areas: i) increased niche overlap, ii) narrower niches or iii) niches skewed towards increasing productivity (Figure 10).

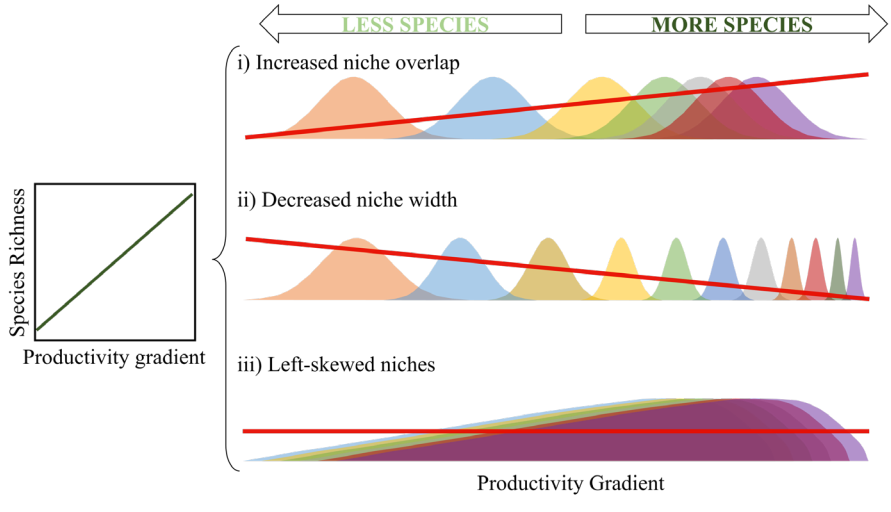

Figure 10. Schematic representation of hypothetical relationships between species niches and productivity, all causing higher alpha diversity with increasing productivity. The red line depicts the expected behaviour of species prevalence at both low vs high productivity sites under these scenarios.

However, none of these scenarios were borne out by any of my findings. Rather, I found the increase in species richness at high productive sites to emerge from **a majority of species having wide niches covering the whole productivity gradient ("common"),** combined with **subsets of specific species ("specialists") occurring exclusively at low- and high-productive sites – with the latter group being bigger.** Furthermore, species-specific prevalence did not differ between the low and the high end of the productivity gradient (Figure 11), and similar proportions of the species pools were shared among sites under both conditions (**Paper II**).

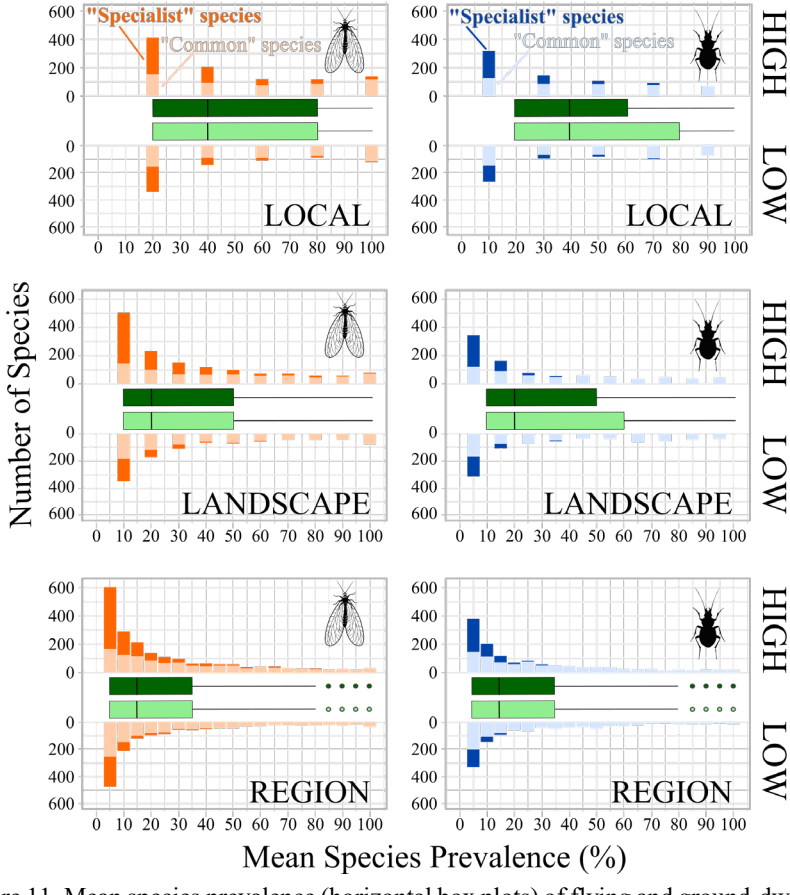

Figure 11. Mean species prevalence (horizontal box plots) of flying and ground-dwelling arthropods at low- and high-productivity sites across scales. Bar plots on top and below each corresponding low or high productivity boxplot show the proportion in numbers of "common" (light coloured) vs "specialist" (vivid coloured) species.

Arthropod assemblages tend to be dominated by numerous "rare" species, encountered at a low frequency across sampling sites. In my study, I found arthropod communities to be dominated by a majority of species being widely-distributed across the landscape, showing little association with productivity patterns. This finding contrasts with other studies, where communities have been found to be heavily dominated by habitat specialists displaying species-specific niche differentiation (Beckers et al., 2018; Hein et al., 2024).

I also found that **the differential amount of species specific to either low or high productivity did not reflect into differences in dissimilarity between community pairs at the respective ends: pairs of communities were no more different under conditions of high productivity than under conditions of low productivity** (**Paper II**; Figure 12). This pattern occurred despite a difference in species richness between these two extremes. This can only be explained by the low impact of "rare/specialists" species on pairwise comparisons between sites, since most of these species were singletons and doubletons (see vivid coloured bars in Figure 11) – causing differences in species-specific prevalence to even out between sites. **This pattern was consistent across scales, once again showing the consistency of the mechanisms shaping arthropod communities from local to regional scales in subarctic landscapes** (**Paper II**; Figures 11 and 12).

4.5 Highly-dispersive species form communities more distinct in space than poorly-dispersive species

At a local scale, frequent dispersal between sites (the so-called mass effects) can be expected to reduce species turnover. This should decrease any differences between communities in poorly or highly productivity sites, since most species can disperse freely across sampling sites. As a counter-force, efficient sampling of the landscape by highly-dispersive species should allow them to aggregate in the most favourable sites, causing strong species sorting on arthropod communities. By comparison, species turnover is expected to be maximal at the regional scale (Figure. 4), owing to low dispersal rates among communities and to the differences in species pools between regions. Nonetheless, we expect no difference in species turnover between low- and high-productivity sites at the regional scale, since the scale of environmental

variation will exceed the scale of dispersal. Such dispersal-limitation should prevent efficient sampling of the environment by all the species.

Contrary to these expectations, **I found no consistent dissimilarities in community composition between low and high productivity areas across any of the scales assessed** (**Paper II**; Figure 12). What I did observe was that, as predicted, **the turnover component of beta diversity increased consistently with spatial extent**. That is, **I found higher species replacement when comparing arthropod communities at the regional scale than at the local scale (Paper II).** This is a common pattern in nature, where communities tend to be more similar to each other the closer they are in space (Soininen et al., (2007) and references therein). In fact, I did find the same pattern when assessing community dissimilarity of multiple taxa at the local scale with increasing geographical space in **paper III** (Figure 13).

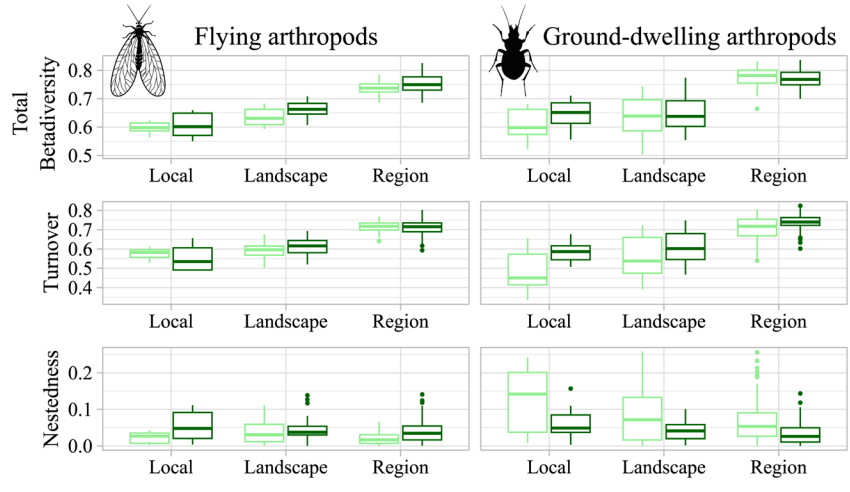

Figure 12. Community dissimilarity values among flying and ground-dwelling communities at each of the scales addressed (local, landscape and region). Shown in each panel is the overall distribution of pairwise total beta diversity, turnover and nestedness values between each pair of sampling sites between either low- (light green) or high-productivity (dark green) sites.

What was less intuitive and clearly in contrast with previous research (Qian, 2009; Jiménez-Valverde et al., 2010) was that at the local scale, **species groups with higher dispersal ability (fungi and plants) showed higher species replacement with geographical distance than species with**

lower dispersal abilities (arthropods) (**Paper III**; Figure 13**)** – despite the longer reach of the former. This finding suggest that at the local scale, the imprint of environmental filtering will vastly exceed the imprints of mass-effects in the strongly-dispersive groups of fungi and plants. Rather than homogenising community composition, high dispersal capacity among these groups will thus allow species to seek out the most beneficial conditions within the landscape. This result agrees with the findings in **paper I**, where the dispersal capacity of flying arthropods showed a decoupled effect between their obligatory development habitats (characterized by high moisture) and their preferred habitats as adults (characterized by high soil temperature). In **paper II**, I found almost no differences in turnover of arthropods within each scale across the full gradient of productivity, as reflecting the wide distribution of arthropods across all productivity conditions. This finding is in accordance with the lower turnover change with increasing geographical distance found for arthropods – but not fungi or plants – in **paper III**. Therefore, high dispersal during specific parts of the life cycle will thus result in efficient "species sorting" by environmental filters (Kraft et al., 2015).

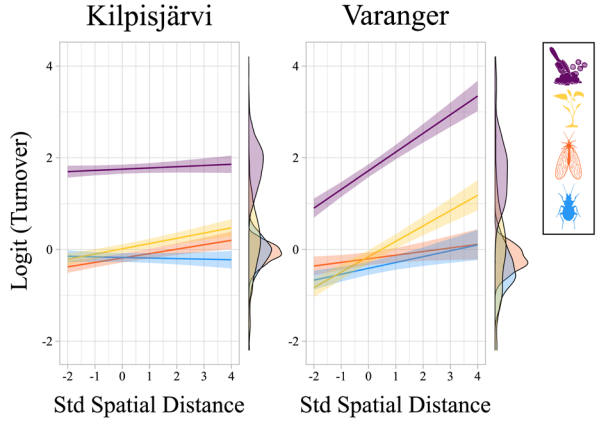

Figure 13. Species replacement (turnover on the logit-scale) across increasing spatial distance within each region for each taxon. Shown in each panel are the fitted slopes of pairwise community dissimilarity against standardized pairwise spatial distances between each pair of sampling sites. Shown on the right side of each panel are the marginal distribution of turnover values. Colours correspond to each taxon, with soil fungi shown in purple, vascular plants in yellow, flying arthropods in orange, and ground-dwelling arthropods in blue.

5. Conclusions and implications under climate change

Climate change is reshaping ecosystems worldwide, driving significant shifts in biodiversity patterns and community dynamics. One of the most striking consequences of climate warming is the alteration of regional species pools. As temperatures rise, species disperse towards higher latitudes, leading to an increase in regional species richness. This shift enriches the fundamental pool from which species are recruited to local communities, fundamentally altering their composition and structure. Changes in environmental conditions may have further implications for the communities inhabiting sub-arctic landscapes.

In my study, I show how environmental variability at the landscape level shapes species richness primarily through the effects of elevation, soil moisture, and soil temperature. Alterations in these conditions can profoundly impact species survival and ecosystem functioning. For instance, earlier snow melt, attributed to shifts in snowfall and increased average temperatures, may redistribute species in space and time across the landscape, potentially causing phenological mismatches between arthropods and plants. Conversely, plant productivity is anticipated to increase under climate change due to the shrubification of high latitude tundra landscapes and the lengthening of the growing season (Mekonnen et al., 2021). As shown in my study, higher plant productivity typically correlates with greater abundance and richness of arthropods, while higher plant richness does not necessarily follow suit. Therefore, the specific consequences of warming for biodiversity are hard to predict.

Variation in species composition across landscapes differs among species groups, due to the combined effects of environmental filtering and dispersal capacity. Among groups, vascular plants and fungi exhibit the highest

dispersal capacity – but display the greatest turnover across spatial distances. This finding underscores the high capacity of plants and fungi to efficiently sample their environment, thus being subject to the strongest environmental filtering. I thus posit that shifts in conditions with climate change will modify community composition, and cause changes in the set of species co-occurring in local communities, but will not necessarily result in a decrease in species richness or abundances.

Our endeavour as ecologists is to comprehensively study current processes at various scales and landscapes, with the aspiration that our work will yield lasting insights into community assembly processes. It is through the evaluation of these patterns over time that we can attain a thorough ecological understanding of the processes studied and discern the sign and direction of changes in patterns. My intention in this thesis has been to understand how communities of different groups are shaped by abiotic factors, energy inputs, and dispersal capacity across two subarctic landscapes. In doing so, I realise that I have merely touched upon present community assembly patterns. While much work remains to be done, I am proud to have extended the key concepts of community assembly to understudied groups in these regions. I hope that my comparative study across a taxonomically comprehensive set of hyperdiverse taxa will contribute to assessing the generality of topical theory and concepts.

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Popular science summary

Have you ever used Google Maps to explore remote corners of the world? I find myself doing this quite often and over the years, I have noticed a pattern: I'm drawn to the most isolated places, where you can virtually immerse yourself in a specific spot through a 360º photograph uploaded by someone else. These places are typically found in extremely remote areas like the Tibetan plateau, Greenland, or the Siberian tundra above the Arctic Circle. When you look at these vast tundra landscapes, where wilderness seems to stretch uninterrupted, it is easy to assume that nature remains untouched by the hand of humanity. However, we now know that even in these sparsely populated and distant regions, the effects of anthropogenic climate change are acutely felt.

One of the most visible signs of climate change is the migration of species into regions where they previously did not exist. For instance, there have been reports of cold-adapted plants shifting towards higher altitudes in search of suitable conditions, not only in the Arctic but also in subarctic and alpine areas. A parallel process is the phenomenon known as “the greening of the Arctic”, which exemplifies the lengthening of the growing season and the expansion of woody plants across the tundra as the consequence of the warmer temperatures. Another well-known example is the northward expansion of red fox populations, which are displacing Arctic foxes in some Arctic regions. In addition, two geometrid moth species have recently expanded their ranges in northern Fennoscandia. They are now causing significant defoliation and occasional mortality of mountain birch forests just a few kilometres away from my study site in Varanger – a phenomenon which has been linked to climate change.

