

ARTICLE

Elevational variation of spider and insect communities in the Swedish mountains

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Abstract

Mountain topography gives rise to often dramatic climate-driven elevation gradients in primary productivity, which can generate substantial biodiversity variation. Therefore, mountain areas may be particularly useful for evaluating the ecological consequences of climate change. Arthropods are the most diverse animal phylum, which play important roles in most ecosystems. However, despite their ecological importance, we have limited information on how arthropods vary along elevation gradients. We investigated how taxonomic richness, taxonomic composition, and spatial structuring of spider and insect communities varied along elevation gradients and among three geographic locations in a mountain region of northern Sweden. The locations provided a latitude gradient spanning approximately 3° (from 62° N to 65° N), but were otherwise selected to contain similar environmental characteristics. Taxonomic richness of both spiders and insects declined monotonically with increasing elevation, and there were limited differences between the geographic locations in such declines. Taxonomic composition varied with elevation for both taxonomic groups, but also differed among the three sites. Linyphiid spiders were more widely distributed along the elevation gradients than other spider taxa, whereas a broad taxonomic range of insects occurred over almost all elevations. We observed nested as well as modular spatial distributions of both spider and insect communities along the elevation gradients. While the modular patterns suggest that species turnover has generated distinct communities at different elevations, some generalist species were still widespread throughout large parts of the gradients. Our results point to smaller differences among geographic locations than among taxonomic groups in how taxonomic richness and community structuring varied with elevation. We interpret these results as support for taxonomically specific adaptations to environmental conditions being important for structuring arthropod communities. We also suggest that climate-driven changes to arthropod communities in mountain environments may be regulated by two not mutually exclusive processes, one in which generalist species may become more dominant

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and shift their ranges upward and one in which high-elevation specialists may go extinct because of increasingly fragmented habitats.

KEYWORDS

altitude, Araneae, Arthropoda, Insecta, latitude, mountain ecology, spatial structure, species composition, species richness, taxonomic diversity

INTRODUCTION

The early naturalists, for example, von Humboldt (1849) and Darwin (1859), acknowledged that latitudinal and elevational gradients generate substantial variation in environmental conditions that have profound effects on the distribution of species (Lomolino, 2001). Both elevation and latitude gradients represent gradual changes in both abiotic conditions and the biota that give rise to different habitats that shape biodiversity patterns in space and time (Currie, 1991; Piel, 2018; Rosenzweig, 1995; Willig et al., 2003). In terrestrial environments, general declines in species richness with increasing elevation and latitude have been frequently observed across a wide range of organisms, geographic regions, and spatial scales. Even though biodiversity declines are correlated with decreased temperature and net available energy (Gillman et al., 2015; Hillebrand, 2004), the underlying causes of these patterns are debated (e.g., Currie et al., 2004; Rosenzweig, 1995; Willig et al., 2003). Additionally, declines in biodiversity along environmental gradients are not necessarily uniform among geographic areas, taxonomic groups, or spatial scales (Bruun et al., 2006; Måsviken et al., 2020; Naud et al., 2019; Nogués-Bravo et al., 2008; Rahbek, 1995, 2005).

Elevation and latitudinal gradients in environmental conditions do not only give rise to general declines in taxonomic richness but can also lead to changes in the functional and phylogenetic composition of species communities (Franzén & Dieker, 2014; Lenoir et al., 2013; Rönquist et al., 2020; Wilson & Nilsson, 2009). Such differences in community composition can have profound ecological and evolutionary consequences (Chesson, 2000; Danks, 1994). For instance, phenotypic variation within communities may influence both ecosystem function and resilience (Tilman, 2001), and phylogenetic variation may be linked to the opportunity of communities to respond to future environmental changes (Dalerum, 2013). In addition, differences in the composition of species communities may indicate spatial structuring along environmental gradients. Distribution patterns are nested when the most widespread species also are dispersed where more localized species occur (Galeano et al., 2009). Thus, in truly nested communities, species-rich sites contain unique species while species-poor sites do not contribute to overall

species richness (Ślipiński et al., 2012). Modularity, on the other hand, describes the extent to which species are clustered into “modules,” where species are more ecologically associated within than across modules (Fortuna et al., 2010). Modular structures along environmental gradients indicate species turnover, and subsequently that each site is inhabited by environmental specialists (Hausdorf & Hennig, 2007; Thébault, 2013). Community structuring along environmental gradients may also indicate the underlying processes of community assembly, since nested structures have been related to environmental regulation and modular structures to antagonistic interactions possibly leading to competitive exclusions (Brännström et al., 2012).

Due to the tight coupling between elevation and climate, mountain areas, especially mountains at high latitudes, are particularly useful for evaluating the ecological consequences of ongoing and future climate change. Through elevation gradients, mountains provide an excellent way of testing large climatic variations within small areas with similar geological and evolutionary history (Körner, 2000). Furthermore, mountains and high-latitude areas have experienced substantially higher temperature increases compared with the global average (Bekryaev et al., 2010; Beniston et al., 1997; Pepin et al., 2015). Mountain areas are characterized by low primary production and consequently harbor relatively species-poor ecosystems. Due to the relatively low number of species, the ecosystems are potentially more vulnerable to alterations in community structure than species-rich areas. Additionally, many species groups are still poorly studied (Karlsson et al., 2020) and such taxonomic bias is likely to be more pronounced for mountain areas, which tend to be under-sampled or underrepresented in many inventories (e.g., Penado et al., 2016; Rönquist et al., 2020).

Arthropods, that is, members of the phylum Arthropoda, form an extraordinarily diverse organism group that contains more species than all other animal phyla in the world (Zhang, 2011). Arthropods are common in almost all environments, and they play vital roles in most ecosystems as predators, prey, decomposers, pest regulators, and pollinators (Seastedt & Crossley, 1984). Spiders (order Araneae) and insects (class Insecta) are two taxonomically rich and ecologically important groups of arthropods (Foelix, 1996; Gullan & Cranston, 2005). Elevational variations in diversity

have been quantified previously for both spiders and insects, but the patterns have not been uniform among different studies. For instance, the taxonomic diversity of spiders has shown declines with elevation (Winkler et al., 2018), hyperbolic relationships with elevation (Gilgado et al., 2022), and no elevational variation (Dolson et al., 2020). Similar variation has been observed in how insect communities respond to elevational gradients (e.g., Despland et al., 2012; Winkler et al., 2018). Hence, there appear both taxonomic and geographic variations in how spider and insect communities respond to shifting elevations.

