












# 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.

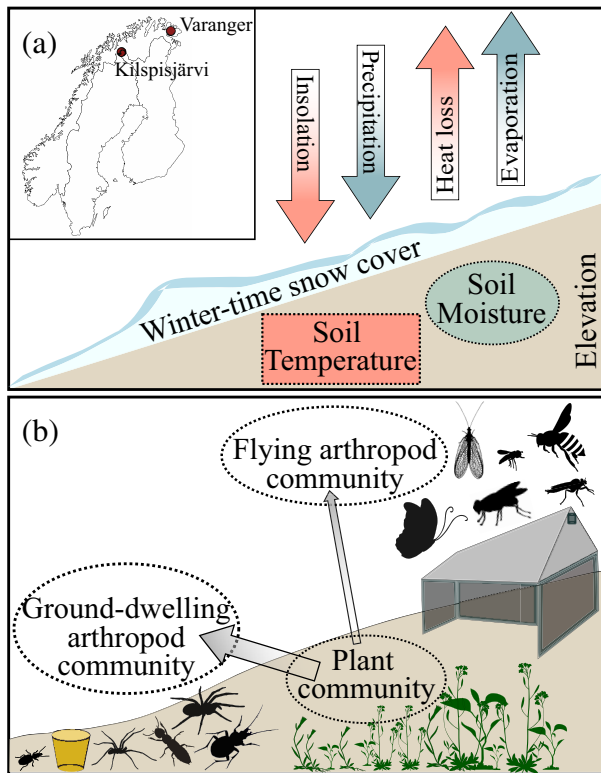
The role of microclimate in explaining local community patterns is likely accentuated in heterogeneous landscapes characterised by high microclimatic variability in space and in time, which is typically the case at high latitudes. In polar regions, species may be strongly

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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>) 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; Kempainen 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 *Vaccinium* 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  $-1.3^{\circ}\text{C}$  and the annual precipitation is 508 mm (1990–2021; Kyläkeskus meteorological station:  $69^{\circ}04' \text{ N}$ ,  $20^{\circ}80' \text{ E}$ ; 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 ( $0\text{--}2^{\circ}\text{C}$ ), while in the interior highland areas rising to 600 m a.s.l. the average annual temperature is below zero ( $-3\text{--}0^{\circ}\text{C}$ ) 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:  $70^{\circ}37' \text{ N}$ ,  $31^{\circ}09' \text{ W}$ ; 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<sup>®</sup>, 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<sup>™</sup> 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  $-18^{\circ}\text{C}$  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<sup>2</sup> 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<sub>2</sub>O, 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).

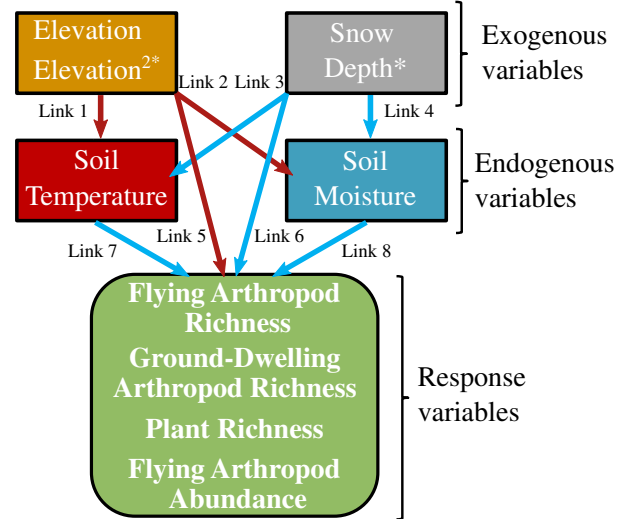
### Comparisons of species pools

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



**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.

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.

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 ( $\chi^2$ ). 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