The impact of these range expansions and distribution changes on subarctic ecosystems and their inhabitants varies with the perspective. While

some species may benefit, others may struggle. For instance, some researchers have noted that the expansion of shrubs in high tundra landscapes delays snowmelt, thus prolonging the protective snow cover on the ground. This benefits many species by protecting them from extreme frost, wind abrasion, or desiccation. However, other studies have warned that shrub dominance could lead to drier, colder, and less fertile soils, potentially affecting the entire tundra system. These examples underscore two important points: community structure is likely to change due to climate change, and understanding the differential responses of different organism groups is crucial, as these species are interconnected within the broader ecosystem. My thesis work aims to shed light on understudied communities of vascular plants, soil fungi and arthropods across the subarctic region. Specifically, I am interested in understanding the patterns of community diversity and the factors influencing them.

The environment plays a significant role in shaping the richness of species and their abundance across landscapes. Based on the community assembly framework, in Paper I, I explored the extent to which local microclimate structures communities through its impacts on species richness and abundance across landscapes. Given the intense effort required for adequately characterizing arthropods, I also investigated whether plant richness could serve as a proxy for arthropod richness across subarctic landscapes

Ecologists have long known that the amount of energy (productivity) within an area is related with the number of species that it can support. In Paper II, I asked myself whether arthropod communities inhabiting the subarctic region are not an exception to this pattern. Moreover, I explored whether communities in high-productive areas exhibit greater species variation compared to those at low-productive areas – and investigated the scale-dependency of this pattern.

In Paper III, I evaluated how the species composition of plant, fungi, and arthropod communities changes across landscapes. To study these patterns, I focused on the dispersal capacity of each taxon, and how differences in presumed dispersal create more or less similar communities across the landscape.

I found that the species richness of subarctic communities of plants and arthropods are strongly influenced by elevation, soil temperature and soil moisture across landscapes. In brief, the higher, colder and drier the

landscape, the less species you will find. In contrast, warmer soils are found in the lower parts of the landscape, where the mountain birch forests – *or at least the ones not yet eaten by an outbreak of the geometrid moths* – occur. These areas are characterized by a higher productivity, which is linked to a higher species richness, suggesting that the subarctic landscapes is no exception to the positive species richness-productivity relationship. However, while the high-productive areas sustained a higher number of species, I did *not* find significantly greater variation in species composition among highly-productive areas than among poorly-productive ones. In fact, across the landscape, subarctic communities of arthropods consist of a combination of very many and common species occurring in both poorly- (*high tundra*) and highly- (*the mountain birch forest*) productive areas, with some other species occurring only at one of the two ends of the productivity gradient. More importantly, these patterns were constant across different scales, from the local, through the landscape to the regional level. When inspecting the communities of plants, fungi and arthropods, the groups with higher dispersal ability – those that are able to travel further across the landscape in search of the ideal conditions to live – showed more structure across the geographical space. This result suggests that these groups (fungi and plants) are strongly shaped by the environment, occurring in areas were conditions are optimal. On the other hand, the less dispersive groups (flying and ground-dwelling arthropods) form communities more similar to each other, composed of species that can inhabit most areas within the landscape.

One final finding of my thesis is that studying different taxa spanning three kingdoms, across different scales and using fine spatiotemporal resolution, often raises more questions than it resolves. However, it is through the evaluation of these patterns over time that we can attain a thorough ecological understanding of the processes at play. Given the time constraints associated with a typical PhD thesis, my findings are based on a snapshot of two years alone. Nonetheless, my results add further knowledge about the subarctic communities of plants, fungi and arthropods. They highlight the interdependency of factors influencing species distribution and richness, and point to some consistent patterns across scales. Both the environment and the topography create areas within landscapes and landscapes within regions that differ in conditions such as temperature, moisture or productivity. To inhabit certain areas, species first need to be able to reach them through dispersal. To survive in these areas, they need to

cope with the local conditions. With this information at hand, it will be easier to discern the sign and direction of changes in patterns. Since high-latitude areas are experiencing a higher increase in temperatures compared to other parts of the globe, they will be ones first affected by the impacts of anthropogenic climate change. Thus, I find continued studies of the communities inhabiting these regions a key priority for future research.

I bet that many of us "researchers, academics and the like" have confronted that classic moment when a beloved family member or a friend comes up at us asking the most typical question. "*So… what exactly do you do in your job?*" I wrote this section, in the spirit of simplification, to explain in plain words what I have worked on for the last four years, what I have learnt from it and why it is worthy of attention.

Populärvetenskaplig sammanfattning

Har du någonsin använt Google Maps för att utforska avlägsna hörn av världen? Jag kommer ofta på mig själv med att göra just det. Under årens lopp har jag upptäckt ett mönster: jag dras till jordens mest isolerade regioner, där jag kan fördjupa mig i en specifik plats genom ett fotografi på 360º som laddats upp av någon annan. Dessa platser återfinns oftast i extremt avlägsna områden såsom den tibetanska platån, Grönland eller den sibiriska tundran ovanför polcirkeln. När man granskar dessa vidsträckta tundralandskap, där vildmarken tycks sträcka sig obruten, är det lätt att anta att naturen här har förblivit orörd av människans hand. Numera vet vi dock att även dessa glesbefolkade och avlägsna regioner berörs av klimatförändringar som direkt har orsakats av människan.

Ett av de mest synliga tecknen på klimatförändringar är att arter sprider sig till regioner där de tidigare saknats. Till exempel har det förekommit rapporter om köldanpassade växter som flyttar mot högre höjder i jakt på lämpliga förhållanden, inte bara i Arktis utan även i subarktiska och alpina områden. En parallell process är det fenomen som kallas "Arktis växling mot grönt". Fenomenet återspeglar en förlängning av den lokala tillväxtperioden och en expansion av vedartade växter över tundran. Båda är konsekvenser av de allt varmare temperaturerna. Ett annat välkänt exempel är den nordliga expansionen av rödrävspopulationer, som nu tränger undan fjällrävar i vissa arktiska regioner. Dessutom har två arter av mätarfjärilar nyligen vidgat sina utbredningsområden i norra Fennoskandien. De orsakar nu betydande avlövning och ibland även dödlighet i fjällbjörkskogar – ett fenomen som även det har kopplats till klimatförändringar.

Hur dessa förändringar i arternas utbredning påverkar subarktiska ekosystem och deras invånare varierar beroende på vems perspektiv man antar. Medan vissa arter kan gynnas av förändringarna kan andra arter lida

av dem. Till exempel har vissa forskare noterat att buskarnas expansion i tundralandskapen på höga breddgrader kan fördröja snösmältningen, vilket resulterar i en längre period av skyddande snötäcke på marken. Denna förlängning gynnar många arter genom att skydda dem från extrem frost, piskande vindar eller uttorkning. Andra studier har varnat för att en ökad dominans av buskar kan leda till torrare, kallare och mindre bördiga jordar, vilket potentiellt kan påverka hela tundrasystemet. Dessa exempel understryker två viktiga punkter: att strukturen på arktiska organismsamhällen sannolikt kommer att förändras på grund av klimatförändringar, och att det är avgörande att förstå hur olika organismgrupper reagerar på förändringana, eftersom de arter som berörs är sammanlänkade inom det bredare ekosystemet. Mitt examensarbete syftar till att belysa understuderade samhällen av kärlväxter, av svampar i jordmånen, och av leddjur i den subarktiska regionen. Specifikt är jag intresserad av att förstå mönster i organismsamhällenas mångfald och de faktorer som påverkar dem.

Miljön spelar en betydande roll för att forma mönster i arternas rikedom och individantal över landskapet. Jag tog min utgångspunkt i teoretiska ramverk kring organismsamhällenas uppbyggnad. I kapitel I undersökte jag i vilken utsträckning det lokala mikroklimatet formar samhällena genom sin inverkan på variationen i art- och individantal över landskapet. Med tanke på den intensiva ansträngning som krävs för att beskriva leddjurssamhällen, så undersökte jag också om växternas artrikedom kunde erbjuda en skattning av leddjurens artrikedom i olika delar av subarktiska landskap

Ekologer har länge vetat att den mängd energi som är tillgänglig inom ett område (genom produktivitet) är relaterat till det antal arter som området kan livnära. I kapitel II utredde jag om leddjurssamhällena i den subarktiska regionen är ett undantag från detta mönster. Dessutom undersökte jag om samhällen i högproduktiva områden uppvisar större lokala skillnader jämfört med samhällen i lågproduktiva områden – och om dessa mönster varierar i olika rumsliga omfattningar.

I artikel III utvärderade jag hur artsammansättningen i växt-, svamp- och leddjurssamhällen varierar över landskapet. För att studera dessa mönster fokuserade jag på spridningskapaciteten för varje organsimsgrupp för sig, och hur skillnader i förmodad spridning skapar mer eller mindre liknande samhällen över landskapet i olika grupper.

Jag fann att artrikedomen i subarktiska samhällen av växter och leddjur starkt påverkas av den lokala höjden över havsytan, av marktemperaturen och av markens fukthalt. Kort sagt, ju högre, kallare och torrare landskapet är, desto färre arter kommer du att hitta. Däremot finns varmare jordar i de nedre delarna av landskapet, där fjällbjörkskogarna förekommer – eller åtminstone *de skogar som ännu inte ätits upp av ett utbrott av mätarlarver.* Dessa områden kännetecknas av en högre produktivitet, som är kopplat till en högre artrikedom. Allt detta tyder på att de subarktiska landskapen inte är något undantag från ett allmänt, positivt förhållande mellan artrikedom och produktivitet. Men även om högproduktiva områdena upprätthöll ett högre antal arter, så fann jag *inte* signifikant större variation i artsammansättning mellan högproduktiva områden än mellan lågproduktiva områden. Faktum är att subarktiska samhällen av leddjur består av en kombination av väldigt många och vanliga arter som förekommer i både lågproduktiva (*hög tundra*) och högproduktiva områden (*fjällbjörkskog*) över hela landskapet, med ett mindre inslag av andra arter som endast förekommer i någondera ändan av produktivitetsgradienten. Ännu viktigare är att samma mönster uppträdde konsekvent över olika rumsliga skalor, från den lokala nivån, genom landskapsnivån till den regionala nivån. Bland artsamhällen av växter, svampar och leddjur fann jag en klarare geografisk struktur inom de grupper som kännetecknas av en högre spridningsförmåga – dvs. de grupper som kan röra sig längre över landskapet i jakt på ideala förhållanden. Detta resultat tyder på att dessa grupper (svampar och växter) är starkt formade av miljön och förekommer i områden där förhållandena är optimala. Å andra sidan bildar organismgrupper med lägre spridningsförmåga (flygande och marklevande leddjur) mer snarlika lokala artsamhällen, sammansatta av arter som kan bebo de flesta områden i landskapet.

Ett sista fynd i min avhandling är hur komplexa förhållandena är i naturen. Därför väcker studier som spänner över tre riken (svampar, leddjur och växter), över olika rumsliga skalor och som bygger på hög upplösning i både tid och rum, ofta fler frågor än det löser. Genom att följa dessa mönster över en längre tid kunde vi uppnå en djupare ekologisk förståelse av de underliggande processerna. På grund av tidsbegränsningen för en typisk doktorsavhandling är mina resultat baserade på en ögonblicksbild på bara två år. Ändå tillför mina resultat ytterligare kunskap om de subarktiska samhällena av växter, svampar och leddjur. De belyser den komplicerade samverkan mellan de faktorer som påverkar arternas distribution och

rikedom, och de pekar ut några konsekventa mönster som håller över olika rumsliga skalor. Både miljön och topografin skapar variation i förhållanden som temperatur, fukt eller produktivitet mellan olika områden inom landskap, och olika landskap inom större regioner. För att kunna bebo ett område måste arter först kunna nå dem genom spridning, och för att överleva i dessa områden måste arterna klara de lokala förhållandena. På basis av denna information blir det lättare att urskilja riktningen för olika förändringar i organismsamhällenas mönster. Eftersom områden på höga breddgrader genomgår en snabbare temperaturökning än andra delar av världen, så berörs de allra först av effekterna av klimatförändringar. Därför ser jag fortsatta studier av organismsamhällen i dessa regioner som en nyckelprioritet för framtida forskning.

Jag är övertygad om att många av oss "forskare, akademiker och liknande" har mött det klassiska ögonblick när en älskad familjemedlem eller en vän närmar sig oss med den typiska frågan. "*Så... vad exakt gör du i ditt jobb?*" Jag skrev detta avsnitt i förenklingens anda för att härmed förklara vad jag har studerat de senaste fyra åren, vad jag har lärt mig och varför detta är värt att uppmärksammas.

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I

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ORIGINAL ARTICLE

Consistent imprints of elevation, soil temperature and moisture on plant and arthropod communities across two subarctic landscapes

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Abstract

1. Factors shaping arthropod and plant community structure at fine spatial scales are poorly understood. This includes microclimate, which likely plays a large role in shaping local community patterns, especially in heterogeneous landscapes characterised by high microclimatic variability in space and in time.
2. We explored differences in local microclimatic conditions and regional species pools in two subarctic regions: Kilpisjärvi in north-west Finland and Varanger in north-east Norway. We then investigated the relationship between fine-scale climatic variation and local community characteristics (species richness and abundance) among plants and arthropods, differentiating the latter into two groups: flying and ground-dwelling arthropods collected by Malaise and pitfall traps, respectively. Arthropod taxa were identified through DNA metabarcoding. Finally, we examined if plant richness can be used to predict patterns in arthropod communities.
3. Variation in soil temperature, moisture and snow depth proved similar between regions, despite differences in absolute elevation. For each group of organisms, we found that about half of the species were shared between Kilpisjärvi and Varanger, with a quarter unique to each region.
4. Plants and arthropods responded largely to the same drivers. The richness and abundance of both groups decreased as elevation increased and were positively correlated with higher soil moisture and temperature values. Plant species richness was a poor predictor of local arthropod richness, in particular for ground-dwelling arthropods.
5. Our results reveal how microclimatic variation within each region carves pronounced, yet consistent patterns in local community richness and abundance out of a joint species pool.

KEYWORDS
abundance, Malaise traps, microclimate, pitfall traps, snow conditions, species richness, structural equation models

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INTRODUCTION

How species communities are structured by climatic variation is of utmost concern. With the ongoing global shift in climatic conditions (Pörtner et al., 2022), we may also expect shifts in community composition (Pecl et al., 2017; Warren et al., 2018) and in emergent features, such as overall species richness and abundances (Antão et al., 2022; Kankaanpää et al., 2020). In evidence of changes in progress, shifts in the distribution and abundance of both individual species and community parameters have already been detected at both small and larger spatial scales (Lembrechts et al., 2019; Lenoir & Svenning, 2015; Parmesan, 2006; van Beest et al., 2021). At large scales, species have shifted towards higher latitudes and elevations as a response to changing climatic conditions (Hallinger et al., 2010; Kemppinen, Niittynen, Virkkala, et al., 2021; Mamantov et al., 2021; Myers-Smith & Hik, 2018; Wilson & Nilsson, 2009). Understanding how climatic variation shapes current communities is the key to understanding how future climatic changes will likely affect community structure.

