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Alpha diversity patterns are unmatched by beta diversity across productivity gradients of the subarctic

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Abstract

The mechanisms linking productivity to patterns of species richness, species prevalence, and beta diversity remain contested and may be scale-dependent. We address productivity–diversity relationships in arthropod communities across two subarctic landscapes. Using the normalized difference vegetation index (NDVI) as a proxy for plant productivity, we targeted three different spatial scales: the local scale (0–10 km), the landscape scale (10–50 km), and the regional scale (>300 km). At each scale, we examined variation in species richness (alpha diversity), in species prevalence patterns, and in spatial turnover (beta diversity) along gradients of productivity. We hypothesized that alpha diversity will increase towards highly productive areas regardless of the scale assessed, and that this increase will be associated with either (a) higher, (b) equal, or (c) lower mean species prevalence towards increasing productivity. We expected to encounter the biggest difference in species turnover between low- and high-productivity sites at the landscape scale, owing to maximized effects of both environmental filtering and dispersal constraints at these two ends of the gradient. We found a positive relationship between alpha diversity and productivity across all scales and arthropod community types. Species-specific prevalence did not differ between the low and high ends of the productivity gradient, and similar proportions of the species pools were shared among sites under both conditions. As a net outcome, the increase in alpha diversity did not translate into higher community dissimilarity at the highly productive sites. Our findings also suggest that while higher productivity can sustain a larger species pool, this is not reflected in higher turnover among sites. Rather, the majority of species are widely represented along the productivity gradient, with a specific subset of species present in high- and low-productive sites. The same patterns prevail across scales and across flying and ground-dwelling arthropods. We conclude that patterns of alpha and beta diversity observed here are consistent with scenario (b) advanced a priori, that is, with equal mean species prevalence across the productivity gradient. A

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fraction of the local species pool is restricted to conditions of either low or high productivity, causing variation in species richness but not in species turnover.

KEYWORDS
community dissimilarity, flying arthropods, ground-dwelling arthropods, mean species prevalence, NDVI, spatial scale, species richness, species turnover

INTRODUCTION

Variation in species richness and community composition has fascinated biologists for long (Darwin, 1859; von Humboldt, 1860; Wallace, 1878). Within a considerable body of literature, many authors have ascribed diversity patterns to differences in energy availability across and within ecosystems (Brown, 1981; Evans et al., 2005; Gaston, 2000; Hutchinson, 1959; Rosenzweig, 1995). Overall, a higher resource base is assumed to sustain more species, but the finer mechanisms are contested (Willig, 2011).

Net primary productivity offers a key proxy for the energetic capacity of an ecosystem, since for heterotrophs, the amount of vegetation locally present usually reflects the rate at which solar energy is converted to energy accessible to organisms at higher trophic levels. Since the mid-1960s, this feature has consistently been used to explain patterns of species richness and diversity (Gillman & Wright, 2006; Leigh, 1965; MacArthur, 1965; Waide et al., 1999). However, ever since proposed, the relationship between productivity and species diversity, and the causal mechanisms behind it, have been subject to heated dispute (e.g., Cusens et al., 2012; Gillman & Wright, 2006; Mittelbach et al., 2001; Waide et al., 1999).

Empirical studies at local, regional, and global scales have revealed mostly positive relationships between species richness (alpha diversity) and productivity. Focusing on plants, Gillman and Wright (2006) found a dominance of positive relationships between productivity and species richness regardless of the scale assessed. In a meta-analysis focused on animals, Cusens et al. (2012) found 72% of relationships between species richness and productivity to be positive across both terrestrial and freshwater ecosystems. However, some studies have reported unimodal and negative relationships, suggesting a scale dependence of mechanisms (Bonn et al., 2004; Chase & Leibold, 2002; Fraser et al., 2015; Gardezi & Gonzalez, 2008; Grace et al., 2016).

To explain how local species (alpha) diversity changes along productivity gradients, the theory of ecological gradients provides a useful framework for understanding how communities assemble across varying environments (Whittaker, 1956, 1967). This theory brings out that changes in species prevalence—the average number of sites occupied by a species—offer insights into the mechanisms underlying richness patterns. Mean prevalence may increase if higher productivity sustains not only a greater number of species but also larger populations, leading to more frequent occurrence of species across sites (Figure 1a). In contrast, prevalence may remain relatively unchanged if resource availability scales proportionally from low to high productivity, with species maintaining similar levels of occurrence across sites despite differences in richness (Figure 1b). Finally, prevalence may decrease if the additional species found at the high end of the gradient are primarily rare taxa. In that case, greater environmental heterogeneity in productive areas may be fostering specialization, in which case many species are observed at only a few sites and site-specific community composition will become more spatially heterogeneous (Figure 1c). Each of these scenarios highlights how ecological gradients can shape diversity not only by influencing how many species are present but also by determining how widely they are distributed across the landscape (Figure 1).