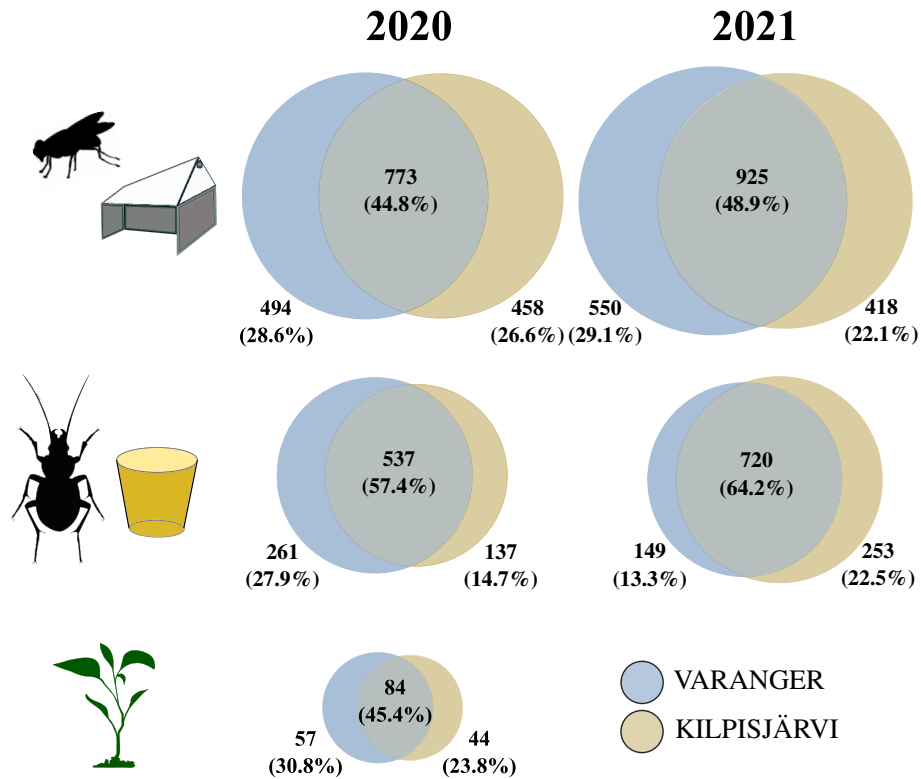
Altogether, we sampled 12,521 g of arthropods (mean  $5.85 \pm \text{SD } 4.42$  and mean  $7.42 \pm \text{SD } 5.94$  grams per site for Malaise in 2020 and 2021, respectively). In this mass, we detected a total of 31,125 ZOTUs of which 30,907 ZOTUs (representing 99.9% of all sequences) were resolved to species (i.e. BINs). The resulting 3399 BINs concerned 22 insect orders and 222 families (mean  $44.82 \pm \text{SD } 19.32$  BINs per site for Malaise data in 2020, mean  $33.18 \pm \text{SD } 26.23$  BINs per site for pitfall data in 2020, mean  $53.97 \pm \text{SD } 23.43$  BINs per site for Malaise data in 2021 and mean  $28.52 \pm \text{SD } 21.24$  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  $23.41 \pm \text{SD } 12.06$  plant species per site).

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

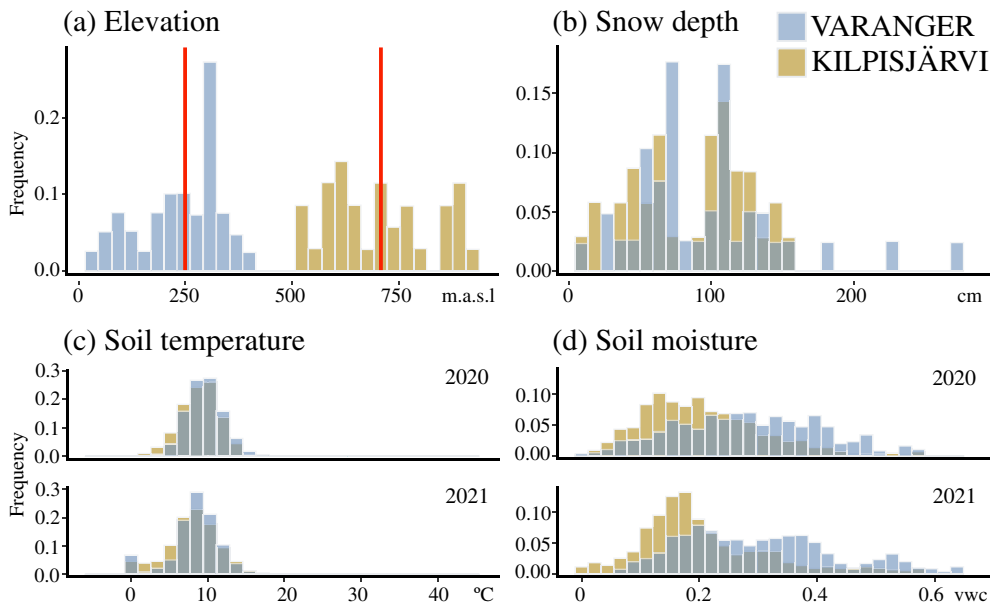
The highest species richness was found in flying arthropods, followed by ground-dwelling arthropods and plants (Figure 3). For all three organism groups, Varanger proved more species-rich than Kilpisjärvi, except for ground-dwelling arthropods in 2021 (Figure 3). Within each group, the two study regions 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 shown 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