The structure of contemporary communities will reflect impacts from multiple scales (HilleRisLambers et al., 2012; Vellend, 2016). While regional species pools are shaped by longer-term evolutionary and geological processes, local communities are formed as subsets thereof, with biotic and abiotic processes acting as filters in between regional and local species pools. In the search for the assembly rules behind present-day local communities, much interest has been invested in macroclimate—that is, average conditions characterising wider regions (Elith & Leathwick, 2009; Lembrechts et al., 2019). This is likely because current climatic predictions are usually generated at comparatively low resolution for relatively large areas and because data on species distribution tend to be associated with environmental data at an equally crude spatial scale (Bütikofer et al., 2020; Potter et al., 2013). By comparison, the impact of climate at smaller spatial scales—likely more relevant to individuals or populations—tends to be less well established. There is a general lack of direct empirical evidence of the effects of microclimate on present-day community features such as species richness and diversity. Moreover, the few studies that account for fine-scale environmental variation are usually limited to a few focal taxa only (Ashcroft et al., 2014; Davis et al., 2016; Gillingham et al., 2012; Nielsen et al., 2010) or use estimates of microclimate derived from simplified models (Randin et al., 2009; Trivedi et al., 2008).

The current mismatch between the scale at which organisms experience climate and the scale at which ecological analyses and predictions are made is unfortunate, given that microclimatic variation within a region can be more pronounced than macroclimatic variation between regions (Maclean et al., 2019). As a result, analyses at low resolution may result in correspondingly low power in terms of identifying the climatic drivers of current community composition, as variation in relevant descriptors is blurred over space.

The role of microclimate in explaining local community patterns is likely accentuated in heterogeneous landscapes characterised by high microclimatic variability in space and in time, which is typically the case at high latitudes. In polar regions, species may be strongly constrained by climatic conditions, with many species living near their tolerance limits in terms of available energy (Bahrndorff et al., 2021) and moisture (Strathdee & Bale, 1998). Of particular interest are communities of ectotherms such as plants and arthropods, which constitute the primary trophic building blocks of most communities. As these taxa rely on external temperatures for their metabolism, their communities are more likely to be strongly shaped by small-scale variation in ambient conditions than are most other taxa.

Importantly, species or individuals within a given taxonomic group are prone to experience somewhat different conditions and will be affected by different aspects of small-scale climatic variation, even when co-occurring in the same environment. For example, temperatures in the air utilised by flying arthropods may be partly decoupled from conditions at the soil surface. The ability of the soil to absorb radiation (Trew et al., 2022) and the insulating effect of snow (Aalto & Luoto, 2014; Kankaanpää et al., 2018; Niittynen, Heikkinen, & Luoto, 2020) and vegetation (De Frenne et al., 2019) give rise to such differences, creating complex mosaics of microclimates across landscapes (Convey et al., 2018; Sears et al., 2011). Thus, depending on the exact environmental stratum occupied by a specific group of organisms, it may experience and respond differently to local conditions (Figure 1). The effects of soil temperature are modulated by variation in snow cover and soil moisture (Tan et al., 2022; Zhao et al., 2022). Warmer temperatures and changes in snow dynamics have been proposed to negatively affect species abundance of arthropods (Bowden et al., 2018; Høye et al., 2020, 2021) and positively affect the growth of plants (Elmendorf et al., 2012; Myers-Smith et al., 2011; Scharn et al., 2021; Tape et al., 2006). Differential responses by different groups of organisms are of particular interest, since these groups are tied to the same wider community by their interactions, moulding community structure across trophic levels and landscapes (Kankaanpää et al., 2021; Koltz et al., 2018; Schmidt et al., 2017).

However, relating microclimatic variation to small-scale variation in community composition is no easy task. Merely sampling and describing local communities among highly diverse taxa such as arthropods is a challenge in itself. As a vivid illustration of the complexities involved, an initiative aimed at characterising some 70 local arthropod communities in Sweden by using Malaise traps yielded an estimated 80 million insect individuals (Karlsson et al., 2020). In the 17 years that followed, this material was sorted into 350 taxonomic fractions and shipped to more than 100 taxonomists across the globe. To date, only 2% of the material has been identified to species (Karlsson et al., 2020). In practice, DNA-based identification techniques will thus provide the only realistic approach to such tasks.

Given the difficulties and labour intensity involved in measuring these species-rich communities (Basset et al., 2015), several authors have proposed that patterns of species richness among plants could be adopted as efficient proxies for patterns of arthropod richness (Basset et al., 2012; Lewinsohn & Roslin, 2008). To what extent this holds true at a landscape level will depend on how similarly plants and arthropods respond to the same drivers. In fact, the exact scale for potential congruence in community patterns among plants and arthropods is yet to be established.

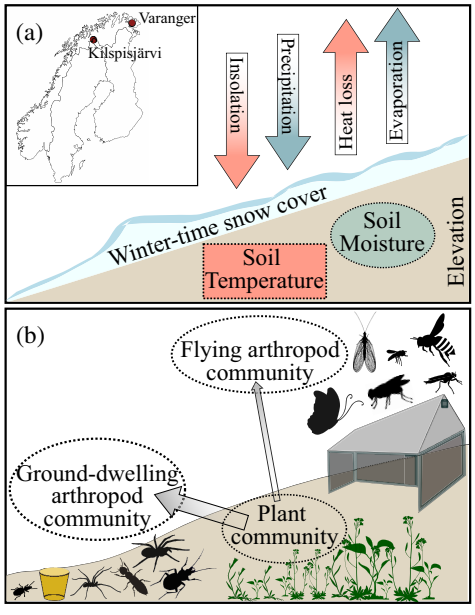

FIGURE 1 Schematic representation of our subarctic study areas (see map) showing (a) the environment and its microclimatic drivers and (b) the three focal taxa groups. (a) Across subarctic landscapes, local variation in topography, aspect and elevation create differences in, for example, insolation, heat loss, precipitation and evaporation. These fluxes may be strongly modified by the insulating effect of winter-time snow coverage, resulting in different microclimatic conditions above and below ground. (b) The resulting microclimatic differences should be experienced differently by the focal species groups, with plants and ground-dwelling arthropods sharing more similar conditions than do plants and flying arthropods (with similarities between groups represented by the width of the arrows). For each group we identify the method employed in sampling them: a Malaise trap for flying arthropods and a pitfall trap for ground-dwelling arthropods were used.

In this paper, we explore the relationship between fine-scale climatic variation and the community characteristics of plants and arthropods. We distinguish between two groups of arthropods, which experience different parts of the environment as adults: flying and ground-dwelling arthropods (Figure 1). In the low subarctic vegetation, ground-dwelling and flying arthropods will experience different conditions due to their ecology and dispersal capacity. Plants and ground-dwelling arthropods spend their full life cycle in or on the soil, and thus experience climate conditions prevailing near the soil surface both in winter and summer. While plants are sessile, arthropods are mobile and may thus seek out the most favourable conditions within their movement range. Flying arthropods spend their larval development on plants or in soil, but much of their adult life is spent high up in plants or in the air, experiencing temperatures at some distance above the soil and are able to select favourable conditions over a much wider range.

As a result, we may hypothesise that: (1) variation in topography, winter-time snow cover and vegetation creates different microclimatic conditions; (2) ground-dwelling arthropods and plants respond most similarly to microclimatic drivers, because of the continuous proximity of both taxa to the soil surface; and (3) small-scale variation in plant diversity is reflected in small-scale variation in ground-dwelling arthropod diversity, since these two taxonomic groups share the same microclimate. By targeting two subarctic regions characterised by a similar macroclimate, but each with large variation in local topography, snow cover and vegetation, we examine the identity and consistency of microclimatic drivers on plant and arthropod communities. Specifically, we ask: (1) what fraction of plant and arthropod species do these regions have in common, that is, to what extent do they share the same species pool; (2) how large is the variation in microclimate within and between the two study regions; (3) do communities of plants, ground-dwelling and flying arthropods respond to the same climatic drivers, despite their use of different parts of the environment; (4) are the imprints of these drivers consistent across regions and years; and (5) can patterns in plant communities be used to predict patterns in arthropod communities?

MATERIALS AND METHODS

Study regions

As representative regions of the subarctic realm, we chose the mountain tundra landscapes of Kilpisjärvi (north-western Finnish Lapland, 69°03′ N, 20°51′ E) and the Varanger Peninsula (north-eastern Norway, 70°31′ N, 29°05′ E) (Figure 1). These regions are separated by ca. 350 km. The study area around Kilpisjärvi (hereafter 'Kilpisjärvi') is located within the subarctic region and expands over 14 km^2 between the Lake Kilpisjärvi and Mount Jehkas. Within this area, elevations range from 475 m a.s.l. at the lakefront to 1029 m a.s.l. at the summit of Mount Saana. The Varanger study area (hereafter 'Varanger') rests at the southern edge of the low-arctic tundra (Ims et al., 2013) and extends over 425 km^2 across the north-western region of the Peninsula, with elevations ranging from sea level up to 619 m a.s.l. Within this region, a focal study area of a size identical to Kilpisjärvi (14 km^2) was established along the west and east sides of the Juladalen Valley (Austertana). For maps of the study regions, see Supporting Information (Figure S1).

Both regions are characterised by a topographically heterogeneous landscape, where steep slopes of mountain massifs and topographic features, such as hilltops, ridges and small depressions create broad environmental gradients and spatial contrasts in local climate, moisture run-off and snow deposition over short distances (Ims et al., 2013; Kemppinen et al., 2018). In each area, the dominant vegetation at the lowest elevations to the tree line (at ca. 700 m a.s.l. at Kilpisjärvi and 250 m a.s.l at Varanger) is mountain birch (*Betula pubescens*) forest. Above the tree line, mountain heaths prevail with dwarf shrubs such as *Empetrum nigrum*, *Betula nana*, *Juniperus communis* and *Vaccinum* spp. among the most common plant species.

Overall, average climatic conditions are similar in the two study areas. Both Kilpisjärvi and Varanger are among the most 'arctic' places in Fennoscandia with a growing season of 100 days or less (Tuhkanen, 1980). The climate in Kilpisjärvi is affected by its high-latitude location in the Scandes Mountains and its close proximity to the Arctic Ocean (Aalto & Luoto, 2014). The mean annual temperature is −1.3°C and the annual precipitation is 508 mm (1990–2021; Kyläkeskus meteorological station: 69°04′ N, 20°80′ E; 480 m a.s.l; Finnish Meteorological Institute). Annual average temperature in the Varanger Peninsula is relatively similar, with some differences between coastal and inland areas. At the outer low-lying coastal areas average annual temperature is above zero (0–2°C), while in the interior highland areas rising to 600 m a.s.l. the average annual temperature is below zero (−3–0°C) inducing widespread permafrost (Farbrot et al., 2013). Annual precipitation is the highest in the coastal areas facing the Barents Sea and in the central highlands, equalling some 623 mm (1990–2021; Vardø meteorological station: 70°37′ N, 31°09′ W; 10 m a.s.l; Norwegian Meteorological Institute).

Sampling site selection

To establish links between microclimatic variation and community characteristics of plants and arthropods, we implemented a stratified random sampling design within each study area. In 2020, we selected 35 and 40 sampling sites for Kilpisjärvi and Varanger, respectively. Sampling sites were located at least 100 m apart, covering a range of environmental conditions in terms of topography, vegetation height, snow depth and distance to water bodies. At each sampling site, we characterised microclimatic conditions and the communities of vascular plants, as well as flying and ground-dwelling arthropods.

Microclimate characterisation

To characterise fine-scale microclimatic conditions we installed a TMS-4 datalogger (TOMST®, Prague, Czech Republic) at each sampling site immediately upon local snowmelt. These loggers measured air, ground and soil temperatures (at 15 cm above, 0 cm and 8 cm below the ground, respectively), as well as soil moisture at 8 cm below ground, every 15 min. In addition, we determined the elevation (m a.s.l) and took a four measurements of snow depth (cm) around each sampling site (in March, the time when snow cover is typically deepest). Due to malfunction of a datalogger, one sampling site at Kilpisjärvi had to be excluded from all analyses.

Community characterisation

To characterise the local community of arthropods, we collected flying arthropods with a Malaise trap and ground-dwelling arthropods with two pitfall traps at each sampling site. To examine consistency in patterns and drivers between years, sampling was conducted over 2 years (2020 and 2021). In each year, sampling covered the entire growing season and was initiated as soon as the snow melted, with site-specific onset (between early June and early July depending on the timing of snowmelt) and lasting until early September. Each sampling site was monitored weekly, resulting in a yearly average of 12 and 10 arthropod samples at Kilpisjärvi and Varanger, respectively.

A Malaise trap (manufactured by Terrapolar, Kauhajoki, Finland) was placed at the centre of the sampling site with the collector bottle facing south. The Malaise collector bottles were filled with 96% ethanol as a preservative. Two pitfall traps were placed at a distance of ca. 1 m from each side of the Malaise trap (following Schmidt et al., 2012). Pitfall traps were 10 cm in diameter and contained water mixed with a few drops of odorant- and colour-free detergent to break the surface tension. Once the sample had been secured, collector bottles and pitfall traps were wiped with DNA-AWAY™ surface decontaminant (Molecular BioProducts Inc., Toronto, Canada) and dried with a clean tissue paper. By this procedure, we avoided spatio-temporal cross-contamination between weekly samples. The samples were stored in Falcon tubes filled with 96% ethanol at −18°C before DNA extractions. In total, 796 malaise and 743 pitfall trap samples were collected in 2020 and 861 malaise and 852 pitfall trap samples in 2021. (This material is similar in size to that described by Karlsson et al. (2020), and thus unamenable to morphology-based analysis within a relevant time frame.)

Local plant communities were surveyed during summer 2022 in an area of 100 m^2 surrounding each sampling site, compiling full species lists of all vascular plants using the taxonomy and nomenclature of Gyldendals store nordiske flora (Mossberg, 2018). Site-specific survey effort was scaled to the species richness of the sampling site, which varied vastly (10–47 plant species in Kilpisjärvi and 8–51 plant species in Varanger; see results). Plant species richness was defined as the sum of all plant species present within each sampling site.

Molecular workflow

Species identification of arthropods was based on DNA metabarcoding. To this aim, DNA was extracted from the arthropod samples using a modified non-destructive salt extraction protocol (Aljanabi & Martinez, 1997; Vesterinen et al., 2016). In addition to the environmental samples, a negative extraction control sample was added to each extraction batch, thereby measuring the purity of reagents and controlling for cross-contamination. These negative controls were otherwise treated similarly to the arthropod samples but contained no animal tissue. Furthermore, internal arthropod controls (*Drosophila hydei*) were added to each trap sample. Prior to DNA extraction, the biomass (wet weight) of malaise samples was measured following a standardised protocol (Schwan et al., 1993). Arthropod abundance was defined as the sum of all flying arthropod sample weights (g) throughout the sampling period.