In this study, we quantify how taxonomic richness, taxonomic composition, and spatial structuring of spider and insect communities vary over elevation gradients at three different geographic locations distributed along the Swedish mountains. The Swedish mountains form an area of relatively high latitude consisting of oro-arctic treeless mountain vegetation, which holds components of both arctic and alpine environments (Virtanen et al., 2016). Elevational variation of vascular plant diversity has been shown to differ substantially both along the Swedish mountains (Måsviken et al., 2020) and among massifs within smaller landscape scales (Naud et al., 2019). Considering the previously observed variation in the manner in which elevation influences spider and insect communities, coupled with the observed spatial variation in how plant diversity varies along elevation gradients in the Swedish mountains, we wanted to evaluate the effect of elevation on taxonomic and geographic variation of spider and insect communities in this northern mountain region. We therefore set out to test six specific predictions, all assuming limited geographic and taxonomic variation: (1) both spider and insect species richness will decline monotonically with increasing elevation; (2) there will be limited variation in this decline between geographic locations and taxonomic groups; (3) the taxonomic composition of both spider and insect communities will vary along the elevation gradients; (4) there will be limited differences in this variation between the geographic locations and taxonomic groups; (5) the distribution of species occurrences over the elevation gradient at each geographic location will form a distinct compartmentalized structure due to an elevational turnover in species ranges; and (6) there will be limited variation in this compartmentalization between geographic locations and taxonomic groups.

METHODS

Study area

Sampling for this study was carried out above the tree line at three locations in the Swedish part of the

Scandinavian mountain range. The Scandinavian mountains extend from southern Norway to the north-east along the border between Norway and Sweden for approximately 960 km and are of relatively low elevation. The Swedish part reaches a maximum of 2096 m above sea level (asl). The vegetation above the tree line, classically called alpine vegetation (Körner, 2003), is in the Swedish mountains categorized as oro-arctic tundra, which is a separate sub-biome different from both alpine and arctic vegetation (Virtanen et al., 2016). Vegetation at lower elevations is characterized by sedges and graminoids, whereas the tundra at higher elevations is primarily comprised of heath vegetation characterized by low-lying perennial herbs (*Saxifraga* sp., *Potentilla* sp., and *Ranunculus* sp.), low-growth woody plants (*Vaccinium myrtillus*, *Betula nana*, and *Salix* sp.), mosses, and lichen. Due to higher elevation and more oceanic climate, there is a general gradient of increasing precipitation toward the west in the Swedish mountains (Carlsson et al., 1999). Temperatures follow the expected latitudinal pattern and are lower in the northern parts (9.7°C mean summer, −10.6°C mean winter, Abisko, 68.21° N, 18.48° E) compared with the southern parts (10.9°C mean summer, −7.4°C mean winter, Idre, 61.53° N, 12.51° E; SMHI, 2022).

Sample collection

Sampling was conducted at three locations spaced roughly one latitude degree apart (Figure 1a): Långfjället (62.10° N, 12.43° E), Storulvån (63.21° N, 12.34° E), and Borgafjäll (64.90° N, 15.04° E). These three locations were selected because they offered similar characteristics in terms of topography and geology and allowed relatively easy logistic access to the full evaluation gradients sampled. All sampling was done above the tree line, according to the definition of Körner (2003). The elevation of the tree line is affected by temperature (Körner & Paulsen, 2004), which in turn differs with latitude. Therefore, the tree line varied among our locations from 840 m asl at Långfjället to 800 m asl at Storulvån and 775 m asl at Borgafjäll. We used a stratified random sampling design, where the elevation at each location was independently divided into four strata from the highest peak to the tree line. We used these elevation strata to sample three elevation gradients per geographic location (Figure 1b–d). The sampled elevations ranged from 878 to 1164 m asl at Långfjället, from 868 to 1441 m asl at Storulvån, and from 853 to 1341 m asl at Borgafjäll. In each stratum, we placed one sampling station for insects (one Malaise trap and six pitfall traps; Appendix S1: Figure S1a) and for the spiders also one transect consisting