Interestingly, while all of the three proposed scenarios will result in a higher count of species in more productive areas, they will translate into different patterns of beta diversity, that is, different rates of species turnover between communities at either low- or high-productive areas. Some authors have anticipated a positive relationship between beta diversity and primary productivity, as increased primary productivity will typically imply a broader range of habitat heterogeneity to which diverse species can adapt (Chase & Leibold, 2003; Leibold et al., 2004). This should result in increased variation in species composition among localities characterized by higher productivity and, therefore, increased beta diversity among those locations. However, despite the intuitive appeal of this explanation, its empirical support remains inconclusive (Heino et al., 2015). In an effort to shed some light on the matter, Bora et al. (2019) reviewed the effects of primary productivity on differences in species composition between localities, but found no clear directional patterns.

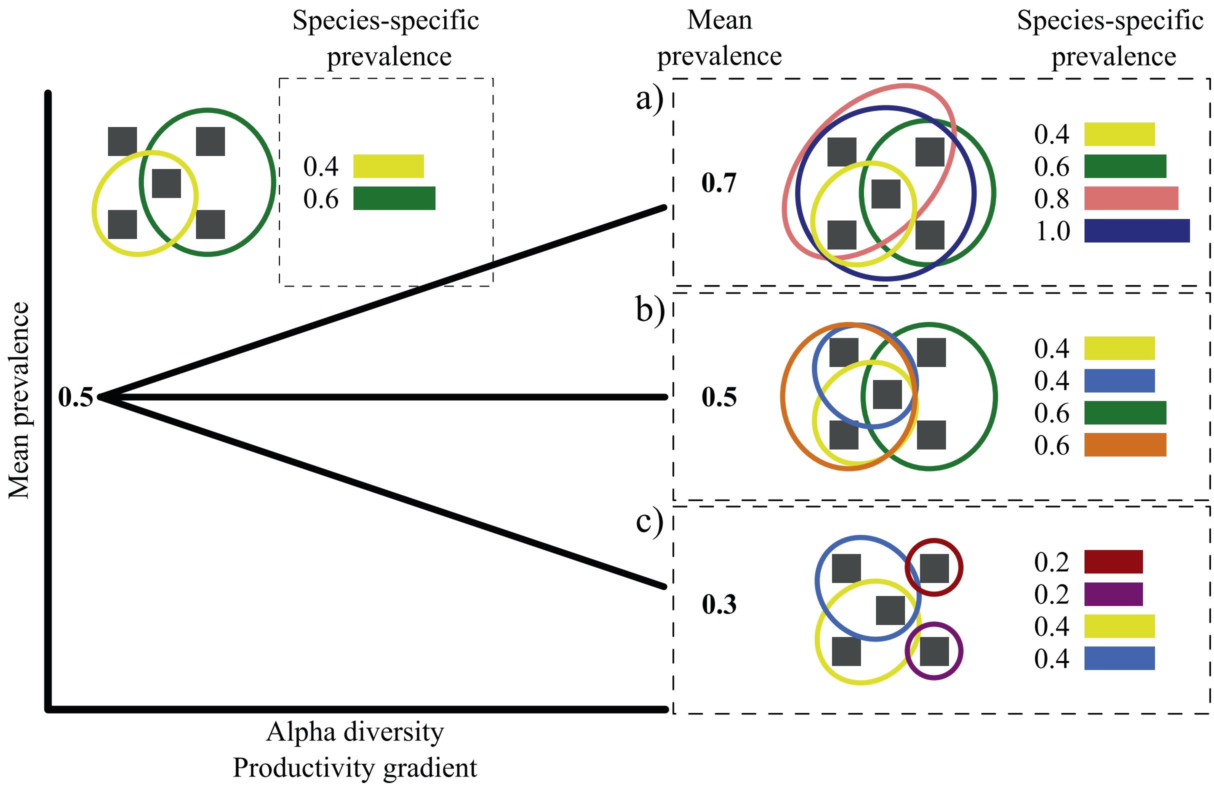

FIGURE 1 Schematic representation of hypothetical changes in mean species prevalence as species richness increases with increasing productivity. The left-hand side of the graph shows imaginary species prevalence at low productivity and low species richness ($n = 2$). Each square represents a sampling site and each colored oval represents the distribution of an individual species. The right-hand side of the graph shows three plausible scenarios for shifts in mean species prevalence with increasing alpha diversity (to $n = 4$) at the high-productive areas. These scenarios correspond to: (a) an increase in mean species prevalence (higher overlap between species distributions), (b) no shift in mean species prevalence (similar values at both low- and high-productive areas, pointing towards a proportional increase of diversity and resources), or (c) a decrease in mean species prevalence (due to a higher specialization of species). The mean species prevalence corresponding to each scenario is shown by the end point of its line (column "Mean prevalence"), with new species added in accordance with the respective scenario (see species ranges and species-specific prevalence values across sampling sites in the right-most part of the figure, compared to those in the left-hand side of the figure).