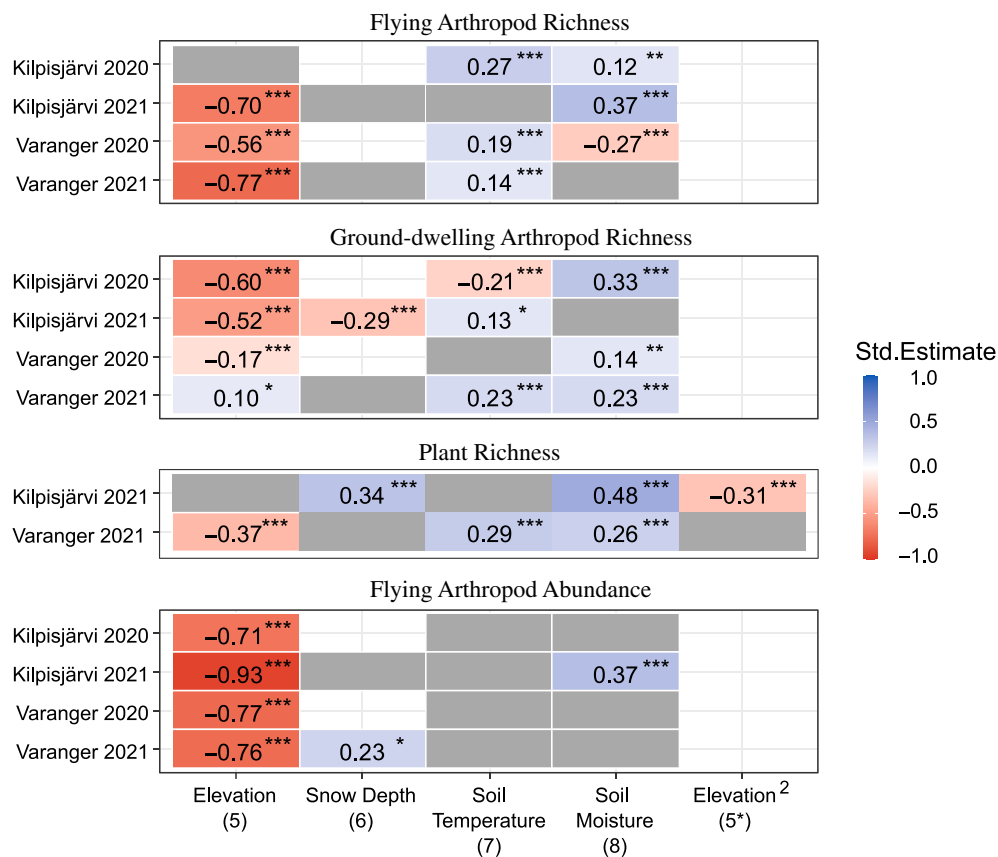
temperatures were roughly similar between the regions, with conditions at individual sites ranging from 0°C to 20°C, and a few sites recorded temperatures higher than 30°C. Likewise, soil moisture was similar between regions, with conditions in Varanger being slightly wetter than conditions in Kilpisjärvi 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?

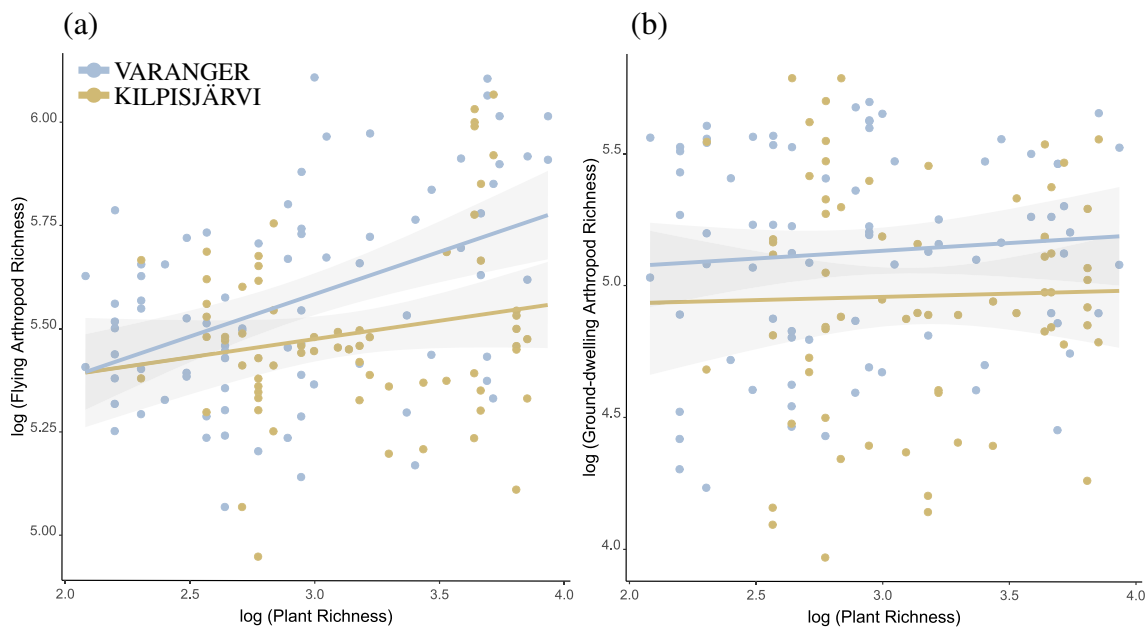
Arthropod species richness as such did not significantly differ between study areas (Table 1). However, flying and ground-dwelling arthropod species richness showed significantly different associations with plant species richness (plant richness × arthropod community type:  $p = 0.006$ ; Table 1). In 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 (Eidsen 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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