From the extracted DNA, a 419-bp fragment of the mitochondrial cytochrome c oxidase subunit I gene fragment (COI) was amplified using primers BF3 5′-CCH GAY ATR GCH TTY CCH CG-3′

(Elbrecht et al., 2019) and BR2 5′-TCD GGR TGN CCR AAR AAY CA-3′ (Elbrecht & Leese, 2017). All the primers included a linker-tag enabling the subsequent attachment of unique indexes to label the samples and Illumina specific sequencing primers. To increase the amplicon library diversity, each primer was used in four different versions, including heterogeneity spacers between the linker-tag and the actual locus-specific oligo (0, 1, 2 or 3 extra nucleotides). Again, a blank PCR control was added to each PCR batch to measure the purity of reagents and the level of cross-contamination. All PCR reactions were carried out as two technical replicates, and each replicate contained two heterogeneity versions of each primer. The reaction setup followed Kankaanpää et al. (2021) with a reaction volume of 10 μL and included 5 μL of 2× MyTaq HS Red Mix (Bioline, UK), 2.4 μL of H_2O, 150 nM of each primer (two forward and two reverse primer versions) and 2 μL of DNA extract of a sample. The optimal number of cycles was tested using real-time quantitative PCR. To decrease the potential bias between rare and common species, the number of cycles was selected from the stage of exponential growth, before the reaction reached a plateau. To balance the sufficient amplification of low-biomass and high-biomass samples, a variable number of cycles were chosen for both trap types and each of the two replicates, based on the results of pilot analyses. For Malaise trap samples we used 21 and 24 cycles and for pitfall trap samples we used 29 and 32 cycles for each replicate, respectively. The PCR cycling conditions were 5 min at 95°C, then a replicate-specific number of 30 s cycles at 95°C, 30 s at 48°C and 2 min at 72°C, and ending with 10 min at 72°C.

For library construction, combinatorial indexing with a unique combination of indexes per sample was used. All index combinations were perfectly balanced in their nucleotide positions to ensure high-quality sequencing. Library preparation followed Vesterinen et al. (2016) with the following minor modifications: for a reaction volume of 10 μL, we used 5 μL of MyTaq HS RedMix, 500 nM of each tagged and indexed primer (i7 and i5) and 3 μL of locus-specific PCR product from the first PCR phase. For PCR cycling, the following cycling conditions were used: 3 min at 98°C, then 12 cycles of 20 s at 95°C, 15 s at 60°C and 30 s at 72°C, followed by 3 min at 72°C. All the replicates, as well as all the control samples received a unique index combination and were included in the final library. All the indexed reactions were pooled, concentrated and purified using magnetic beads following Vesterinen et al. (2016). Sequencing was done at the Turku Centre for Biotechnology, Turku, Finland, on an Illumina NovaSeq6000 SP platform v1.5 using PE 2 × 250 (Illumina Inc., San Diego, California, USA) and including a PhiX control library.

For Malaise samples from 2020, pitfall samples from 2020, Malaise samples from 2021 and pitfall samples from 2021, respectively, sequencing yielded 558,880,841, 309,134,391, 648,168,050 and 465,889,979 paired-end reads identified to original samples and replicates with unique dual-index combinations. Paired-end reads were merged and trimmed for quality using 64-bit VSEARCH v.2.14.2 (Rognes et al., 2016) with the command '*fastq_mergepairs*'. The primers were removed from the merged reads using software CUTADAPT v.2.7 (Martin, 2011) with 20% rate for primer mismatches and strict length parameters (400–420 bp). The reads were then collapsed into unique sequences (singletons removed) with the command '*fastx_uniques*' using VSEARCH. Unique reads were denoised (i.e. chimeras were removed) and clustered into zero-radius operational taxonomic units (ZOTUs) with the command '*unoise3*' using 32-bit USEARCH v.11 (Edgar, 2010). The UNOISE algorithm performs better than traditional clustering of OTUs in (i) removing chimeras, (ii) PhiX sequences and (iii) Illumina artefacts (Edgar & Flyvbjerg, 2015). Finally, ZOTUs were mapped back to the original primer-trimmed reads to establish the total number of reads in each sample using the VSEARCH '*usearch_global*' algorithm. In total, 92.34%, 95.37%, 95.42% and 94.94% of reads were successfully mapped for Malaise 2020, pitfall 2020, Malaise 2021 and pitfall 2021 samples, respectively. We obtained a total of 25,143 and 43,503 ZOTUs for Malaise and pitfall samples in 2020 and 26,054 and 29,367 ZOTUs for Malaise and pitfall samples in 2021. The PCR blanks yielded very few reads (111,251 (i.e. 0.025% of all reads) and 44,079 (0.020%) reads for Malaise and pitfall in 2020 and 9,555 (0.001%) and 60,812 (0.019%) reads for Malaise and pitfall in 2021), indicating neither cross-contamination among samples nor contamination of the reagents. For further discussion of how to interpret the paired-end read numbers observed in control samples, see Supporting Information (Text S1).

To eliminate 'tag jumping' among samples, the proportion of non-mock reads out of the total number of reads in mock samples was calculated. This revealed a tag-jumping rate of 0.07% and 0.03% in Malaise samples (2020 and 2021, respectively) and 0.06% and 0.00% in pitfall samples (2020 and 2021, respectively). To ensure thorough filtering of tag-jumping results, we removed any ZOTU less than 0.10% of the total read sum of a sample. In the subsequent step, only reads assigned to *Arthropoda* were retained, while non-target taxa were filtered away. ZOTUs occurring at a read count less than 100 were then removed from the data. For the rationale of our overall approach to denoising, see Supporting Information (Text S1).

To allow the usage of all reads, we decided to use Barcode Index Numbers (BINs) as taxonomic units, and for simplicity, we henceforth refer to them as 'species'. Indeed, BINs have been found to closely match morphologically identified species, especially among arthropods (Ratnasingham & Hebert, 2013). To assign ZOTUs to BINs, we used a custom-made script (Vesterinen et al., 2020) that leveraged the Barcode of Life Data System (Ratnasingham & Hebert, 2007) Application Programming Interface (APIs). As our key response for downstream analyses, we extracted the sample-specific count of BINs retained across the steps above. In doing so, we built on a simple rationale: as each sample was collected and processed in the same way, we can assume that an equal sampling effort had been invested in generating each sample. Also, we can expect the impact of different biases imposed by the pipeline to be not removed but comparable across samples. For this reason, we used the observed species richness rather than any rarefied or extrapolated value. In practice, this currency will represent 'the number of species recorded with any reasonable and thereby reliable representation in the data' (for added justification, see Supporting Information, Text S1). The raw sequence datasets generated in the current study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under accession number PRJEB63601.

Statistical analyses

Microclimatic similarity

To evaluate the similarity of microclimatic conditions between the Kilpisjärvi and Varanger study regions, we focused on four key features: summer soil temperatures, summer soil moisture, elevation and snow depth. For each of these variables, we generated frequency histograms of site-specific values for the years 2020 and 2021 and examined their proportional overlap. Summer soil temperatures were calculated as the average of the weekly mean soil temperatures through the sampling season. Summer soil moisture was calculated as the average of the weekly mean volumetric water content (VWC) through the sampling season. The latter variable was obtained by converting raw soil moisture readings using the calibration function *mc_calc_vwc* in the R package *myClim* v.1.0.2 (Matěj Man et al., 2023). Elevation was defined as the altitude of the sampling site (m a.s.l) and snow depth as the average of snow depth measurements (cm) taken at four different sample points (N, S, E and W) ca. 5 m away from the centre of each sampling site. Specific sampling site variability in the selected variables is provided in Supporting Information (Figure S2).

Comparisons of species pools

To characterise differences in the regional species pool of Varanger and Kilpisjärvi, we only included data resolved to the species level. We then calculated the species richness of arthropods as the sum of unique species present in each region for Malaise and pitfall data in 2020 and 2021, respectively. The species richness of plants was scored as the sum of unique species present in each region in 2022. Finally, we calculated the numbers and proportions of species that are unique to each region and shared between them.

Drivers of species richness and abundance

To evaluate the effects of elevation and snow depth on species richness and abundance of arthropods, potentially through their effects on soil moisture and temperature, we used piecewise structural equation modelling (pSEM). This approach allows the simultaneous evaluation of multiple causal hypotheses in a single dataset in which the variables could be interrelated (Lefcheck, 2016). Since inference based on pSEM is always conditional on a hypothetical structure of cause–effect relationships, we invested particular effort in defining how the explanatory variables might drive variation in a response variable (Shipley, 2000).

For all models, we defined elevation and snow depth as exogenous variables, since they are not (elevation) or barely (snow depth) influenced by other variables included in the models. Because elevation and snow depth can clearly influence soil temperature and soil moisture we defined the latter two as endogenous variables. Exogenous variables were always defined as explanatory variables in our models, while endogenous variables were defined as both explanatory (of species richness or abundance) and response variables (influenced by elevation and snow depth) (Figure 2). Again, we stress the rationale behind this path structure: 'Elevation' in itself is clearly a catch-all for multiple environmental features potentially varying in concert (Fontana et al., 2020; McCain & Grytnes, 2010; Peters et al., 2016). Consequently, the links between elevation, as an exogenous variable, and soil temperature and soil moisture, as endogenous variables, will explicitly resolve what fraction of an elevational pattern can be attributed to differences in soil temperature and soil moisture along that elevational gradient.

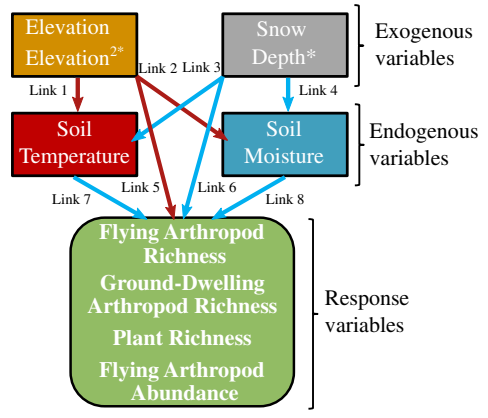

FIGURE 2 Hypothetical path structure of cause–effect relationships. Links 1–4 represent relations between exogenous and endogenous variables, whereas links 5–8 refer to relations between exogenous and endogenous variables and the actual responses, that is, arthropod and plant community features. Arrow colours represent expected positive (blue) or negative (red) associations between variables. *Snow depth was only included in models using data from 2021 and the squared term for elevation was only included in models of plant species richness.

To identify whether community features of ground-dwelling and flying arthropods respond to the same climatic drivers in space (Varanger-Kilpisjärvi) and in time (2020–2021), we fitted a total of 12 pSEMs (8 for arthropod richness and 4 for arthropod abundance). Here, we used separate models to a priori enforce as little joint structure as possible across sites and years. Then, we fitted another two pSEMs to identify whether plant species richness responded to the same climatic drivers as arthropods in space (Varanger-Kilpisjärvi), using only 2021 microclimatic data (i.e. the year previous to vegetation sampling). To account for the fact that plant species richness may peak at intermediate elevation (Bruun et al., 2006; Parviainen et al., 2009), we included the squared term of elevation to explain plant species richness. Within each pSEM, soil temperature and soil moisture (as endogenous variables) were analysed using *linear models*, whereas variation in community features (species richness and abundance) were analysed using generalized linear models. For models of species richness of plants, ground-dwelling and flying arthropods, we

assumed a log-link and Poisson-distributed errors, whereas for flying arthropod abundance (biomass), we assumed an identity link and Gaussian errors, using log-transformation of the response variable to comply with normal distribution of errors. Snow depth was excluded from models using 2020 data. The measurement of this variable was done in March 2021 and we cannot assume a constant distribution of snow between years.

To relate the impact of each variable to its variation within the data range, we standardised each variable to a mean of zero and a standard deviation of one. The resulting estimates of standardised effects are used for assessing the relative size of different paths in the same model. Nonetheless, care should be taken when interpreting these relationships. Since the scaling procedure is done relative to the sample standard deviations, standardised coefficients are not immediately comparable among data derived from different sources (i.e. different datasets), since different datasets have different sample variances. Thus, to assess the quantitative effects of the same variable across several datasets, unstandardised coefficients were used to characterise the change in the response per unit change in the explanatory variable (see Supporting Information: Figure S3). Prior to the analyses, collinearity between predictor variables was checked and showed low absolute correlation values between all pairwise comparisons ($r < 0.53$; Supporting Information: Figure S4).

All pSEM models were fitted in R package '*piecewiseSEM*' (Lefcheck, 2016). pSEMs were estimated using the *psem* function, and the goodness-of-fit was tested by Shipley's test of directed separation (Fisher's *C*), as implemented with the *dSep* function. This test addresses whether there are missing paths between the variables in the pSEM (with values of $p > 0.05$ indicating that the model is indeed consistent with the observed data). In addition, we compared the predicted versus observed covariance matrix using a chi-square test (χ^2). Here, a non-significant test will support an acceptable model fit. Out of the relationships explored (Figure 2), we only included the subset of relationships supported by our analyses in the final pSEM (i.e. only significant associations in the final analyses; $p < 0.05$).

The total standardised effect size of each explanatory variable on each response variable was calculated as the sum of direct and indirect effects. Indirect effect sizes were obtained by multiplying the standardised coefficients of the exogenous-endogenous path and the endogenous-response path. For those exogenous variables with more than one indirect path (through elevation and snow depth), we calculated the total indirect effect as the sum of its partial effects. Finally, all total standardised effect sizes were joined across sampling areas and years to summarise the main effects of each explanatory variable on each response variable (Supporting Information: Figure S5).

Direct effect of plant communities on arthropod richness

To evaluate whether patterns in one species group followed patterns in another (i.e. whether the properties of arthropod communities can be predicted from patterns in plants), we fitted a GLMM of site-specific arthropod species richness as a function of plant species richness. To test for differences between study areas, we included the region (Varanger or Kilpisjärvi) as a categorical fixed effect. To test whether the relationship between arthropod and plant species richness is consistent between communities of flying and ground-dwelling arthropods (Figure 2), we included community type (Malaise or pitfall) and the interaction term between plant species richness and community type as further fixed effects. To account for the fact that the same 74 sampling sites had been sampled in 2020 and 2021, we included sampling site identity as a random effect. The models were fitted using maximum likelihood techniques in R package '*glmmTMB*' (Brooks et al., 2022). All statistical analyses were run in R version 4.2.1.

RESULTS

Altogether, we sampled 12,521 g of arthropods (mean 5.85 ± SD 4.42 and mean 7.42 ± SD 5.94 grams per site for Malaise in 2020 and 2021, respectively). In this mass, we detected a total of 31,125 ZOTUs of which 30,907 ZOTUs (representing 99.9% of all sequences) were resolved to species (i.e. BINs). The resulting 3399 BINs concerned 22 insect orders and 222 families (mean 44.82 ± SD 19.32 BINs per site for Malaise data in 2020, mean 33.18 ± SD 26.23 BINs per site for pitfall data in 2020, mean 53.97 ± SD 23.43 BINs per site for Malaise data in 2021 and mean 28.52 ± SD 21.24 BINs per site for pitfall data in 2021). All BINs were taxonomically vetted against prior records in BOLD and Roslin et al. (2022). The high taxonomic diversity and large number of arthropod individuals per site precluded direct comparison to patterns detectable by traditional taxonomy, since no comparable material could be generated with realistic resources or within a realistic time period. For plants, we detected a total of 185 species representing 29 orders and 42 families (mean 23.41 ± SD 12.06 plant species per site).

What fraction of plant and arthropod species do the study regions share with each other?