What further complicates the relationship between productivity and alpha- and beta diversity is the fact that both the patterns and the underlying processes may be scale-dependent. Ultimately, differences between localities within any spatial scale will depend on both environmental variation and the effect of species sorting—that is, on the extent to which the distribution of individuals within a species will reflect the suitability of the habitat, and thus the niche of the species (Leibold et al., 2004; Soininen, 2014). The latter aspect will critically depend on species' abilities to disperse to the habitats of highest quality. To resolve such scale dependence, Heino et al. (2015) probed for positive relationships between beta diversity and environmental heterogeneity in aquatic invertebrates across different scales, ranging from local streams, through drainage basins to ecoregions. Their findings suggest that the effects of environmental filtering may be masked at small scales due to high dispersal rates (mass effects), where local communities are dominated by an inflow of individuals from nearby habitats. At larger scales, the relation between beta diversity and environmental heterogeneity may be masked by low dispersal rates, as not all species may reach every site. Consequently, the relationship between beta diversity and environmental heterogeneity should be most pronounced at intermediate scales, where dispersal rates among localities are neither too high nor too limiting to allow efficient species sorting (for explicit a priori expectations, see Figure 2).

Given the number of factors with a potential impact on the productivity–biodiversity relationship, it is evident that their relative effect can only be understood by exploring specific community assembly mechanisms operating at local scales, and by assessing how these translate to larger scales. Here, arthropods in the subarctic realm offer an ideal study system. Their ectothermic life style (Danks, 2007; Strathdee & Bale, 1998) renders