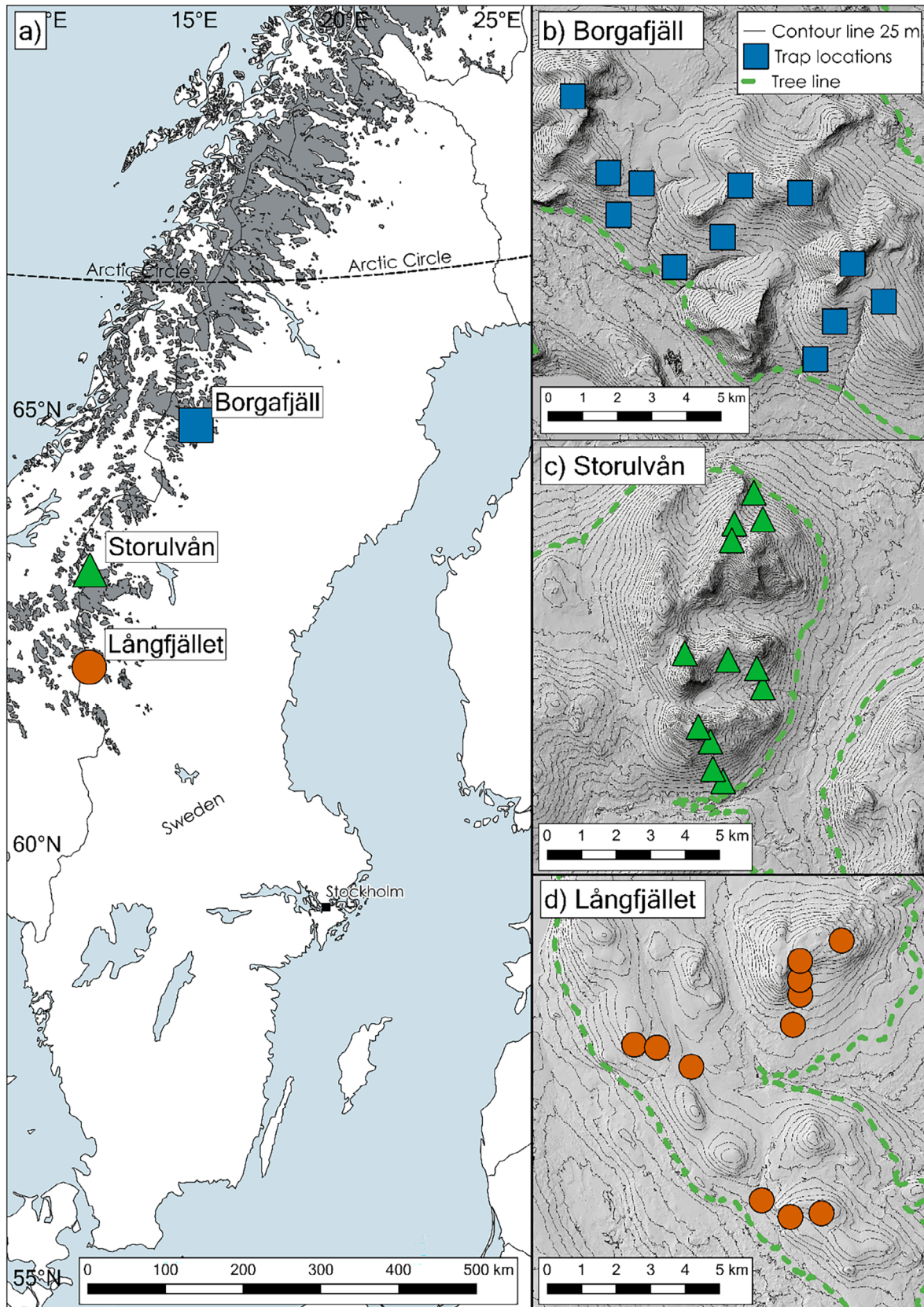


FIGURE 1 The three studied geographic locations within the Swedish mountains (gray areas) (a), as well as detailed maps of the sampling transects at Borgafjäll (b), Storulvån (c), and Långfjället (d).

of 15 additional pitfall traps (Appendix S1: Figure S1b). This resulted in 11–12 sampling units per geographic location, distributed across the full elevation range from the tree line to the highest peak. The Malaise trap collection bottles were filled with 95% ethanol and refilled if needed. The pitfall traps were filled with water and a nonscented detergent to break surface tension and were generally not serviced prior to being collected. All traps were left out for five days before collection. Sampling was done during July to early August in 2018 at Långfjället and Storulvån and 2019 at Borgafjäll. One Malaise trap at Storulvån and one at Borgafjäll had collapsed. In addition, all pitfall traps on that transect at Borgafjäll were completely frozen, amounting to 8% of the sampling effort on this location and less than 3% of the efforts on all locations. We therefore excluded these sample locations from our analyses. All spiders were separated into individual tubes for morphological identification while the rest of the arthropods were kept as one bulk sample per trap. All samples were stored in 95% ethanol at -20°C until further processing.

Taxonomic identification

Spiders were identified morphologically using taxonomic expertise to species or lowest possible taxonomic level, following the taxonomy of the database Dyntaxa (SLU Artdatabanken, 2021).

Insects were identified from the bulk arthropod samples using DNA metabarcoding following the NCBI Taxonomy (Schoch et al., 2020). We analyzed each Malaise trap and each of the six surrounding pitfall traps as a separate sample. Metabarcoding is the most common genetic method of taxonomic identification, particularly for large-scale surveys. This method relies on the amplification and sequencing of short fragments of some hundred base pairs (bp), the so-called barcodes, of taxonomically variable DNA regions that are used for taxonomic identification (Taberlet et al., 2012). Barcodes are often genetic regions or genes from cell organelles since they occur at a much higher frequency than the nuclear DNA, which simplifies extraction and detection. We conducted the metabarcoding using the primer pair BF3 and BR2. These primers target a 418 bp long fragment of the cytochrome *c* oxidase I (COI) region of the mitochondrial genome and are developed specifically for metabarcoding of arthropods (Elbrecht & Leese, 2015). The COI region is the most commonly used barcode region for animals, including arthropods (Andújar et al., 2018; Liu et al., 2020). We have reported the taxonomic units of insects as molecular operational taxonomic units (MOTUs). MOTUs are clusters of similar sequences identified using a predefined similarity

threshold (Blaxter et al., 2005) and are routinely used for metabarcoding of taxonomic groups where the taxonomic cover is low. Although we treated each MOTU as an individual taxon for our analyses (see below), we still assigned a taxonomic name to them by referencing each MOTU against all available sequences of terrestrial arthropods in the BOLD database (Ratnasingham & Hebert, 2007). A detailed protocol for the metabarcoding and associated taxonomic assignments is given in Appendix S2.

Of the 236 individual samples used for metabarcoding, that is, bulk samples from Malaise traps or individual pitfall traps, 11 were regarded as empty and not sequenced. We were able to retrieve sequences from 212 of the 226 sequenced samples. Metabarcoding of the content from these samples yielded ~ 3.2 million reads. After removing contaminants (misclassified sequences), low-quality MOTUs (best identity < 0.85), and reads assigned to taxonomic levels above family level, the reads were distributed among 625 MOTUs. The majority, 95%, of the 625 identified MOTUs belonged to insects (595 MOTUs), while 4% (23 MOTUs) belonged to springtails (class Collembola) and 1% (7 MOTUs) to arachnids (class Arachnida).

Data analysis

For data analysis, we pooled the number of morphologically identified spider taxa and the number of identified MOTUs of insects from each sample (i.e., one transect for spiders and one Malaise trap and its six associated pitfall traps for insects). All MOTUs were treated as different taxonomic entities and will be referred to as taxa. We have refrained from using our read data quantitatively, as an organism's body size and composition affect the amount of DNA released during the lysis process, which biases the amount of identified sequences for certain taxa (Marquina et al., 2022). We have therefore used all data as a measure of presence–absence of occurrences at each sample location. Although we have abundance data on spiders, we have used the data as presence–absence to allow for meaningful comparisons with insects.

We evaluated the effects of elevation and location on taxonomic richness of the three arthropod groups using generalized linear models with a log link function and a quasi-Poisson error structure. We used a quasi-Poisson error structure because the data on both spiders and insects were overdispersed with dispersion parameters of 2.27 and 9.62, respectively. We constructed one model for each arthropod group with the taxonomic richness of each sample as the response variable. The models included elevation, geographic location, and their two-way interaction as predictors. We evaluated the significance of all

terms using likelihood ratio tests. If no significant interaction was found, we simplified the models by removing the interaction term. To enable comparisons of the effect of elevation among locations, we normalized elevation by subtracting the average tree line elevation at each location from the measured elevation at every sampling location. Tree line elevation at each location was estimated using areal images with a 0.48-m resolution and a digital elevation model with 2-m resolution. Both datasets were obtained from the Swedish land survey (Lantmäteriet, 2022).

We used permutational multivariate analysis of variance, based on Bray–Curtis distances calculated from the presence–absence matrices, to evaluate the effects of elevation and locations on the taxonomic composition of the three arthropod groups. Similar to our analysis of species richness, we evaluated species composition using one model for each taxonomic group and included elevation (above tree line), geographic location, and their two-way interaction as predictors. For models in which we found a significant interaction effect, we ran subset models to evaluate the effect of elevation within each location and differences in the effect of elevation among all pairs of locations. For models with only a significant main effect of location, we similarly used subset models containing each pair of locations to test for pairwise differences in species composition. We corrected *p* values from all subset models by adjusting for the false discovery rate (Benjamini & Hochberg, 1995). Variation in taxonomic composition along the elevation gradients and among locations was visualized using nonmetric multidimensional scaling (NMDS) fitted to two dimensions using a Bray–Curtis distance matrix (Minchin, 1987).