The highest species richness was found in flying arthropods, followed by ground-dwelling arthropods and plants (Figure 3). For all three organism groups, Varanger proved more species-rich than Kilpisjärvi, except for ground-dwelling arthropods in 2021 (Figure 3). Within each group, the two study regions shared a major part of their species pools (44.8% to 64.2%). Across plants, ground-dwelling and flying arthropods, about half of the species were common to both regions, with about one-quarter being unique to Kilpisjärvi and another quarter to Varanger (Figure 3).

How much does microclimate vary within and between study regions?

Within both Kilpisjärvi and Varanger, individual sites showed large variation in microclimatic conditions (Figure 4, Figure S2). Within each

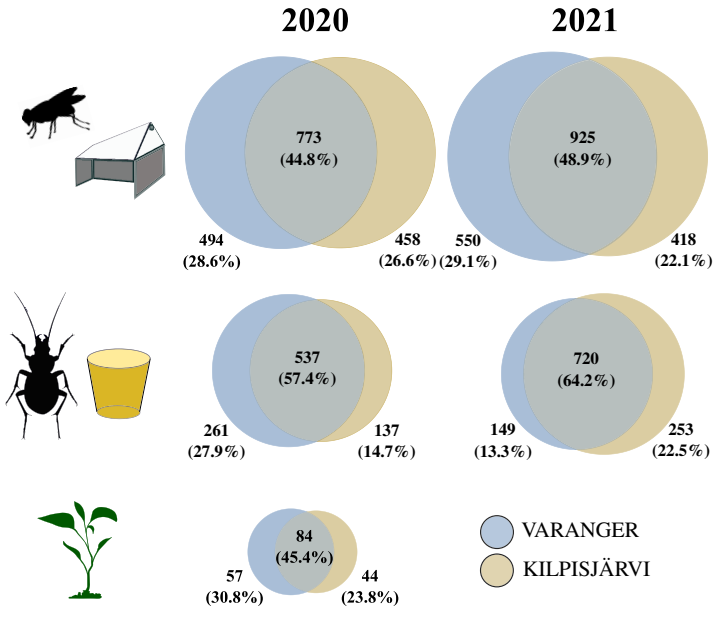

FIGURE 3 Total number and percentage of unique and shared species between Varanger and Kilpisjärvi in the years 2020 and 2021. From top to bottom: flying arthropods from Malaise traps, ground-dwelling arthropods from pitfall traps and vascular plant species. Circle sizes are proportional to the number of species.

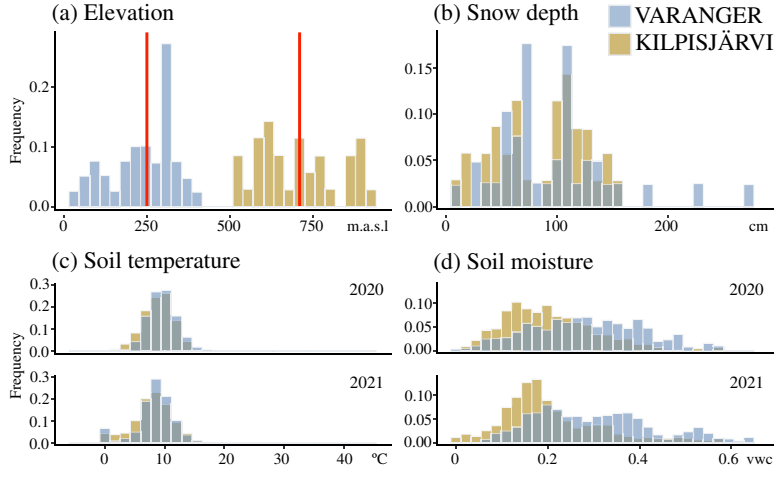

FIGURE 4 Frequency distribution histograms showing microclimatic variability across Varanger and Kilpisjärvi sampling sites. Plotted are the fraction of site-specific values of (a) elevation (m a.s.l), (b) snow depth in 2021 (cm), (c) soil temperature (°C) and (d) soil moisture (volumetric water content, VWC), with the latter two for the years 2020 and 2021, separately. The tree line limit is showed in red at graph (a).

study region, we had deliberately targeted sampling sites along an approximately 500-m elevation gradient covering both sides of the tree limit. However, the elevation of this tree limit differed greatly between the two regions and thereby the range in elevation, with Varanger sites going from sea level to 450 m a.s.l. and Kilpisjärvi sites from 500 m to almost 1000 m a.s.l (Figure 4). Nonetheless, soil

temperatures were roughly similar between the regions, with conditions at individual sites ranging from 0°C to 20°C, and a few sites recorded temperatures higher than 30°C. Likewise, soil moisture was similar between regions, with conditions in Varanger being slightly wetter than conditions in Kilpisjärvi in both years. Snow depth was also similar in both regions, but Varanger displayed odd sites with snow depths over 160 cm.

Do communities of plants, ground-dwelling and flying arthropods respond to the same climatic drivers, and how consistent are these responses across regions and years?

The final piecewise SEMs ($n = 14$) were all consistent with the observed data (p-values associated with Fisher's C > 0.05, and p-values associated with chi-square goodness-of-fit test >0.05; see Table S1), suggesting no missing paths in any of the models. Consistent with this interpretation, all individual r^2 terms for the dependent variables were high and exceeded 0.51 (Table S1).

In terms of variable-specific impacts, elevation had by far the largest effect on arthropod species richness (Figure 5). Species richness consistently declined with increasing elevation, with a statistically significant direct effect detected in six out of eight models. This effect seemed more consistent for flying arthropod communities than for the ground-dwelling arthropods.

Most of the altitudinal effect on species richness appeared direct. However, an additional indirect soil temperature-mediated effect of altitude was detected in five out of eight models, with soil temperature decreasing significantly with an increase in elevation in all models (Figure 5; Figure S6). We only detected an indirect soil moisture-mediated effect of elevation in flying and ground-dwelling arthropod communities of Varanger in 2020, with soil moisture significantly decreasing with increasing elevation (Figure S6). In two cases (i.e. for the flying arthropod communities of Kilpisjärvi in 2020 and the ground-dwelling arthropod communities of Varanger in 2021), we did not detect any significant negative direct effect of elevation on species richness. In both cases, species richness increased with soil temperature and soil moisture (Figure 5). For all but two cases (i.e. the flying arthropod communities of Varanger in 2020 and the ground-dwelling

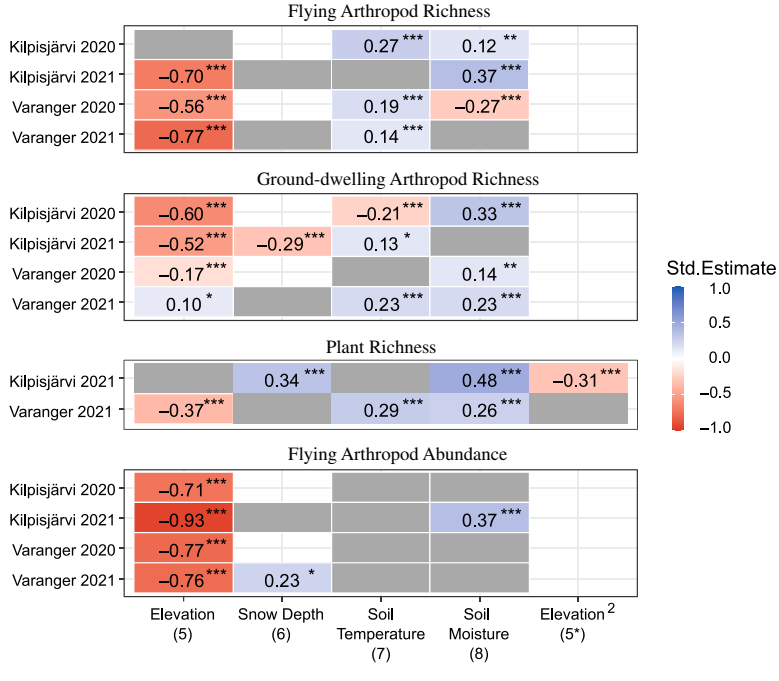

FIGURE 5 Heat map of the standardised coefficients of each potential driver of species richness and abundance across Varanger and Kilpisjärvi in 2020 and 2021. Shown are values for the final piecewise structural equation modeling (pSEM). Models, with the numbering of variables (*x*-axis) referring to the hypothetical paths of Figure 2. Colours show the sign and strength of direct effects on the species richness of flying arthropods, ground-dwelling arthropods and plants, and on the abundance (biomass) of flying arthropods. Elements shown in grey correspond to variables with no statistically detectable direct effect, whereas elements shown in white represent variables excluded from the model. The number of asterisks indicate the level of significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. We reiterate that snow depth was only included in models using data from 2021 and that the squared term for elevation was only included in models of plant species richness.

arthropod communities of Kilpisjärvi in 2020) did we detect an increase in species richness with increasing soil temperature and soil moisture (Figure 5).

As for species richness, flying arthropod abundance significantly decreased with elevation in all models, and this effect was always direct. In Kilpisjärvi, arthropod abundance increased with increasing soil moisture in 2021. In Varanger, arthropod abundance also increased with increasing snow depth in 2021. Soil temperature had no detectable effect on arthropod abundances, even though soil temperature significantly decreased with increasing elevation—a pattern found across all models (Figure 5; Figure S6).

Plant species richness significantly increased with decreasing elevation and with increasing soil temperature and soil moisture. These patterns were found for both Kilpisjärvi and Varanger. However, the strength of the direct effect of elevation was higher in Varanger, while the direct effect of moisture on plant species richness was stronger in Kilpisjärvi than in Varanger (Figure 5).

Can patterns in one species group predict patterns in another?

Arthropod species richness as such did not significantly differ between study areas (Table 1). However, flying and ground-dwelling arthropod species richness showed significantly different associations with plant species richness (plant richness × arthropod community type: $p = 0.006$; Table 1). In fact, flying arthropod species richness increased with increasing plant species richness within both Varanger and Kilpisjärvi, whereas for ground-dwelling arthropod communities, we did not find any detectable association with plant richness (Table 1; Figure 6).

DISCUSSION

With climate-induced changes in community composition and ecosystem functioning unfolding around the world, the challenge of

TABLE 1 Generalized linear mixed model (GLMM) of arthropod species richness as a function of plant species richness, study area (Varanger vs Kilpisjärvi), arthropod community type (ground-dwelling or flying arthropods) and the interaction between plant species richness and arthropod community type.

Response variable	Predictor variable	Estimate	Std. error	*Z* value	*p*-value
Arthropod species richness	Intercept	190.344	12.238	15.553	<0.001***
	Plant species richness	1.868	0.415	4.497	<0.001***
	Study area	15.287	8.170	1.871	0.061
	Arthropod community type	−65.458	15.501	−4.221	<0.001***
	Plant species richness × Arthropod community type	−1.590	0.583	−2.728	0.00637**

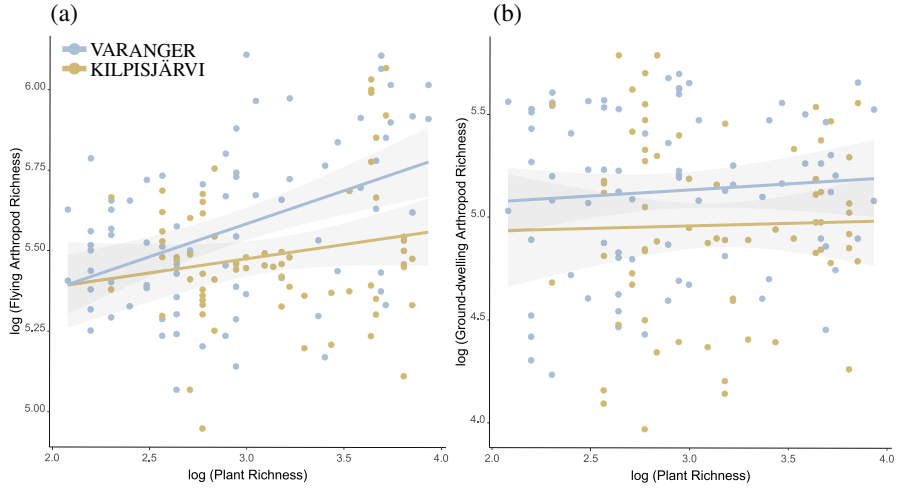

FIGURE 6 Relationships between arthropod species richness (ln) on plant species richness (ln) for (a) flying arthropods from Malaise traps and (b) ground-dwelling arthropods from pitfall traps, as estimated by the generalized linear mixed model (GLMM) described in Table 1. The blue line represents data from Varanger while the yellow line represents data from Kilpisjärvi.

linking community composition to climatic variation is more topical than ever. In this study, we found a strong imprint of microclimatic variation on emergent features of local arthropod and plant communities across two subarctic landscapes. While differences in microclimatic conditions between these regions were small and roughly half of their arthropod and plant species were shared, microclimatic variation within each region created vast differences in local species richness and arthropod abundance. Plants and arthropods consistently responded to the same drivers; yet, local variation in plant species richness was a poor predictor of arthropod species richness, in particular for ground-dwelling arthropods. Below, we will discuss each finding in turn.

Species pools are largely shared between regions

Local communities will always form subsets of wider, regional species pools. Importantly, the regional species pool will be shaped by the longer-term processes of speciation and species redistribution with biogeographical history. Of this raw material, local communities are formed by local assembly processes, with biotic and abiotic processes acting as filters in between regional and local species pools (HilleRisLambers et al., 2012; Vellend, 2016). Before examining the role of microclimatic variation, we should therefore establish the extent to which the two regions host the same or different species, that is, whether microclimatic filters will be acting on the same or different raw material in the two focal regions.

Overall, the two regions showed substantial overlap in their species pools. This concerned both plants and arthropods to a very similar degree. Nonetheless, while a major part of the whole species pool for each group of organisms was found in both areas (~ 50%), about a quarter of species was also unique to each region. Varanger showed slightly higher diversity than Kilpisjärvi for all three species groups, as reflected in a slightly higher number of species unique to this region than species unique to Kilpisjärvi. The relative similarity in species pools can likely be attributed to the relative geographical proximity of the regions (ca. 350 km apart) and to a similar geological history (e.g. Donner, 2005). As most or all of these regions were covered by ice as recently as 11–14 ka years ago (Romundset et al., 2017; Stroeven et al., 2016), there has been little speciation in situ, but rather postglacial immigration from source communities outside of the former extent of the ice (Hewitt, 1999). Slight differences in contemporary species pools might then result from differences in the postglacial colonisation history of different taxa. Nonetheless, the evidence of dispersal from potential northern refugia remains debated, as does the relative imprint of contemporary forces versus legacy effects from the last ice age (Eidesen et al., 2013; Shikano et al., 2010; Stewart et al., 2016; Tzedakis et al., 2013). Since our comparison remains unreplicated across regions, we will abstain from inferring causality at the level of regional species pools, and rather focus on patterns within regions.