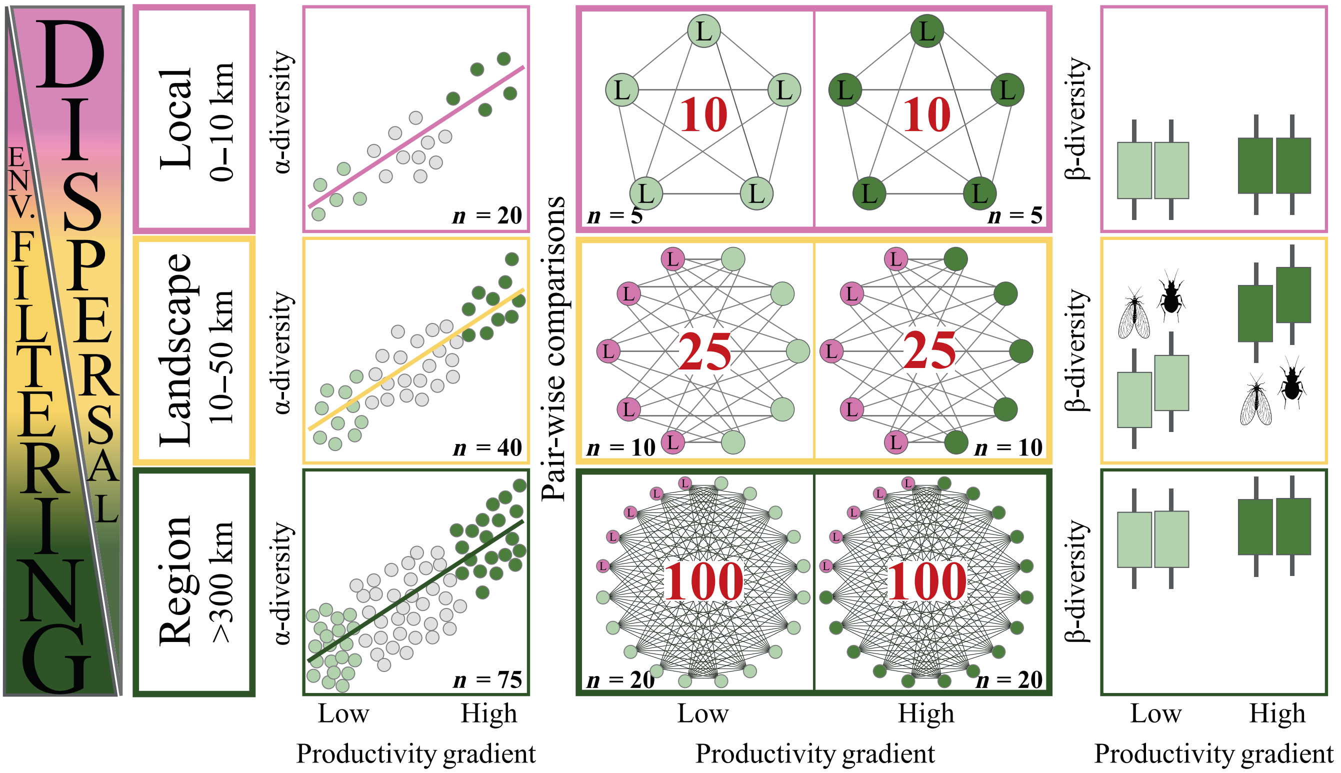

FIGURE 2 Schematic representation of hypothetical patterns in alpha and beta diversity patterns, and their resolution through the pair-wise comparisons implemented in this study. The two gradients on the left represent the expected imprints of dispersal versus environmental filtering on community assembly across scales (with dispersal increasing upwards and environmental filtering increasing downwards). The graphs on the left show the expected relationship between alpha diversity and the productivity gradient at each scale, with the number of sampling sites identified as *n*. The middle part of the illustration outlines pair-wise comparisons of community dissimilarity at each end of the productivity gradient. Here, red numbers in the middle of each graph identify the number of pair-wise comparisons made at each scale, while *n* represents the number of sampling sites characterized as either "low" or "high" productivity. Note that for comparisons at the landscape and regional scales, one-half and one-quarter of the sampling sites (identified in pink and by the letter "L"), respectively, were also included in comparisons at the local scale. Across the illustration, light green and dark green circles represent low- and high-productivity sites, respectively. Gray circles represent sampling sites at the middle of the productivity gradient, which were omitted for analyses of beta diversity. The graphs on the right denote the relationships expected a priori between beta diversity and productivity across scales. At the local scale (in pink), minimal species turnover is expected due to mass effects, resulting in no discernible differences between communities at low- or high-productivity sites. At the regional scale (in green), species turnover is expected to be maximal, owing to low dispersal rates among communities. Nonetheless, at the regional scale, we expect no difference in species turnover between low- and high-productivity sites, since the scale of environmental variation will exceed the scale of dispersal, and thus prevent efficient sampling of the environment by the species. At the landscape level (in yellow), we expect significant impacts of both environmental filtering and dispersal rates, resulting in differences in species similarity between low- and high-productivity sites. Due to variation in dispersal capacity, we expect more pronounced differences between low- and high-productive areas for ground-dwelling than flying insect communities at the landscape scale, as due to the limited dispersal ability of the former.

them sensitive to variation in local climates, whereas interspecific variation in dispersal capacities creates variation in the expected imprints of dispersal on local community composition (Danks, 2007; Strathdee & Bale, 1998). Given the inherently low energy availability within the subarctic environment, the imprints of both dispersal capacity and environmental filtering should be particularly accentuated in this region (Høye & Sikes, 2013).

In this study, we aimed to unravel how alpha and beta diversity patterns vary with productivity, whether and how they reflect changes in mean species prevalence, and to what extent these patterns are scale-dependent. To this aim, we explored patterns in terrestrial arthropod communities across gradients of productivity at increasing spatial scales in subarctic landscapes. To characterize local productivity, we used the normalized difference vegetation index (NDVI), as reflecting the level of locally available energy funneled into terrestrial food chains through uptake by primary producers. To explore the scale dependence of patterns, we adopted the approach of

Heino et al. (2015), defining three geographical scales: the local, landscape, and regional scale. To further evaluate the influence of dispersal capacity on community similarity between sites, we compared two arthropod groups with differing mobility: ground-dwelling and flying arthropods, of which the latter will likely show stronger dispersal.

We asked the following questions: (1) Does alpha diversity (i.e., local species richness) increase with productivity and (2) if so, which of the scenarios outlined in Figure 1 does the pattern support—that is, how does mean prevalence change along the productivity gradient? (3) Does beta diversity (i.e., species turnover) increase with productivity, and is this change more pronounced at the landscape scale? (4) Does the relationship between alpha and beta diversity versus productivity vary with the spatial scale assessed? (5) Does the dispersal capacity of organisms produce different patterns of alpha and beta diversity across productivity gradients and across scales?

Given the general energy limitation of the target system, we a priori anticipated higher species richness in highly productive areas, regardless of the scale (local, landscape, or regional) or the type of organisms under study (flying or ground-dwelling arthropods). Following Heino et al. (2015), we expected to find the most pronounced impacts of both environmental filtering and dispersal rates at intermediate scales—in other words, that a positive correlation between beta diversity and productivity would be clearest at the landscape level. At the local and regional scales, we expected a dampening of this association, as due to either mass effects (at a local scale) or limited sampling of the environment through dispersal limitation (at the regional scale). Based on variation in the dispersal capacities of the target taxa, we anticipate more pronounced differences between low- and high-productive areas for ground-dwelling than for flying insect communities at the landscape scale, due to the limited dispersal ability of the former.

MATERIALS AND METHODS

Study regions

As representative regions of the subarctic realm, we selected 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). The study area in the Varanger Peninsula (henceforth referred to as "Varanger") lies at the southern edge of the low-arctic tundra (Ims et al., 2013), whereas the Kilpisjärvi study area (referred to as "Kilpisjärvi") is located within the subarctic region. Both regions feature similar topographically diverse landscapes, marked by steep slopes of mountain massifs and various topographic elements such as hilltops, ridges, and small depressions. These features create broad environmental gradients and spatial variations in local climate, moisture run-off, and snow deposition over short distances (Ims et al., 2013; Kemppinen et al., 2018). In both areas, mountain birch (*Betula pubescens*) forest dominates from the lowest elevations to the tree line (~700 m above sea level [asl] at Kilpisjärvi and 250 m asl at Varanger). Beyond the tree line, mountain heaths prevail, featuring dwarf shrubs like *Empetrum nigrum*, *Betula nana*, *Juniperus communis*, and *Vaccinium* spp. as the most common plant species.