We analyzed the patterns of spatial community structuring using methods based on mathematical graph theory (Dale, 2017). We focused these analyses on the detection of nested and modular structures, and evaluations of whether these structures followed the elevation gradients. We tested for nested and modular structures since these have been suggested as ecologically relevant for both arthropods (e.g., Dalerum et al., 2017, 2019) and elevation gradients (da Silva et al., 2018; Jacquemyn et al., 2007; Ramos-Jiliberto et al., 2010). We made separate analyses for nestedness and modularity, and calculations were done separately for spiders and insects at each geographic location. All analyses were based on presence–absence matrices, which consisted of each sample as rows and the detected species or taxa as columns.

For nestedness, we sorted taxa by the number of occurrences and sites by elevation and calculated nestedness using the NODF (nestedness metric based on overlap and decreasing fill) index (Almeida-Neto et al., 2008; Basella, 2012). It generates a value that ranges between

0 (no nestedness) and 100 (perfect nestedness) but is not fully interpretable unless it is compared against a null model randomization. We therefore compared the estimated nestedness to values obtained from 1000 randomized matrices, generated by randomly shuffling the cell values while preserving the same number of occurrences of each taxon. This null model has been suggested as appropriate for evaluating the influence of environmental conditions on community structuring (Jonsson, 2001). If the matrices having sites ordered by elevation did not result in a nested structure, we also evaluated matrices in which sites were ordered by taxonomic richness, since this ordering generates an optimally nested pattern for any given matrix (Ulrich et al., 2009). Hence, ordering the sites by elevation explicitly tests whether there was a nested structure along the elevation gradients, whereas ordering sites by taxonomic richness tests whether there was a nested structure in the communities, although this structure did not follow elevation.

For modularity, taxa were ordered by the scores from reciprocal averaging. As with nestedness, we first tested for modularity using matrices in which the samples were ordered by elevation, and, if no modular structures were identified, we also evaluated the modularity in matrices in which the samples were ordered by reciprocal averaging scores. Reciprocal averaging has been suggested as a useful method for ordering matrices along latent environmental gradients (Gauch et al., 1977; Hill, 1973). We quantified modularity using the *Q* statistic after we had identified modules using Barber's (2007) bipartite extension of Newman and Girvan's (2004) recursive induced model. The *Q* statistic is based on the probability that a given edge (in our matrices the occurrence of a taxon within a given location) falls within a given module in relation to the probability that any random edge falls within that module. It can range from 0 to 1. As with nestedness, we compared the observed modularity values to those obtained from the 1000 randomized matrices described above.

All analyses were performed in the R statistical environment (version 4.0.5, <http://www.r-project.org>) and the contributed packages bipartite (version 2.17, Dormann et al., 2008), emmeans (version 1.7.3, Lenth, 2022), metacom (version 1.5.1 and version 1.5.3, Dallas, 2014), pairwiseAdonis (version 0.4, Martinez Arbizu, 2017), and vegan (version 2.6-2, Oksanen et al., 2022).

RESULTS

A total of 2844 spiders were collected, distributed among eight different families and 85 taxa. Of these 85 taxa, 68 (80%) were identified to species, 13 (15%) to

genus, and 4 (5%) to family level. All families except Araneidae, Philodromidae, and Hahniidae were represented at all locations, but occurrences varied considerably among families along the elevation gradients (Figure 2a). Linyphiidae was the most widely observed spider family followed by Lycosidae, Gnaphosidae, and Thomisidae, although the latter three were never observed at higher elevations. Moreover, Thomisidae was only found at very low elevations at the northern location, Borgafjäll.

Of the 595 insect taxa (i.e., MOTUs), 332 (53%) were taxonomically referenced to species level, 177 (28%) to genus, 18 (3%) to subfamily, and 98 (16%) to family. The insect taxa were distributed among 12 different orders (Figure 2b). Diptera accounted for approximately 68% of the taxa and was the only order found at all elevations and sampling locations where we collected arthropods and from which we retrieved metabarcoding sequences. Coleoptera, Hemiptera, and Hymenoptera were found from low to high elevation at all locations but were