Microclimate creates vast variation among local communities within regions

Within each of the two regions of Varanger and Kilpisjärvi, the range of microclimatic conditions was similar. This consistency was not caused by the sampling design as such, since within each region sampling sites varied with respect to, for example, elevation and topography, but by the similar range of conditions present within each region. The main difference between regions was the absolute elevation at which these microclimatic conditions prevailed. In Kilpisjärvi, the tree line occurs at ca. 700 m a.s.l., whereas in Varanger at ca. 250 m a.s.l. As a consequence, when distributed on both sides of the tree line, sites in Varanger spanned in absolute elevation from the sea level to almost 450 m a.s.l, while sites at Kilpisjärvi ranged from 500 m a.s.l to almost 1000 m a.s.l. Thus, between the two regions, the occurrence of identical conditions is shifted some 450 m in a vertical dimension, whereas within each landscape, the range of values is effectively the same.

This variation in local microclimate was associated with substantial variation in local species pools within regions. Local species richness in plants varied by a factor of four within the Kilpisjärvi region and a factor of six within the Varanger region. Within each year and region, the most species rich arthropod communities were on average more than three times diverse than the least rich sites. Overall, the patterns detected add evidence for strong microclimatic forcing of community structure in subarctic landscapes, that is, for microclimate acting as a strong abiotic filter during local community assembly.

Communities of plants, ground-dwelling and flying arthropods largely respond to the same microclimatic drivers

The drivers of local species richness were largely consistent between species groups and years. Hence, across plants and arthropods, and across different arthropod guilds, local species richness generally decreased with elevation, and increased with soil temperature and soil moisture. With the same causal pathways being consistently distilled by pSEMs across years and regions, we find conclusive evidence for their impacts.

Among individual drivers, variation in elevation emerged as a common predictor for all community features considered, irrespectively of the region. Nonetheless, elevation in itself is basically a catch-all for variation in other features with more immediate impact on the performance of plants and arthropods. Here, only part of the effect of elevation as such could be attributed to effects acting through the impact of elevation on local temperature and soil moisture. While the degree of determination (r^2) was uniformly high for all path models (Table S1), this does suggest that the impact of elevation is mediated by further factors beyond its impact on local temperature and soil moisture. This is an important take-away, since it implies that of environmental variation across elevation, multiple dimensions will have a true impact on local animal and plant richness. One such likely

factor is the existence of an elevational pattern in nutrient limitation. Nonetheless, in the current data, there was no detectable effect of nutrient limitation (soil C to N ratio) on arthropod species richness. For plant species, we saw a trend towards decreasing richness with increasing nutrient limitation, as consistent with the 'paradox of enrichment' (Cleland & Harpole, 2010; Supporting information; Figure S7).

In terms of the specific direct impacts of snow, temperature and soil moisture, the patterns uncovered were largely consistent with suggestions from previous studies (Lembrechts et al., 2018; Ohler et al., 2020). Snow cover had a pronounced effect on the species richness of plants—but this was driven by data from Kilpisjärvi, with no clear effect for Varanger. Snow has previously been identified as a major modulator of air-to-soil conditions (Aalto et al., 2018; Kearney, 2020; Niittynen et al., 2018) by providing protection against extreme frost, wind abrasion or desiccation (Rapacz et al., 2014) and retaining water and nutrients (Blankinship et al., 2014; Edwards et al., 2007; Semenchuk et al., 2015). Snow dynamics strongly modulate soil temperature and moisture (Bokhorst et al., 2016; Niittynen, Heikkinen, Aalto, et al., 2020), creating spatiotemporal variability in microclimatic conditions (Aalto et al., 2018), shaping plant species distributions (Niittynen, Heikkinen, & Luoto, 2020; Niittynen & Luoto, 2018; Rissanen et al., 2021) and determining the length of the growing season (Høye & Forchhammer, 2008; Kankaanpää et al., 2018; Pedersen et al., 2018).

Snow has also been found to shape local arthropod communities (Bowden et al., 2018; Kankaanpää et al., 2018). However, in the current study, the imprint of spring-time snow depth on arthropod communities was less consistent. Here, we should first acknowledge some limitations in our study design. Snow conditions were only measured at a single time during our study, representing the peak in snow depth. For arthropods, this measurement might not be as significant as the length of snow coverage or the time of snowmelt would be (Slatyer et al., 2022). Snowmelt patterns change significantly over time (Kankaanpää et al., 2018; Kearney, 2020) due to variations in yearly wind drift (Filhol & Sturm, 2015; Mott et al., 2018) or winter rainfall (Cooper et al., 2011). Moreover, individual arthropod species are known to be affected by snow cover in diverse ways (Høye & Forchhammer, 2008; Randin et al., 2009), whereas we focused just on net species richness as a summary measure of species occurrence across taxa. Together, these considerations will act to diffuse the effects of snow depth on local communities and might obscure the contribution of this variable to the patterns observed in our study. If this is the case, then it highlights the risk of using temporal average values as well as macro-scale geographical averages for predictions.

Regarding the influence of soil temperature and moisture, we found a distinct imprint of small-scale heterogeneity in these factors on the spatial distribution of plant species and arthropod richness. Soil moisture, which varied considerably over short distances at our study sites, is considered another key driver of plant community composition and species richness in high-latitude areas (le Roux et al., 2013; Nabe-Nielsen et al., 2017; Stewart et al., 2018). In this respect, our results are also clearly in line with those from Hansen, Hansen, Bowden, Normand, et al. (2016), showing that moisture and soil temperature are important factors in determining arthropod species patterns at the local scale.

A priori, we had hypothesised that ground-dwelling arthropod communities and plant communities would be most strongly influenced by soil temperature, due to their proximity to the ground. Nevertheless, soil temperature seemed to have a more clear-cut positive effect on flying arthropod species richness than on ground-dwelling arthropod richness or plant richness. Flying arthropods may exhibit a more efficient behavioural response across the landscape, as they actively aggregate under locally favourable conditions, ultimately resulting in higher species richness within those areas. Here, the current methods fail to distinguish between local demographic rates and individual redistribution, which will be an important focus of future work.

Increasing soil moisture proved more influential than temperature in promoting ground-dwelling arthropod species richness. Indeed, soil moisture is known as an important factor for the development and distribution of several species of Coleoptera, spiders and other ground-dwelling arthropods (Bowden et al., 2018; Hansen, Hansen, Bowden, Treier, et al., 2016; Hodkinson, 2005; Høye et al., 2018; Koltz et al., 2018). What may deflate a similar result for flying arthropods is the high variability in larval habitats, with some species using vegetation structures and others using the ground (Danks, 1991, 2004). A considerable amount of these flying arthropods are in fact aquatic as larvae (including dipteran, plecopteran, trichopteran or coleopteran species)—or terrestrial, but overwintering in particularly sheltered or moist habitats (Danks, 2004). These taxa will naturally contribute to the total species richness observed, but their distribution across the landscape at the adult stage may poorly reflect soil moisture conditions. Again, this emphasises the need for quantifying the relative role of local recruitment versus adult redistribution in shaping the contemporary composition of adult arthropod communities.

Among plants, we found a general increase in richness with increasing moisture. These results echo those of several authors, who reported higher plant richness with increasing moisture across landscapes (le Roux et al., 2013; le Roux & Luoto, 2014; Nabe-Nielsen et al., 2017). Beyond the effects observed here, these microclimatic effects on plant communities may not only affect species richness and its distribution, but also drive other community features such as inter- and intraspecific trait variation (Bjorkman et al., 2018; Kemppinen, Niittynen, le Roux, et al., 2021; Niittynen, Heikkinen, & Luoto, 2020).

Patterns in plant communities poorly predict patterns in arthropod communities

Because of the large sampling effort required to characterise arthropod communities, it would be convenient if microclimatic impacts could be gleaned from a single indicator taxon (i.e. plants) and applied to other groups (Basset et al., 2015; Lewinsohn & Roslin, 2008). Several authors have proposed that patterns of species richness among plants could be adopted as efficient proxies for patterns of

arthropod species richness (Basset et al., 2012; Lewinsohn & Roslin, 2008). Indeed, within landscapes, increased plant productivity in warmer areas is expected to positively affect the richness of both herbivores and flower visitors (Duchicela et al., 2021; Ohler et al., 2020).

Nonetheless, where multiple studies have found an association between plant and arthropod richness (Høye et al., 2018; Rich et al., 2013; Schaffers et al., 2008), we found only a weak pattern. While the principal climatic drivers shaping arthropods and plant communities were fundamentally similar, variation in taxon-specific response still causes a weak association at the level of overall species richness (Figure 6). For the ground-dwelling taxa, this might be caused by the composition of the arthropod fauna. Here, the predatory guild accounts for a major element. For such taxa, plant diversity per se will have less of a direct impact than on herbivorous arthropods, with vegetation acting mainly as a buffer to extreme conditions. Similar patterns have previously been found in several studies where, regardless of plant diversity, vegetation provides the habitat structure needed for predatory arthropods in terms of hunting habitat (Bowden & Buddle, 2010), complexity and heterogeneity (Brose et al., 2003; Jiménez-Valverde & Lobo, 2007).

Moreover, the shape of the associations with individual drivers may be different between arthropods and plants. In half of the models explaining plant species richness, we found a significant quadratic effect of elevation. By comparison, models of ground-dwelling arthropods always came with a linear effect of elevation and showed both positive and negative associations. Therefore, while we might expect higher plant species richness at intermediate elevations, higher soil arthropod diversity is mostly found at lower elevations.

For flying arthropods, we found a slightly closer association with plant species richness, especially at Varanger (Figure 6). This may reflect a closer trophic association. A major fraction of flying arthropods are herbivores, parasitoids of herbivores or pollinators sensu *lato*. Nonetheless, even for them the association was weak and scattered—probably for reasons akin to those discussed above. In addition, we should note that many of the taxa involved will shift between functional guilds, diet and feeding mode between their life cycle stages, thus causing 'trophic omnivory' and obfuscating the link between species occurrence, abundance and specific resources.

Implications for subarctic communities under climate change

With ongoing climate warming, local communities are likely to experience multiple effects. Our study identifies several avenues through which these changes may manifest. First, global shifts in climatic conditions (Pörtner et al., 2022) are leading to major shifts in the regional species pools, with species moving northwards and increasing local species richness (Kemppinen, Niittynen, Virkkala, et al., 2021; Mamantov et al., 2021). Consequently, the fundamental pool from which species are recruited to local communities is enriched.

Against this backdrop, general warming will result in varying changes in the landscape-level distribution of microclimatic variability. For instance, increasing average temperatures will likely cause the timing of snowmelt to advance, resulting in multiple consequences for the ecology of several species. Earlier snowmelt will expose arthropod species to more extreme conditions, whose survival and reproduction may be reliant on the buffer function that snowpack exerts. Additionally, shorter snow cover duration could lead to earlier emergence, causing phenological mismatches between arthropod species and their host plants and potentially leading to population declines. Thus, the impacts of climate change will not only change large-scale average conditions, but also redistribute local microclimatic variability. Our study indicates that the impacts of such changes may be substantial, with local species richness varying by almost an order of magnitude among sites with different conditions.

Nonetheless, our study also points to the limits of extrapolations from contemporary studies in space to predictions across time. In the present study, we found a clear-cut imprint of elevation as such, without corresponding paths through well-resolved environmental factors. We emphasise that elevation, in essence, serves as a broad indicator of other features that have a more direct impact on the performance of plants and arthropods. Thus, our findings suggest that the impact of elevation is mediated by further factors beyond its impact on local temperature, humidity or nutrients (see above). As a consequence, we believe that added, unresolved dimensions of microclimatic variation drove the patterns observed. This finding has strong implications when adopting the current patterns for any kind of space-for-time substitution, that is, for predicting future change over time from current patterns in space. As both microclimate in space and future climate over time involve many dimensions, we should shun away from predictions based on changes in temperature and precipitation alone.

What has hampered large-scale work on hyper-diverse arthropod communities is the difficulty of measuring the very diversity involved. Our study points to molecular tools as the way forward, by allowing us to include truly diverse taxa in assessments of microclimatic impacts on diversity patterns. By adopting these methods, we were also able to evaluate a topical notion—that when faced with a scarcity of data on one taxon, we may use patterns from another as a proxy. Here, we found that plant species richness proved a poor surrogate of arthropod species richness in the subarctic. For understanding the impacts of microclimatic variation, we are then confined to quantifying separate patterns in individual taxa. Besides, the differential responses observed in different taxa suggest a key consequence of climate change. If different taxa respond differently to changing conditions, then this may cause an ecological dissociation in key relations—echoing previous warnings by, for example, Kankaanpää et al. (2021).

CONCLUSIONS

Arthropod and plant communities are shaped by microclimatic conditions. Our study shows strong imprints of such conditions, and suggests that ongoing climate change may come with corresponding changes in arthropod and plant communities. In particular, we find

that contemporary patterns along elevational gradients cannot be resolved to imprints of temperatures or moisture alone, and that impacts on arthropods cannot be gleaned from impacts on plants. These patterns urge prudence in extrapolations from space to time, and from one taxon to another. Here, a key piece of the puzzle emerges as missing. Where our study pertains to communities of adult arthropods, their larval stages may still depend on partly different resources in different habitats. The observed communities of adult arthropods therefore integrate both larval performance and adult behavioural choice. Dissecting these two elements calls for further work, but is needed to understand the processes behind the patterns resolved here.

AUTHOR CONTRIBUTIONS

Pablo Peña-Aguilera: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; software; formal analysis; data curation; resources; project administration; validation. **Niels M. Schmidt:** Conceptualization; writing – review and editing; resources; supervision. **Lærke Stewart:** Writing – review and editing; resources; investigation; methodology. **Bastien Parisy:** Investigation; writing – review and editing; resources. **René van der Wal:** Conceptualization; writing – review and editing; supervision. **Ly Lindman:** Conceptualization; writing – review and editing; supervision. **Eero J. Vesterinen:** Writing – review and editing; data curation; software; methodology. **Ilya M. D. Maclean:** Writing – review and editing; conceptualization; supervision. **Tuomas Kankaanpää:** Investigation; writing – review and editing; resources; methodology. **Helena Wirta:** Investigation; writing – review and editing; resources; methodology. **Tomas Roslin:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; project administration; supervision; resources; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in European Nucleotide Archive at https://www.ebi.ac.uk/ena/browser/search, reference number PRJEB63601.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information.

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Supplementary material

Consistent imprints of elevation, soil temperature and moisture on plant and arthropod communities across two subarctic

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Text S1. Further details on the bioinformatics analysis

Rationale adopted in denoising the data

Our analysis pipeline, as any other approach, will yield observations of true ecological signal, with added "noise" on top. What we then need to do is to separate between "real" ecological signal and the "noise" generated by a wealth of factors. The former component consists of real sequences present in the ecological sample, whereas the latter consists of spurious sequence variants originating from any step of analysis. The noise does not usually offer any biologically informative insight and should thus be pruned from the data by denoising (sensu lato). Such denoising actually happens at several steps of analysis, for example: 1) at the sequencing platform, when performing base calling, 2) in demultiplexing, when only good hits to indices/barcodes are accepted (as typically judged by maximally 1 mismatch), 3) during FASTQ filtering/merging, when poor-quality reads are discarded, 4) during otutable (Zotutable) construction, when only good-enough matches of sequence variants (here ZOTUs) to the trimmed data are accepted, 5) during primer trimming, where only reads with primers are passed on to subsequent steps, 6) during negative filtering, where information from the negative controls are taken into account, and 7) based on information from the positive controls. Each of these steps are naturally included in our analysis pipeline.