Climatic conditions are generally similar in the two study areas. Both Kilpisjärvi and Varanger rank among the most "arctic" locations in Fennoscandia, with a growing season of 100 days or less (Tuhkanen, 1980). The climate in Kilpisjärvi is influenced by its high-latitude position in the Scandinavian Mountains and its proximity to the Arctic Ocean (Aalto & Luoto, 2014) with a mean annual temperature of −1.3°C, and mean annual precipitation of 508 mm (1990–2021; Kyläkeskus meteorological station: 69°04′ N, 20°80′ E; 480 m asl; Finnish Meteorological Institute). The average annual temperature in the Varanger Peninsula is relatively similar, with some variation between coastal and inland areas. Coastal areas are characterized by temperatures above zero (0–2°C), while inland highland areas, rising to 600 m asl, have temperatures below zero (−3 to 0°C), maintaining widespread permafrost (Farbrot et al., 2013). Annual precipitation is highest in the coastal areas facing the Barents Sea and in the central highlands, reaching around 623 mm (1990–2021; Vardø meteorological station: 70°37′ N, 31°09′ W; 10 m asl; Norwegian Meteorological Institute).

Selection of sampling sites

To establish links between variation in productivity and in arthropod community characteristics, we implemented a stratified random sampling design within each study area. We selected a total of 35 and 40 sampling sites for Kilpisjärvi and Varanger, respectively. All sampling sites were located at least 100 m apart, covering a range of environmental conditions in terms of topography, vegetation, snow depth, and distance to water bodies. At each sampling site, we characterized net productivity and surveyed both flying and ground-dwelling arthropod communities.

Characterization of productivity

To assess local plant productivity, we used the NDVI. With values ranging from −1 to 1, NDVI distinguishes the reflectance properties of vegetation. As such, the metric is strongly linked to factors like photosynthetic capacity, net primary production, leaf area index (LAI), carbon assimilation, and evapotranspiration (Buermann et al., 2002; Hicke et al., 2002; Myneni et al., 1995; Wang et al., 2005). Positive values indicate areas with living green vegetation, while negative values represent water bodies, snow, clouds, and non-vegetated surfaces (Holben, 1986; Vermote et al., 2014). Overall, we used this measure as a proxy of local energy availability and the amount of energy funneled into local food chains by primary producers.

NDVI values were computed using the red (RED, 627–703 nm) and near-infrared (NIR, 697–987 nm) spectral bands with the formula:

$$\mathrm{NDVI} = \frac{(\mathrm{NIR} - \mathrm{RED})}{(\mathrm{NIR} + \mathrm{RED})}. \tag{1}$$

This spectral information was derived from atmospherically corrected Level-2A satellite imagery from the European Space Agency Copernicus Open Access Hub (https://www.copernicus.eu/en/access-data). The Copernicus Sentinel-2 satellite constellation provides data at high spatiotemporal resolution (10 m × 10 m every 3–5 days), enabling precise monitoring of vegetation productivity.

To enhance the reliability of our NDVI estimates, we collected all available satellite images ($n = 13$ and $n = 11$ for Kilpisjärvi and Varanger, respectively) between 2017 and 2023 for July and August, coinciding with the vegetation peak. We specifically chose images with less than 10% cloud cover and visually confirmed the absence of clouds in the sampling region. For each sampling site, we calculated an NDVI value by averaging the NDVI values of the pixels within a 150-m radius in each picture. Finally, to determine the overall productivity for each sampling site, we calculated the average NDVI using all available images. These analyses were performed in QGIS Desktop 3.34.7 version.

Community characterization

To characterize the local arthropod community at each sampling site, we employed a Malaise trap (manufactured by Terrapolar, Kauhajoki, Finland) to collect flying arthropods and two pitfall traps to collect ground-dwelling arthropods. The pitfall traps were placed approximately 1 m on each side of the Malaise trap. Sampling spanned 2 years (2020 and 2021) and encompassed the entire plant growing season from early June to early September each year. Malaise and pitfall traps were deployed at each sampling site as soon as snow had melted and the soil surface was exposed. The collecting bottle was exchanged every week, resulting in a yearly average of 12- and 10-week-long arthropod samples at Kilpisjärvi and Varanger, respectively.

Malaise trap collector bottles were filled with 96% ethanol to euthanize and preserve the arthropods captured. Pitfall traps, measuring 10 cm in diameter, contained water mixed with a small amount of odorant- and color-free detergent to break the surface tension. After securing the samples, they were stored in Falcon tubes filled with 96% ethanol at −18°C until DNA extractions. In total, 796 Malaise and 743 pitfall trap samples were collected in 2020, and 861 Malaise and 852 pitfall trap samples were collected in 2021.

Arthropods were identified through DNA metabarcoding, using the CO1 region. As a basis for our analyses, we considered only zero-radius operational taxonomic units (ZOTUs) taxonomically assigned to arthropod species using the CO1 region reference database—which is particularly comprehensive for this region (Roslin et al., 2022). As species proxies, we used Barcode Index Numbers (BINs; Ratnasingham & Hebert, 2013). These operational taxonomic units have been shown to closely align with morphologically identified species, particularly among arthropods (Ratnasingham & Hebert, 2013). Laboratory workflows, bioinformatics, and taxonomic assignment procedures are detailed in Peña-Aguilera et al. (2023). 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.