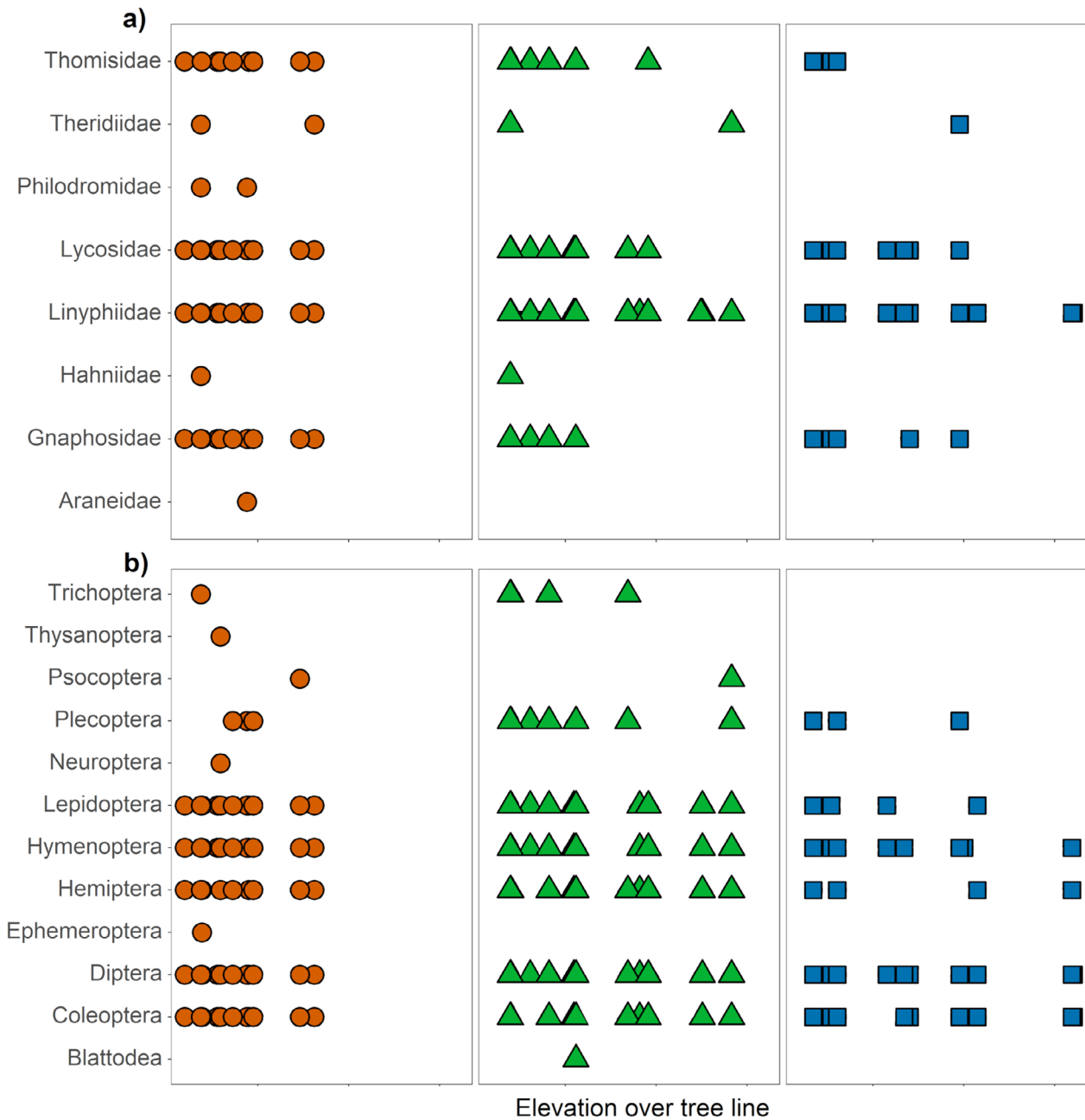


FIGURE 2 The distribution of spider families (a) and insect orders (b) along the elevation gradients at three geographic locations along the Swedish mountains: Långfjället (red circles), Storulvån (green triangles), and Borgafjäll (blue squares). Elevation is expressed as meters over the average tree line at each location.

missing at some sampling units along the elevation gradient. Lepidoptera showed a similar pattern but were not present at higher elevations at the northern location, Borgafjäll. The other seven insect orders were found in much fewer locations.

Taxonomic richness

There were significant monotonic declines in the taxonomic richness of spiders ($\beta = -1.41 \times 10^{-3}$, $SE = 4.82 \times 10^{-4}$, $p = 0.006$; Figure 3a) and insects ($\beta = -1.07 \times 10^{-3}$, $SE = 5.17 \times 10^{-4}$, $p = 0.046$; Figure 3b) with increasing elevation. There were no differences in the effect of elevation among geographic locations for either taxonomic group (spiders: $X^2 = 3.42$, $df = 2$, $p = 0.461$; insects: $X^2 = 12.96$, $df = 2$, $p = 0.507$), nor differences in taxonomic richness among locations, pooled across the elevation gradients, for spiders ($X^2 = 2.53$, $df = 2$, $p = 0.564$). However, there were differences between geographic locations for insects ($X^2 = 129.40$, $df = 2$, $p = 0.001$). The northern location Borgafjäll had lower taxonomic richness of insects compared with the central location Storulvån ($\beta = -0.63$, $SE = 0.20$, $p = 0.004$), while there were no differences between the southern location Långfjället and Borgafjäll ($\beta = 0.30$,

$SE = 0.27$, $p = 0.520$) nor between Långfjället and Storulvån ($\beta = -0.33$, $SE = 0.25$, $p = 0.378$).

Taxonomic composition

There was a significant interaction between elevation and location on the taxonomic composition of spiders ($F = 2.57$, $df = 2$, 28 , $p = 0.004$; Figure 4a). At all three geographic locations, there were significant effects of elevation on spider taxonomic composition (the southern location Långfjället: $F = 1.99$, $df = 1$, 9 , $p_{adj} = 0.055$; the central location Storulvån: $F = 6.95$, $df = 1$, 10 , $p_{adj} < 0.001$; the northern location Borgafjäll: $F = 7.14$, $df = 1$, 9 , $p_{adj} = 0.002$), but these effects differed between all pairs of locations (Långfjället and Storulvån: $F = 8.32$, $df = 1$, 21 , $p_{adj} < 0.001$; Långfjället and Borgafjäll: $F = 9.22$, $df = 1$, 20 , $p_{adj} < 0.001$; Borgafjäll and Storulvån: $F = 9.28$, $df = 1$, 21 , $p_{adj} < 0.001$). For insects there were significant effects of elevation on taxonomic composition, pooled across all locations (insects: $F = 2.79$, $df = 1$, 27 , $p < 0.001$; Figure 4b). There were also significant differences in the taxonomic composition among locations, pooled across the elevation gradients, for both spiders ($F = 4.05$, $df = 2$, 28 , $p < 0.091$) and insects ($F = 4.21$, $df = 2$, 28 , $p < 0.001$). There were differences among all

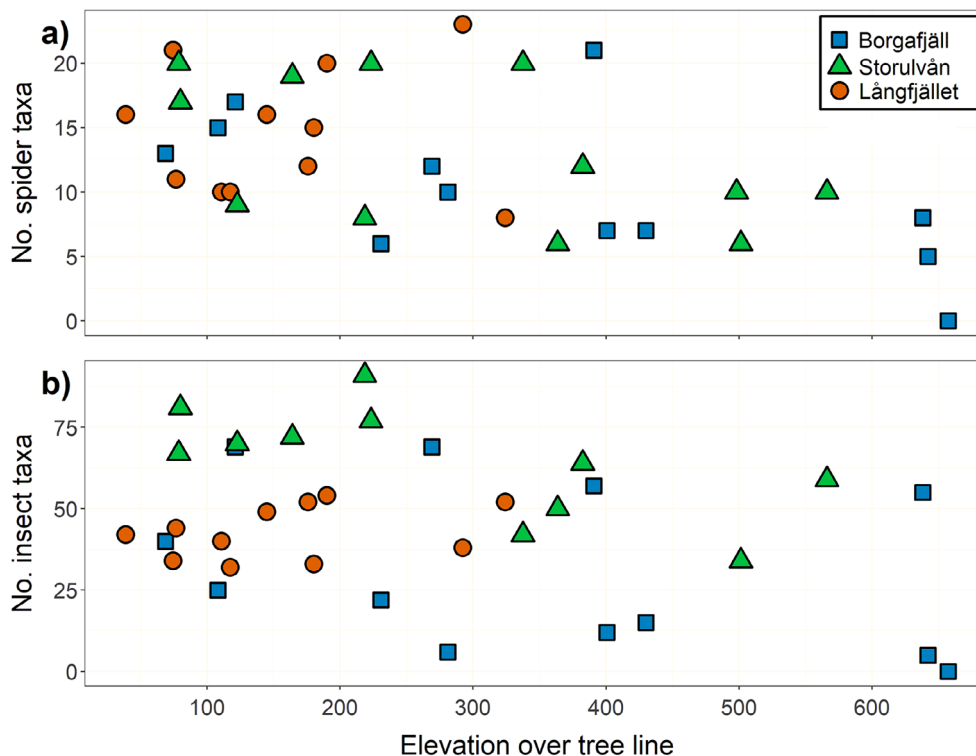


FIGURE 3 Taxonomic richness of spiders (a) and insects (b) over varying elevation for three geographic locations along the Swedish mountains: Långfjället, Borgafjäll, and Storulvån. Elevation is expressed as meters over the average tree line at each site. Taxonomic richness was quantified as the number of identified taxa from morphologic identification of spiders and the number of identified molecular taxonomic units identified using genetic metabarcoding for insects.