In applying these steps, we do not claim that our approach is the only correct one, or that ZOTUs are free of any disadvantages. What we argue is that any pipeline should be based on explicit and justified choices rather than built on arbitrary examples. In the latter context, we note that many studies today still start by clustering their data at 97% similarity – whereas we have opted to retain all biological sequence variants (as represented by ZOTUs). With respect to the rarest variants, there is then a high risk (but clearly no certainty) that they may represent noise rather than true signal. To decrease the impact of this element of noise, we will want to remove them. Importantly, the effect of rare sequence removal on the information content of the remaining sample will depend on sequencing depth. Removing 0.1% of the sample read sum will imply something completely different if one applies this proportion to a sample of 1000, 10 000, 100 000 or 1 000 000 reads. In our case, the sequence output was deep enough to allow removal of rare sequence variants from samples, without fearing to lose too many "real" biological members of the community.

To appreciate how different solutions for clustering vs denoising will affect the sample, we may turn to advice by Robert Edgar (the original author of key software used in both clustering and denoising, including UPARSE, UNOISE etc.). As summarised in Edgar (2018), the main disadvantage of resorting to 97% clustering is that we discard the information on some true biological entities present in the reads – as the corresponding reads are lumped into OTUs mixing several such entities. If these entities represent real strains or species, then we lose relevant information on the numbers and frequencies. The main advantage of ZOTU-based denoising is then that we achieve better resolution by retaining all the biological sequences.

By comparison, the main disadvantage of denoising is first that species often show variation between individuals and paralogs that are not 100% identical. Thus, there will frequently be many ZOTUs per species, and these ZOTUs will still need to be clustered by e.g. taxonomic assignment and pooling per species (as we did). Second, more low-abundance sequences are lost: with UPARSE, singletons (abundance=1) are discarded, but with UNOISE, uniques with abundance <8 are discarded. Nonetheless, the impact is likely to be subtle as most. As summarised by Edgar (2018), "For typical studies, this shouldn't make much difference because samples should be pooled, so a sequence with abundance <8 will probably be a singleton in a few samples and singletons in the OTU table should not be considered significant because they could be spurious with any method."

In our case, we conclude that the sequence output was deep enough to allow removal of rare sequence variants from samples, without fearing to lose too many "real" biological members of the community. This justifies denoising by removal of ZOTU's with a proportion of less than 0.1% of the sample read sum.

Taxonomic assignments

To assign the sequence variants (here, ZOTUs) to taxa, we applied the SINTAX algorithm (Edgar 2016. "SINTAX: A Simple Non-Bayesian Taxonomy Classifier for 16S and ITS Sequences." Preprint available at BioRxiv, https://doi.org/10.1101/074161). SINTAX returns a probability for each level of taxonomy in the reference database for each query sequence. We used a local database that was constructed from all the public sequences in the BOLD database (~500M unique taxa/sequences) and extended with sequences from the organisms in the mock community samples. We used the information from the mock samples to deduce the optimal probability threshold to reliably identify sequence variants. It seemed that even a lower probability of ~0.55 would still achieve correct identification. However, as the mock community sample only consists of ~10 species, we used a more cautious probability threshold for species level identification: 0.70.

Sometimes, the SINTAX does not return any match at all. In these cases, we retrieved the taxonomical matches from the BOLD Systems using the bold-retriever API script (Vesterinen et al. 2020. "A Global Class Reunion with Multiple Groups Feasting on the Declining Insect Smorgasbord." Scientific Reports 10 (1): 16595. https://doi.org/10.1038/s41598-020-73609-9.). Through this combined approach, we were able to identify more than 83% of the sequences to species level, and over 90% to family level. Some of these assignations concerned non-target taxa beyond arthropods, but this fraction was tiny overall. Most of the non-targets were naturally-occurring microbes or vertebrates, such as reindeer, shrews, or birds, and were likely included in insect blood meals or occurred in the vicinity of the traps (see Lynggaard et al. 2019. "Vertebrate diversity revealed by metabarcoding of bulk arthropod samples from tropical forests." Environmental DNA, 1(4), 329-341.).

After taxonomic assignment, we merged all the ZOTUs with the same species identity, using plain R commands in the tidyverse ecosystem. As a substitute for species, we adopted the BIN (Barcode Index Number) concept of Ratnasingham & Hebert 2013. "A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System." PLoS ONE 8 (7). https://doi.org/10.1371/journal.pone.0066213. These BINs are well documented and can be tracked to individual specimen and species names. For the records that were not automatically paired with full taxonomy for each BIN, we used a custom UNIX script utilising BOLD APIs (http://www.boldsystems.org/index.php/api_home) to retrieve species names and full taxonomy for nearly all assignations. For a minority of sequences, this approach still left the ZOTU without a valid BIN-level assignation. Luckily, Norway and Finland hold the two most extensively barcoded insect faunas in the world (see Roslin et al. 2022. A molecular-based identification resource for the arthropods of Finland. Molecular Ecology Resources, 22(2), 803-822),

thus minimizing the relative bias incurred. In total, only 0.70 % of all ZOTUs and 0.12 % of all sequences could not be assigned to BINs. In other words, the slight uncertainty in species numbers emanating from the current approach will relate to a tiny minority of the rarest species – i.e. to the part of the species abundance distribution which is poorly quantified by any approach. Overall, we conclude that this solution will have little impact on our main inference.

Interpretation of sequence yields from blank control samples

Any molecular analysis will yield some spurious sequences – i.e., what we call "noise" above. The amount of this noise in a molecular approach is best measured using different types of control samples: A) positive controls (so called mock community samples), b) negative DNA extraction controls, where a sterile water sample is processed instead of a real sample, and c) PCR blank control, where a sterile water sample is amplified instead of a real sample. If the proportion of noise is constant, then the more one gathers data, the higher is the absolute amount of noise (i.e. the more sequences are encountered in control samples). As another rule of thumb applicable to negative controls, the earlier in the process the control is introduced, the more noise it will gather. This is a logical consequence of the fact that that the control sample will travel through the whole process, from the point of introduction to the end. In other words, it is normal for DNA extraction controls to yield more reads than PCR blanks will do.

In our analysis, we produced data for two trap types: Malaise and Pitfall traps. We included two replicates of each real samples, as well as several replicates of control samples. In terms of the controls, we included at least one set of controls for each batch or plateful of samples. For sequencing, we then adopted the highest-yielding sequencing platform available: Illumina NovaSeq6000, which produces massive amounts of data. As a consequence, we naturally observed some number of sequences for each type of control sample (for exact number, see main text). Nonetheless, in terms of proportions, the corresponding figures were very low: In the Malaise set, 99.5780 % of the reads derived from the real samples, 0.3343 % from the Mock samples, 0.0629 % from the Negative extraction controls, and 0.0249 % from PCR blank controls. For the Pitfall set, the corresponding numbers were 99.2235 %, 0.6813 %, 0.0756 %, and 0.0196 %. Thus, even though the absolute read counts observed in the controls may be higher than observed in many other studies, this pattern was due to the massive amount of data. As the proportions were uniformly low, we find that the controls indicate well prepared and clean data.

FIGURE S1. Study areas.

Maps showing the location of our two sampling areas within two subarctic regions: Kilpisjärvi (north-western Finnish Lapland; top panel; location within Fennoscandia indicated by yellow circle in inset map) and Varanger Peninsula (north-eastern Norway; bottom panel; location within Fennoscandia indicated by blue circle in inset map). Within these areas, the location of individual sampling sites (n=35 in Kilpisjärvi and n=40 in Varanger) are shown by red circles. Please notice the different scales used in the two maps, as motivated by the smaller extent of the overall study area in Kilpisjärvi (top) than Varanger (bottom).

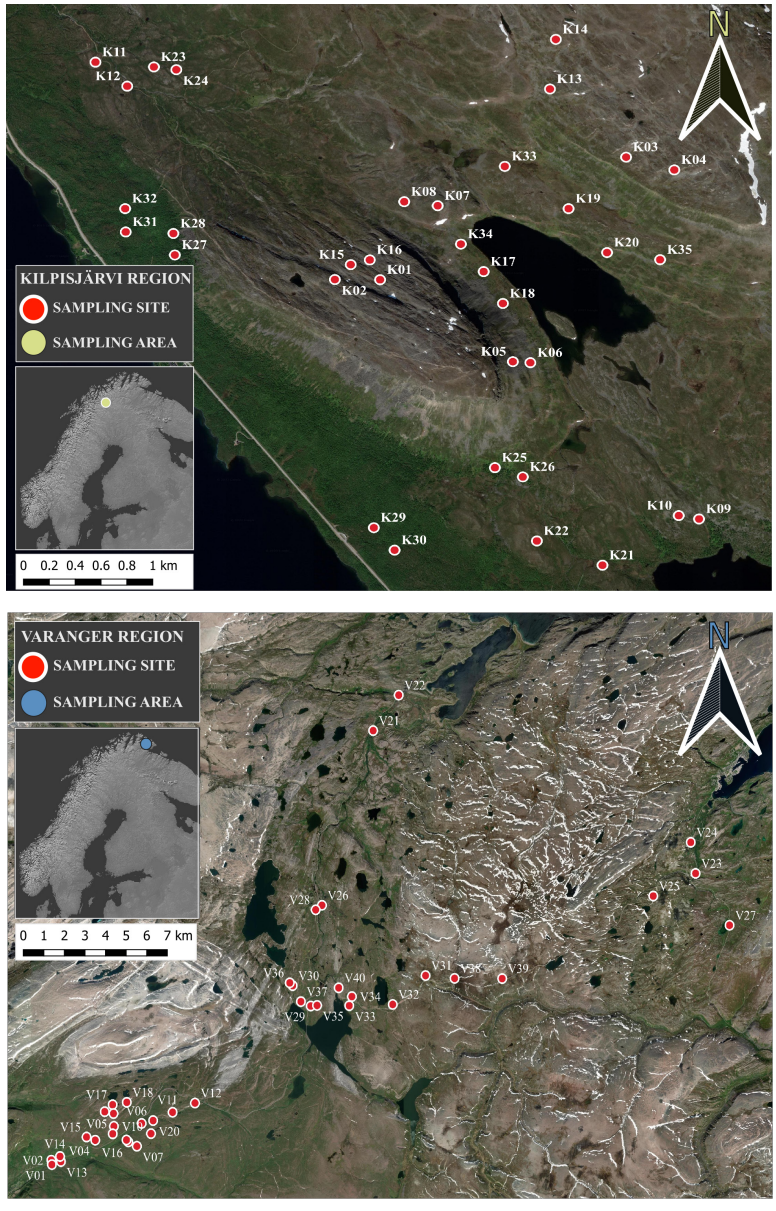


FIGURE S2. Site-specific microclimatic variability

Site-specific microclimatic variability in A) soil temperature, B) soil moisture, C) elevation and D) snow depth for Varanger and Kilpisjärvi, as observed in 2020 and 2021. For A) and B) boxplots show the variation in summer conditions recorded between June and September. The median is represented by a line, the box limits correspond to the first and third quartiles (the 25th and 75th percentiles), and the upper and lower whiskers extend from the hinge to the largest value. Different colours indicate the sampling site identity. For C) and D) bar plots show the measured elevation (in metres above sea level) and snow depth (in cm), respectively. Colour gradient ranges from blue (low values) to red (high values).

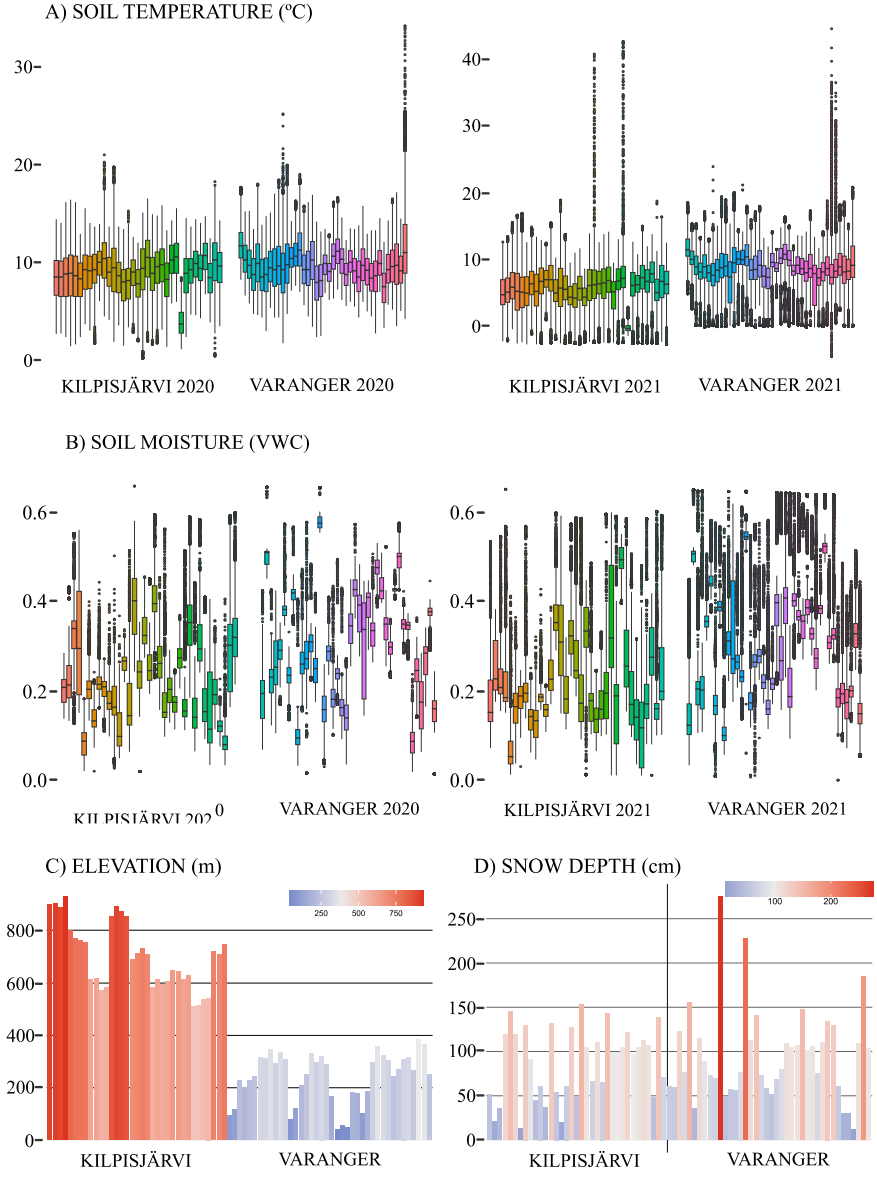


FIGURE S3.

Heat map of the coefficients of each potential driver of species richness and abundance across Varanger and Kilpisjärvi in 2020 and 2021. Shown are values for the final piecewise Structural Equation Models, with the numbering of variables (x-axis) referring to the hypothetical paths of Fig. 2. Colours show the sign and strength of direct effects on the species richness of flying arthropods, ground-dwelling arthropods and plants, and on the abundance (biomass) of flying arthropods. Elements shown in grey correspond to variables with no statistically detectable direct effect, whereas elements shown in white represent variables excluded from the model. The number of asterisks indicate the level of significance: *p < 0.05, **p < 0.01, ***p < 0.001. We reiterate that snow depth was only included in models using data from 2021 and the squared term for elevation was only included in models of plant species richness.