Defining scales

To address patterns at different spatial scales, we defined three nested geographical scales (Figure 2). The “local” scale (0–10 km) comprised 20 sampling sites within a 14-km^2 area on the west and east sides of the Juladalen valley (Austertana, Varanger Peninsula; see Appendix S1: Figure S1). This scale corresponds to the spatial range at which dispersal effects are likely to be accentuated, as it roughly matches the seasonal dispersal capacity of arthropods. The “landscape” scale (10–50 km) included 40 sampling sites distributed across the north-western Varanger Peninsula, covering an area of approximately 425 km^2. At this scale, both dispersal and environmental filtering are expected to contribute to variations in species composition. Finally, the regional scale (>300 km) encompassed all 75 sampling sites across both Kilpisjärvi (Finland) and Varanger (Norway), situated about 350 km apart. This broadest scale is associated with low dispersal per generation, and spatial effects are therefore expected to diminish.

Statistical analysis

All statistical analyses were performed in R version 4.2.1. Since the analyses concerned a number of different responses and a series of different scales, we have compiled the definition of each term in Table 1 for quick reference.

Analyzing alpha diversity along the productivity gradient

Alpha diversity was computed by summing the number of species identified at each sampling site, separately for Malaise and pitfall data, for the years 2020 and 2021. To examine how alpha diversity varies with productivity and community type, we fitted two generalized linear mixed models by maximum likelihood techniques implemented with the package "glmmTMB" (Brooks et al., 2022). For both models, we assumed a negative binomial distribution for the response variable (Appendix S1: Table S1). Both models included productivity (NDVI) and community type (flying or ground-dwelling arthropods) as continuous and categorical fixed effects, respectively. Sampling site was included as a random effect, to adjust for the fact that two different community types were sampled at each site. By modeling site-to-site variation as a random intercept, we assumed that a site rich in flying species was also rich in ground-dwelling species—a pattern supported by empirical data (see Figure 3). To assess whether the effect of productivity on alpha diversity differs among different community types, we included an interaction term between productivity and community type in the second model, while the first model maintained separate effects for productivity and community type. Our primary focus was on the interaction term,

TABLE 1 Terms and definitions used in this paper.

Term	Definition
Study area	Either of the mountain tundra landscapes of Kilpisjärvi and Varanger.
Sampling site	Randomly stratified locations within Kilpisjärvi ($n = 35$) and Varanger ($n = 40$), where net productivity was characterized and arthropod communities were surveyed.
Spatial scale	Size of the area that includes a specific set of sampling sites across one or both of the study areas. It can be categorized as local ($n = 20$ sites), landscape (n = 40), or regional ($n = 75$), depending on the spatial extent covered.
Productivity gradient	Variation in NDVI values, representing net productivity, across all sampling sites at a specific scale.
Low-productivity sites	Sampling sites characterized by low values of NDVI at a specific scale. Specifically, these sites are situated below the 25th percentile threshold in terms of NDVI values.
High-productivity sites	Sampling sites characterized by high values of NDVI at a particular scale. Specifically, these sites are located above the 75th percentile threshold in terms of NDVI values.
Community type	Either flying arthropods sampled by Malaise traps or ground-dwelling arthropods sampled by pitfall traps.
Alpha diversity	Overall species richness present within a specific sampling site. In this study, we differentiate between flying and ground-dwelling richness.
Common species	*Common* species are those found consistently across the entire productivity gradient, occurring at both low- and high-productivity sites.
Specialist species	*Specialist* species are those exclusively found at one end of the productivity gradient, meaning that they occur solely at either low- or high-productivity sites.
Beta diversity	Measurements of community dissimilarity using pairwise comparisons of sites with similar productivity (either low vs. low or high vs. high). In this study, we estimated Jaccard community dissimilarity (hereafter total beta diversity) and its turnover (reflecting species replacement across sites) and nestedness (accounting for richness differences between nested sites) components.
Shared species	*Shared* species refers to the no. species that are shared between any pair of sampling sites situated within the same productivity gradient category, either low or high.
Unique species	*Unique* species refers to the no. species found exclusively at a particular sampling site, not present at any other sampling site within the same productivity gradient category.

Abbreviation: NDVI, normalized difference vegetation index.

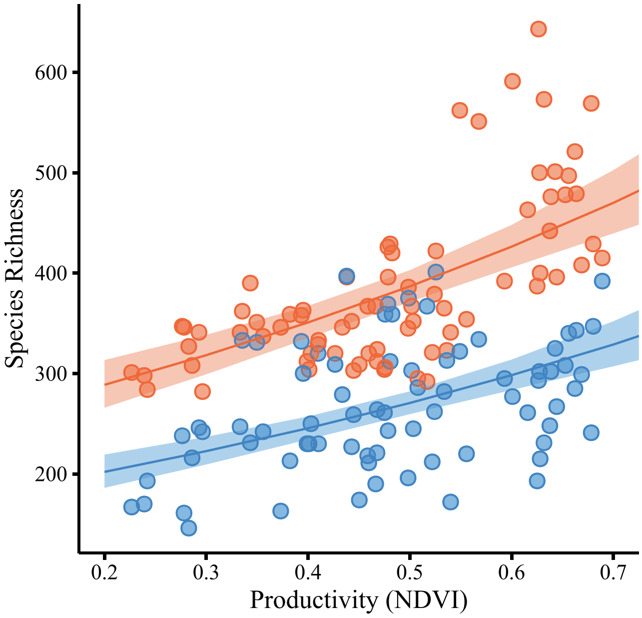

FIGURE 3 Relationship between species richness and productivity (measured by normalized difference vegetation index [NDVI]) for flying arthropods (orange) and ground-dwelling arthropods (blue). Each point represents a sampling site and the lines show the linear regression fit for each group, with shaded areas indicating the 95% CIs (model details in Table 2). Alpha diversity increased along the productivity gradient for each community type, with flying arthropods showing a steeper increase in species richness compared to ground-dwelling arthropods.