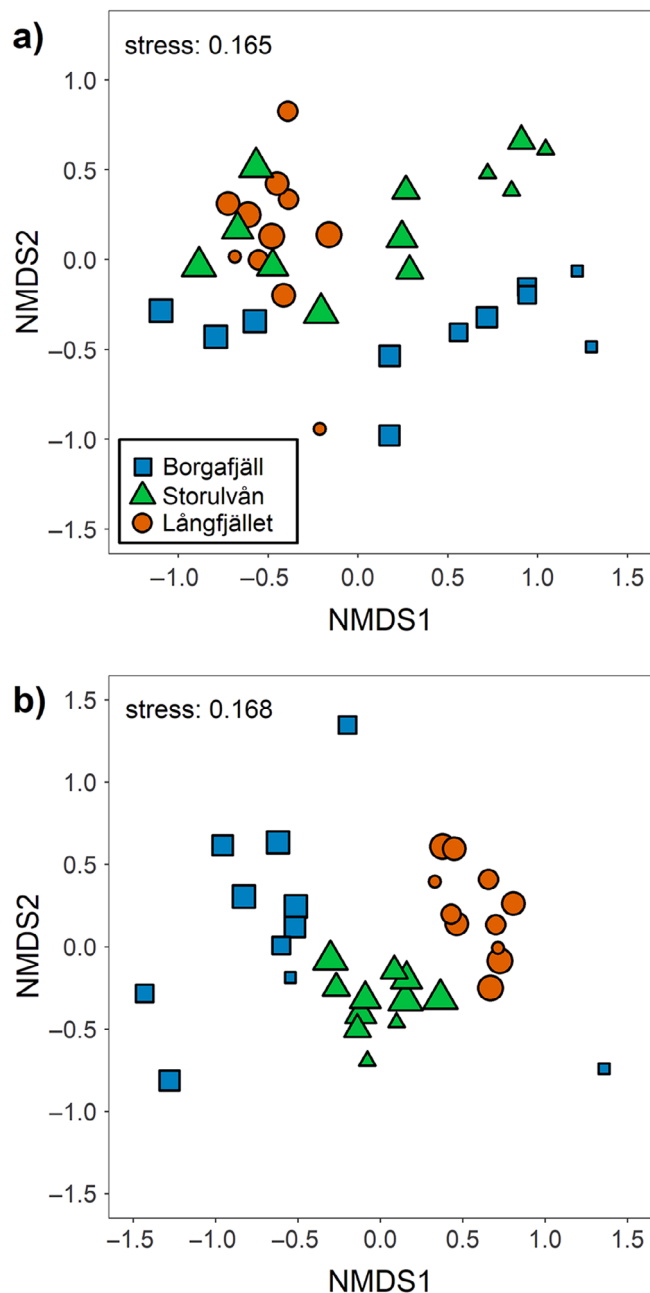


FIGURE 4 Variation in taxonomic composition of spiders (a) and insects (b) at three sites in the Swedish mountains, visualized as nonmetric multidimensional scaling (NMDS) biplots based on Bray–Curtis distances. Each data point represents a sample (i.e., all spiders identified along a 500-m transect or all insect molecular taxonomic units [MOTUs] identified in one Malaise trap and its six associated pitfall traps), and larger symbols indicate lower elevation of this location. Quantifications of taxonomic compositions were based on taxa identified from morphologic characteristics for spiders and from MOTUs identified using genetic metabarcoding for insects.

pairs of locations for both spiders (Långfjället and Storulvån: $F = 4.16$, $df = 1$, 21 , $p_{adj} = 0.003$; Långfjället and Borgafjäll: $F = 4.76$, $df = 6$, 38 , $p_{adj} = 0.003$; Storulvån and

Borgafjäll: $F = 2.70$, $df = 1$, 21 , $p_{adj} = 0.029$) and insects (Långfjället and Storulvån: $F = 5.13$, $df = 1$, 20 , $p_{adj} = 0.001$; Långfjället and Borgafjäll: $F = 4.70$, $df = 1$, 20 , $p_{adj} = 0.001$; Storulvån and Borgafjäll: $F = 3.81$, $df = 1$, 20 , $p_{adj} = 0.001$).

Spatial community structuring

Communities of both spiders and insects showed low to intermediate levels of nestedness along the elevation gradients at all three geographic locations (Figure 5a). The community structuring of both spiders and insects was significantly more nested along the elevation gradients than null model expectations (Table 1).

Communities of both taxonomic groups showed moderate levels of modularity along the elevation gradients at all locations (Figure 5b). Spider communities at all locations were significantly more spatially modular along the elevation gradients than null model expectations (Table 1), with eight modules identified at the southern location Långfjället and six each at the central location Storulvån and the northern location Borgafjäll. Similarly, insect communities at Långfjället and Storulvån were also significantly more spatially modular along the elevation gradients than null model expectations (Table 1), with 9 modules identified at Långfjället and 10 at Storulvån. However, insect communities at Borgafjäll were less modular than null model expectations, both with samples sorted by elevation (Table 1) and reciprocal averaging ($Q_{obs} = 0.50$, $Q_{exp} = 0.51$, $Z = -3.84$, $p < 0.001$).