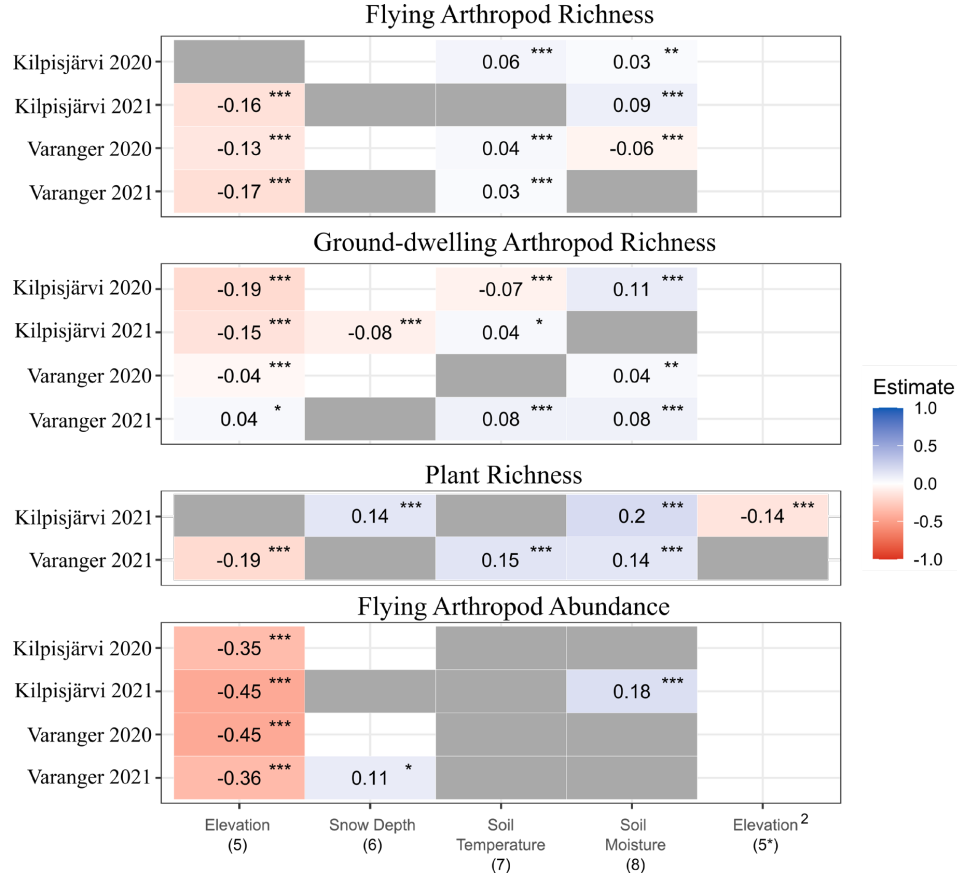


Figure S4.

Pearson moment product correlation values (r) between all explanatory variables for each region (Varanger and Kilpisjärvi) and each year (2020 and 2021).

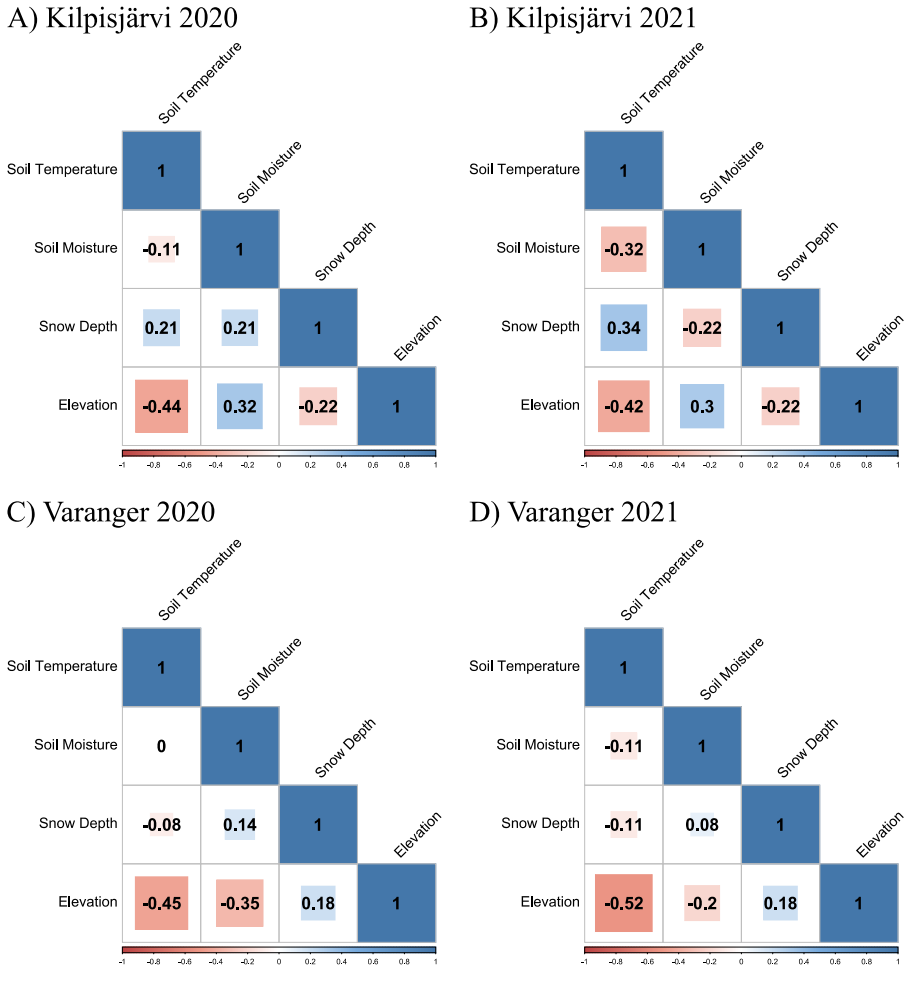


Figure S5.

Bar plots of the total standardized effect sizes for each explanatory variable (with numbers in parentheses referring to the hypothetical paths of Figure 2), shown separately for each response variables (FAR = Flying Arthropod Richness, GDAR = Ground-Dwelling Arthropod Richness, PLR = Plant Species Richness and FAA = Flying Arthropod Abundance). Each bar summarizes the effect sizes for all the pSEM models across regions (Kilpisjärvi and Varanger) and years (2020 and 2021). Direct effects are shown in purple, indirect effects are shown in green and total effects are shown in yellow. Squares with asterisks in the centre show the direct and total effect sizes of the quadratic term of altitude for the model of plant species richness.

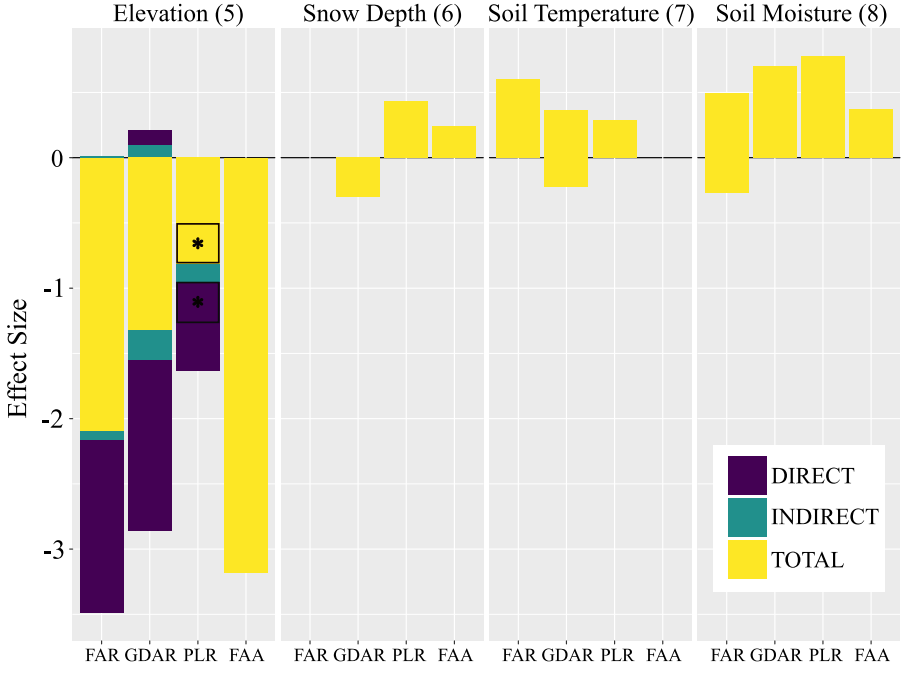


Table S1.

Global goodness-of-fit values for each pSEM model. For each year, organism group and study region, we show Chi-Squared and Fisher´s C values (with associated p-values) for the final model, along with r2 and AIC statistics. We note that the hypothesized relationships are considered consistent with the data when there is weak support for the sum of the conditional independence claims, that is, for the case that the observed collection of relationships could have occurred by chance alone. For such cases, the P-value for the Chi-Square test is greater than the chosen significance threshold (typically $\alpha = 0.05$; Lefcheck, 2016). In other words, when a Chi-Squared test is run on the C statistic and $p < 0.05$, then there is evidence that the model does not offer a good fit. Such a lack of fit will suggest that one or more of the missing paths will contain some useful information, yet is neglected by the model. Conversely, if $p > 0.05$, then we may infer that the model represents the data well, and that there is no suggestion of missing paths.

pSEM Model	Region	χ^2 (p-value)	d.f.	Fisher's C (p-value)	d.f.	R squared	AIC
Flying arthropod sp. richness	Kilpisjärvi 2020	0.889 (0.641)	2	2.447 (0.654)	4	0.62	680.761
	Kilpisjärvi 2021	4.784 (0.188)	3	8.796 (0.185)	6	1	566.544
	Varanger 2020	1.416 (0.234)	1	2.728 (0.256)	2	1	823.943
	Varanger 2021	0 (1)	0	NA	0	1	582.101
Ground-dwelling arthropod sp. richness	Kilpisjärvi 2020	0.066 (0.797)	1	0.427 (0.808)	2	0.94	558.032
	Kilpisjärvi 2021	2.733 (0.098)	1	4.285 (0.117)	2	0.99	682.531
	Varanger 2020	4.252 (0.119)	2	7.497 (0.112)	4	0.58	1099.938
	Varanger 2021	2.710 (0.100)	1	4.312 (0.116)	2	0.57	921.513
Plant species richness	Kilpisjärvi 2021	8.966 (0.176)	6	16.699 (0.161)	12	0.89	372.393
	Varanger 2021	2.710 (0.100)	1	4.312 (0.116)	2	0.93	449.426
Flying arthropod abundance	Kilpisjärvi 2020	0.089 (0.766)	1	0.503 (0.778)	2	0.51	123.532
	Kilpisjärvi 2021	2.588 (0.274)	2	4.988 (0.289)	4	0.80	94.264
	Varanger 2020	5.117 (0.163)	3	10.035 (0.123)	6	0.59	262.188
	Varanger 2021	2.193 (0.334)	2	3.756 (0.440)	4	0.57	133.312

Figure S6.

Heat map of the standardised coefficients of each potential driver of soil temperature and soil moisture across Varanger and Kilpisjärvi in 2020 and 2021. Shown are values for the final piecewise structural equation models, with the numbering of variables (x-axis) referring to the hypothetical paths of Figure 2. Colours show the sign and strength of direct effects on soil temperature and soil moisture. Elements shown in grey correspond to variables with no statistically detectable effect. The number of asterisks indicates the level of significance: *p < 0.05, **p < 0.01, ***p < 0.001.

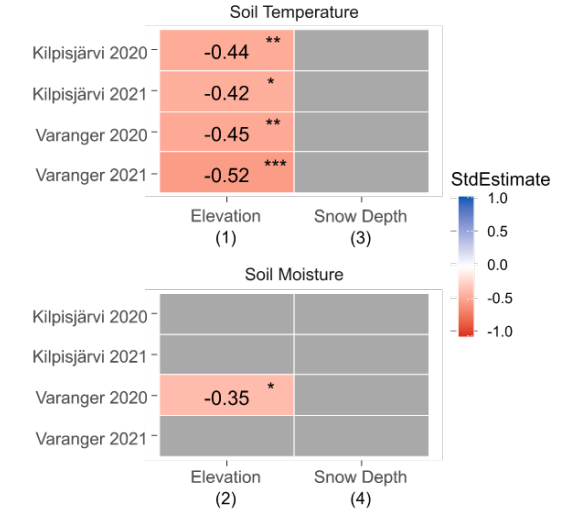
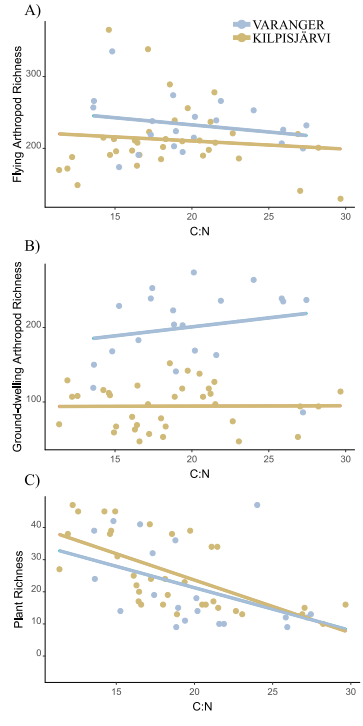


Figure S7.

The relation between community richness and nutrient availability (C to N ratio) for A) flying arthropods from Malaise traps, B) ground-dwelling arthropods from pitfall traps and C) plants. Blue lines represent data from Varanger while yellow lines represent data from Kilpisjärvi. The data is derived from analyses of soil cores extracted at each sampling site in Kilpisjärvi (n = 35) and at half of the sampling sites in Varanger (n = 20). The subset of sites in Varanger represents a focal study area that is similar in size to Kilpisjärvi (see Material and Methods). For each sampling site, we collected five soil cores with a diameter of 5 cm and a depth of 7 cm. We then homogenized the soil cores by hand and pooled them for analysis. The pooled soil samples were oven-dried at 70℃, and further homogenized using a sieve with a 2mm mesh size. From each compound sample, we weighed 0.15mg of soil under air-vacuum, encapsulated it into tin foil, and analysed it for C, N, and pH using Leco series 828 series analyser (Leco, United States). Data source: Bastien Parisy, unpublished.



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Understanding the dynamics of ecological communities is essential for assessing how they form and change over time. This thesis delves into the mechanisms driving community assembly, focusing on the impacts of environmental filtering and dispersal limitations on species richness and composition. Overall, my findings shed light on how abiotic factors, energy inputs, and dispersal capacity shape communities of plants, fungi and arthropods across subarctic landscapes, highlighting the complex interplay of factors in shaping community assembly.

Pablo de la Peña Aguilera Received his PhD education from the Department of Ecology, SLU, Uppsala, and obtained his Master of Applied Ecology at the Inland Norway University of Applied Sciences.

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