which indicates whether the slope of alpha diversity varies with community type along the productivity gradient. Thus, we compared the log-likelihood of the model with and without the interaction term using the *anova* function from the package "stats." As this test deemed the interaction term nonsignificant (Appendix S1: Table S1), subsequent results were based on the model without the interaction. Model fit and adherence to standard assumptions for all models performed were verified using the "DHARMa" package (Hartig, 2018). These involved visually inspecting residuals through quantile–quantile plots to detect overall deviations from the expected distribution, alongside tests for correct distribution (KS test), dispersion, and outliers. The models showed overall satisfactory performance. Additional details on model fitting can be found in Appendix S1: Figure S2, along with a test of the consistency of patterns across scales (Appendix S1: Table S2).

Relating species prevalence to alpha diversity

To understand how patterns of alpha diversity emerge along productivity gradients, we focused on species prevalence—that is, the proportion of sampling sites where each species occurs. We then summarized these patterns by calculating the mean species prevalence across sites, separately for each combination of productivity level (low or high), community type (flying or ground-dwelling arthropods), and spatial scale (local, landscape, or regional). Comparing mean species prevalence between productivity levels allows us to evaluate which of the three hypothetical scenarios (Figure 1) best reflects the observed biological data. A higher mean prevalence in more productive areas suggests greater overlap in species distributions, consistent with larger population sizes or broader environmental tolerances (Figure 1a). In contrast, if mean prevalence remains similar across the gradient, this implies that most species maintain comparable prevalences regardless of productivity, consistent with a proportional increase in resource availability across sites (Figure 1b). Finally, a lower mean prevalence under high productivity indicates that richness gains are driven mainly by rare or specialized species occurring in only a few sites (Figure 1c). Together, these scenarios provide a framework for interpreting how productivity shapes species richness while also influencing the degree of spatial turnover in community composition, thereby linking alpha and beta diversity patterns.

Given the non-normal distribution of the data, we employed Wilcoxon signed-rank tests to examine differences in mean species prevalence between low- and high-productivity sites (Appendix S1: Table S4). These analyses were conducted independently for each scale and community type, employing the *wilcox_test* function from the package "rstatix" (Kassambara, 2020).

To further dissect patterns of species occurrences along productivity gradients, we differentiated between the contributions of *common* versus *specialist* species and explored their respective occurrence (Table 1). *Common* species are those consistently found at both low- and high-productivity sites. *Specialist* species are those exclusively found at one end of the productivity gradient, implying that they occur solely at either low- or high-productivity sites. This differentiation is important because *common* species constitute the basal set of species occurring across the entire productivity gradient and therefore do not contribute to increased species richness at higher productivity sites. In contrast, *specialist* species directly influence the overall species count at both ends of the gradient and may also contribute to differential patterns of species turnover across sampling sites. For *common* species, we compared occurrence patterns along the NDVI range by correlating their prevalence (percentage of occupied sampling sites) at the low and the high end of the gradient. Here, a high correlation would signal similar prevalence at both ends, whereas a low correlation would imply that the species occurrence is centered at one end of the productivity gradient.

Comparing beta diversity between the two ends of the productivity gradient

To examine how productivity influences beta diversity patterns across scales, we focused on comparisons between communities at both extremes of the productivity gradient. In other words, we compared how community dissimilarity differs between sets of sampling sites in either low- or high-productivity areas. This focus on the two ends of the spectrum is motivated by a simple consideration: since analyses of beta diversity are based on pairwise indices, a given difference in productivity can be associated with several different scenarios. Note that a comparison of low versus low productivity and high versus high productivity will both be associated with a low difference in productivity, but represent entirely different ecological settings. For clarity alone, we thus discretized the gradient and targeted selected comparisons only.

As a basis for these analyses, we categorized all sampling sites based on their overall NDVI values. To distinguish the two ends of the productivity gradient, we calculated the 25th and 75th percentiles using the entire set of NDVI values corresponding to each scale (i.e., local, landscape, and region). Subsequently, we designated any sampling site below the 25th percentile threshold as a "low-productivity site" and any site above the 75th percentile threshold as a "high-productivity site" (Table 1). Sampling sites falling between the 25th and 75th percentiles were excluded from these specific analyses, as these may cloud any causal inference (see above).

To ensure the comparability of results between sets of low- and high-productivity sampling sites, we used an equal number of sites at each end of the productivity gradient. Given the hierarchical design of scales in our study, the local scale involves sampling sites also included at both landscape and regional scales (Figure 2). Thus, at the landscape scale, we ensured equal representation of sites of low versus high productivity by drawing sites from across the local scale and the rest of the Varanger Peninsula, thus covering the full geographical region. Similarly, at the regional scale, we drew half of the sites representing both low and high productivity from Kilpisjärvi and the other half from Varanger, thereby achieving the intended coverage of geographical distances. The local, landscape, and regional scales were thus represented by 5, 10, and 20 sampling sites, respectively, at either end of the productivity spectrum (Table 1, Figure 2).