DISCUSSION

Our data generally supported the predictions that taxonomic richness would decline and the taxonomic composition would change with increasing elevation and that there would be limited differences in such elevational variation among geographic locations. For both organism groups, there also appeared to have been distinct taxonomic compositions, pooled across elevations, at each of the three study locations. We note that the lack of geographic differences in elevational variation of taxonomic richness is different from previous findings of vascular plants, which have shown substantial geographic variation in diversity along elevation gradients on both large (Måsviken et al., 2020) and finer spatial scales (Naud et al., 2019) in the same region. Instead, our data indicate differences among taxonomic groups rather than between geographic locations in how arthropod communities have responded to elevation. We suggest that some of these differences imply that plant distributions are more tightly regulated by local environmental conditions than the

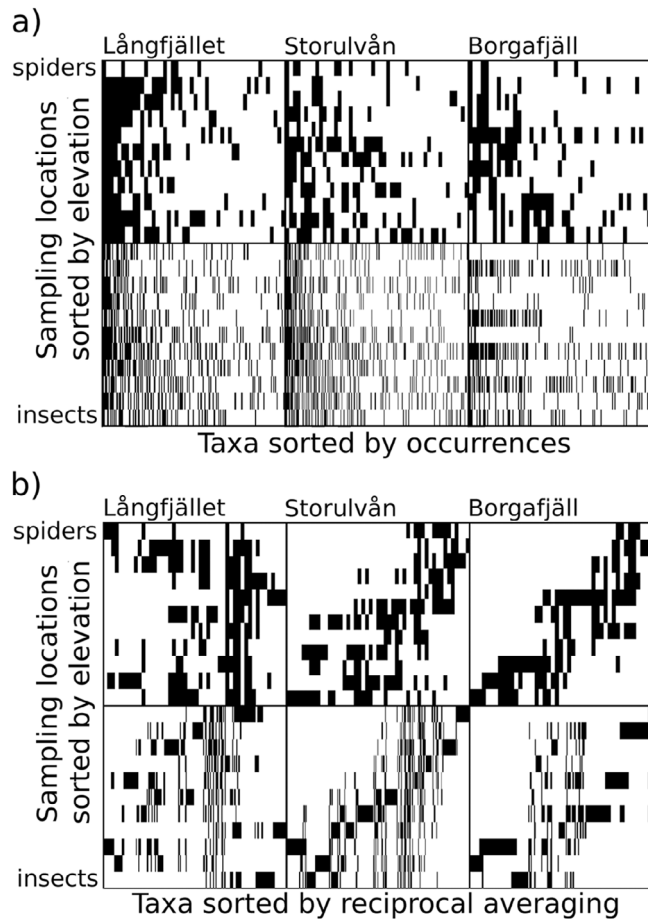


FIGURE 5 Image representations of binary presence–absence matrices of arthropod taxa (rows) within each sample (columns) showing patterns of nestedness (a) and modularity (b) for spiders and insects at three geographic locations along the Swedish mountains: Långfjället, Storulvån, and Borgafjäll. For nestedness, taxa were ordered by decreasing number of occurrences from left to right for matrices evaluating nestedness (a), so that an optimal nested pattern would have all presences packed toward the upper left corner of the matrix. For modularity, taxa were ordered by their reciprocal averaging scores (b), where an optimal modular pattern would not have any overlap in occurrences over different elevations (i.e., rows). In all matrices, samples were ordered by elevation from bottom up. Sorting of matrices was done separately for each site.

distributions of animals (Bradshaw, 1972). Arthropods may instead be regulated by larger environmental contrasts such as broad climate regimes (e.g., Copeland et al., 2010) or by different adaptations associated with resource utilization and resource competition (Andrewartha & Birch, 1954). Also notable is the lack of support for nonlinear patterns of community shifts over the elevation gradients. In particular, unimodal patterns have been frequently observed along elevation gradients for a wide range of organisms (Lenoir et al., 2008; Rahbek, 1995). This pattern has been explained by a shift in community regulation from competitive exclusion at lower

TABLE 1 Observed and expected indices of spatial nestedness (NODF) and modularity (Q) of spiders and insects along elevation gradients at three geographic locations in the Swedish mountains, as well as the number of identified modules for the analyses of modularity.

Location	Observed	Expected	Modules	Z	p
Nestedness (NODF)					
Spiders					
Borgafjäll	34.59	30.45		3.72	<0.001
Storulvån	37.57	33.07		7.19	<0.001
Långfjället	44.12	41.89		12.71	<0.001
Insects					
Borgafjäll	21.60	15.20		34.46	<0.001
Storulvån	23.16	21.96		8.99	<0.001
Långfjället	23.37	23.03		1.64	0.050
Modularity (Q)					
Spiders					
Borgafjäll	0.39	0.33	6	4.75	<0.001
Storulvån	0.33	0.29	6	3.21	<0.001
Långfjället	0.25	0.24	8	1.93	0.027
Insects					
Borgafjäll	0.50	0.51		−3.84	<0.001
Storulvån	0.42	0.41	10	5.72	<0.001
Långfjället	0.40	0.39	9	2.95	0.002

Note: Taxa for the nestedness values were ordered by number of occurrences and for modularity by scores generated from reciprocal averaging. For both nestedness and modularity analyses, samples were ordered by elevation. Expected values were calculated from 1000 randomizations of the observed matrices where the number of occurrences by each taxon had been preserved.

elevations toward a higher importance of environmental filtering with increasing elevation (Rosenzweig, 1992; Rosenzweig & Abramsky, 1993). The observed monotonic declines in species richness with increasing elevation may indicate that such shifts in community regulation were prevalent for both spiders and insects.

In agreement with our finding of differences in taxonomic compositions along the elevation gradients, we also observed modular patterns in the distribution of taxa at different elevations. These observations point to a species turnover in which environmental specialists inhibit specific parts of the elevation gradient. Such specialization is likely tied to the energetic costs associated with inhabiting specific elevations for any given species (Hall et al., 1992). However, we simultaneously observed nested community structuring along the elevation gradients, which suggests that some generalist species occurred along a large range of the elevation gradients. These dual patterns imply that we could possibly face

two consequences of the ongoing global warming in these areas. First, we are likely to lose high-elevation specialists with a warming climate, due to the combined stressors of shifting environmental conditions and increased fragmentation of high-elevation habitats (Dirnböck et al., 2011). As we are already in a potential extinction crisis for arthropods, such losses could have drastic ecological and evolutionary consequences (Goulson, 2019, 2021; Goulson et al., 2015; Hallmann et al., 2017). Second, we are likely to see a dilution in the taxonomic evenness within species communities, where individual taxa or sets of taxa with similar characteristics will become dominant. Such processes have already been observed in arthropod communities worldwide (Sánchez-Bayo & Wyckhuys, 2019) and may further accelerate the ecological consequences of species losses (Hillebrand et al., 2008).

While we observed relatively limited geographic variation in the effect of elevation on taxonomic richness and composition, we did observe substantial differences between spiders and insects in how they varied over elevation gradients in taxonomic richness. Hence, these two taxonomic groups appear to have responded differently to environmental conditions associated with elevation. Taxonomic differences in elevational variation of diversity have been reported previously, for instance, between bacteria and vascular plants (Bryant et al., 2008), and appear to be the norm for both above- and belowground consumers (Sundqvist et al., 2013). While climate has been suggested as a uniform driver of elevational changes at the community level (Peters et al., 2016), we highlight that the observed taxonomic variation still indicates strong effects of taxonomic characteristics in the manner in which each group responds to the environmental variation linked to elevation. The two taxonomic groups in our study inhabit different trophic positions, with spiders being predominantly predatory (Nentwig, 1987) and the insect taxa ranging over several trophic levels (Gullan & Cranston, 2005). In addition, spiders and insects differ dramatically in size and life history strategies, with some insects even inhabiting different biomes and occupying different trophic positions during different life stages (Danks, 1994). We therefore believe that our results highlight how phenotypic characteristics, such as morphology and life history, interact with environmental conditions in shaping the spatial patterns of biodiversity.

We found monotonic declines in spider taxonomic richness with elevation as well as differences in both their taxonomic composition and spatial structuring. Spiders sampled at high elevation were almost exclusively from the family Linyphiidae, which consists of small-bodied species (Hormiga, 1994). Hence, our data indicate that the elevational change in the taxonomic composition of spiders was mainly driven by the disappearance of larger

bodied taxa at higher elevations. Previous studies have made similar observations (e.g., Ameline et al., 2018; Wehner et al., 2023), which also is congruent with larger biogeographic variations in spider body sizes (Entling et al., 2010). Smaller bodied arthropod species need shorter time to reach adulthood, which has been suggested as important at high elevations where the growing season is short and prey availability low (Ameline et al., 2018; Høye & Hammel, 2010). Additionally, vegetation structure may affect the taxonomic composition of the arthropod community (Moran & Southwood, 1982), including spiders in our study region (Måsviken et al., 2023). Thus, we suggest that the observed elevation variation in spider communities may have been the consequence of direct thermal effects associated with physiology and energetic constraints (Kircher, 1987), as well as secondary effects of temperature acting on vegetation structure, which in turn may affect prey diversity and abundance (Måsviken et al., 2023). Such an interpretation is supported by the observed taxonomic distribution of spiders, where we found a larger proportion of actively hunting spiders (e.g., Lycosidae) at lower elevations and conversely mainly passively hunting web-weaving spiders (primarily Linyphiidae) at high elevations. The low primary productivity in high-elevation environments may favor passive hunting modes, since spiders need to rely to a large extent on windblown fallout (Crawford & Edwards, 1989; Swan, 1992). Indeed, the catching of windblown food by spiders has been suggested as an important source of nutrient entrapment in low-productivity ecosystems (Hodkinson et al., 2001), and we therefore propose that spiders may play a key role in maintaining biodiversity in low-productivity/high-elevation environments.

As with spiders, we observed monotonic declines in the taxonomic richness of insects with elevation, as well as differences in both taxonomic composition and spatial structuring. The taxonomic composition also differed between geographic locations, which could be due to site-specific characteristics including habitat structure and regional climate regimes. The insect groups included in this study inhabit several different trophic levels (Barnard, 2011). In addition, several have life stages in different biomes. For such species, the connection between the environments at different life stages can be partly or completely decoupled (Thackeray et al., 2010). This is especially true for insect taxa that spend most of their life in an aquatic environment and have a very short reproductive phase in terrestrial habitats, for example, Ephemeroptera and Plecoptera (Barnard, 2011; Denno & Dingle, 1981). One major difference between insects as compared with spiders is that the vast majority of insect taxa are actively flying as adults. However, despite this characteristic, we still observed distinct elevational variation in insect

communities. Insect declines have been widespread both taxonomically and geographically (Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020), including declines of Diptera in arctic habitats (Loboda et al., 2018) and Lepidoptera in mountains areas (Halsch et al., 2021). Coupled with these observations, our results further highlight that climate change likely will cause strong perturbations to insect communities in areas of high elevation and latitude.

Although we based our study on a substantial field effort and included a comprehensive sampling using a consistent methodology over a large geographic area, we do offer some caveats to our study. First, we have treated all community data as presence–absence data. This has been suggested as a simple and useful measurement of diversity that avoids the often-confusing interpretations of more complex indices (Magurran, 1988). However, we recognize that other biodiversity metrics exist, which also incorporate relative abundance of organisms (reviewed in Magurran, 1988, 2004). However, since no optimal index exists that combines taxonomic richness with relative abundance (Magurran, 2004), we have preferred to maintain this relatively simple metric for ease of interpretation. It is also deeply problematic to estimate relative abundance from genetic metabarcoding (Elbrecht & Leese, 2015), and abundance estimations of invertebrates can also be more sensitive to sampling regimes than estimates of taxonomic richness (Montgomery et al., 2021). Second, we restricted our quantifications to taxonomic diversity. Modern interpretations of the biodiversity concept also include the phenotypic variation among organisms (Petchey & Gaston, 2006) or their joint phylogenetic history (Faith, 1992). Although we regard our taxonomic diversity metric useful, we recognize that adding functional or phylogenetic dimensions may add further insights into the ecological consequences of elevational changes in these arthropod communities and the evolutionary processes that have shaped them. We finally recognize some potential limitations in our sampling design, where particularly temporal fluctuations in local weather conditions may to some extent have influenced the sampling success. While we cannot rule out that weather variation did influence our data, each elevation gradient was sampled simultaneously, which would prevent any major effects on the estimated elevational variation.

To conclude, we observed monotonic declines in the taxonomic richness of both spiders and insects, and the taxonomic composition also varied along the elevation gradients. We also observed both nested and modular spatial structures of community variation along the elevation gradients. However, while we observed geographic differences in the taxonomic composition pooled across

all elevations, our results point to smaller differences among geographic locations than among taxonomic groups in how taxonomic richness and community structuring varied with elevation. We suggest that taxonomically specific adaptations to environmental conditions may be important for structuring spider and insect communities in this high-latitude mountain region. We subsequently suggest that climate change may influence these communities by two not mutually exclusive processes, one in which generalist species shift their ranges upward and become more dominant, and one in which high-elevation specialists may go extinct because of increasingly fragmented habitat patches. However, we urge further studies aimed at providing mechanistic understandings of the factors driving community variation along elevation gradients in northern environments, including studies focusing on functional and phylogenetic dimensions of biodiversity.

AUTHOR CONTRIBUTIONS

Johannes Måsviken and Fredrik Dalerum conceived and designed the study. Johannes Måsviken and Fredrik Dalerum carried out the field sampling. Johannes Måsviken performed the DNA extraction and lab work. Daniel Marquina conducted the bioinformatics and wrote the corresponding parts of the manuscript. Johannes Måsviken and Fredrik Dalerum performed statistical analysis and wrote the manuscript. Love Dalén, Karin Norén, and Daniel Marquina provided feedback on the text. All authors contributed to and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Måsviken et al., 2023) are available from Figshare: <https://doi.org/10.6084/m9.figshare.22491502>.

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SUPPORTING INFORMATION

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

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