To characterize arthropod community dissimilarity across low- and high-productivity sites at local, landscape, and regional scales, we followed the approach proposed by Baselga (2010). Hence, we estimated Jaccard community dissimilarity (hereafter total beta diversity) and its turnover (i.e., species replacement) and nestedness–resultant dissimilarity (defined as the dissimilarity not explained by species turnover, that is, difference in species richness) components. These calculations were done separately for each community type, scale, and productivity category. We excluded self-pairs and included each pairwise comparison only once (since a vs. b equals b vs. a). As previously mentioned, pairwise comparisons included at the local scale were omitted from analyses at the landscape and regional scales, to thereby distil the effect of increasing geographical distances. All calculations were implemented using the package "betapart" (Baselga & Orme, 2012).

To assess the combined effects of productivity and spatial scale on community dissimilarity, we modeled each community beta diversity component separately. Thus, each component of beta diversity was modeled as a separate function of productivity category (low or high), scale (local, landscape, or regional), and their interaction. Since the same sampling site recurred across different scales, the identities of both members of pairwise comparisons were included as random effects. In fitting the models, we note that metrics of beta can be very close to zero and to one. As a robust solution, we assumed a beta distribution in our analyses, which implicitly applies a logit transformation to the response variable. This kind of distribution is more appropriate for variables ranging from zero to one, with variance increasing towards intermediate values. To validate model fit, we conducted the same diagnostic procedures as outlined for alpha diversity models (see above). For each beta diversity component of each community type, we assessed differences between low- and high-productivity sites across scales using estimated marginal means with Tukey adjustment (Appendix S1: Table S3). These post hoc pairwise comparisons were calculated using the *emmeans* function of package "emmeans" (Lenth et al., 2018).

Relating species prevalence to beta diversity

To expose how beta diversity patterns arise from patterns in species prevalence, we explored which species contribute to turnover (species replacement) as the keystone of community dissimilarity. In our study, *unique* species are those found exclusively at a particular sampling site within a productivity category (Table 1). *Shared* species are those species occurring in multiple sampling sites within the same productivity category (Table 1). Our reasoning will be evident from the following considerations:

Based on the approach of Baselga (2012), the species turnover component of Jaccard dissimilarity is calculated as:

$$\beta jtu = \frac{2\min(b,c)}{a + 2\min(b,c)}, \quad (2)$$

where b and c represent the number of species *unique* to sites 1 and 2, respectively, and a represents the number of species *shared* between sites 1 and 2. From this equation, it becomes evident that dissimilarity due to species turnover increases as the number of *shared* species (a) between two sampling sites decreases. Eventually, in the absence of nestedness, the number of *shared* species will be zero. As we anticipated community dissimilarity to be highest between low- and high-productivity sites at the landscape level (Figures 1 and 2), these differences should manifest themselves in the ratios between *unique* and *shared* species. More specifically, those differences should be reflected in disparities in the ratios of species being replaced between each pair (numerator: $2\min(b,c)$) and the number of species that could potentially be replaced (denominator: $a + 2\min(b,c)$). Therefore, to resolve the basis of dissimilarity patterns at the two extremes of the productivity gradient, we explored the variation in and proportion of *unique* versus *shared* species across sets of sampling sites and for each scale. Finally, to visualize patterns of species turnover under different conditions and scales, we constructed chord diagrams of *unique* and *shared* species across sampling sites at the two extremes of productivity, for each taxon and scale separately.

RESULTS

Alpha diversity increases across productivity gradients

Overall, the community of flying arthropods was more diverse than the ground-dwelling community. In general, the species richness of both flying and ground-dwelling arthropods increased with productivity (Table 2, Figure 3). Sampling sites characterized by high productivity exhibited a greater species diversity compared to low-productivity sites, irrespective of community type or assessment scale.

The alpha diversity gradient is driven by more species *specialized* in high-productivity sites

At none of the scales evaluated did mean species prevalence within either community type differ between low- and high-productivity sites (Figure 4; Wilcoxon signed-rank tests >0.05; Appendix S1: Table S4). Interestingly, when dissecting the contribution of *common* versus *specialist* species across the productivity gradient, an average of over 40% of the entire species pool

TABLE 2 Generalized linear mixed model of alpha diversity as a function of productivity (normalized difference vegetation index [NDVI]) and community type (flying and ground-dwelling arthropods) as fixed effects.

Effect	Estimate	SE	CI	*z*	*p*
Fixed effects					
Intercept	237.56	15.47	209.09–269.91	83.98	**<0.001**
NDVI	2.65	0.34	2.07–3.40	7.68	**<0.001**
Comm. type (ground-dwelling)	0.70	0.02	0.66–0.74	−12.82	**<0.001**
Random effects					
σ^2	0.03				
$\tau 00_{\text{Sampling Site}}$	0.00				
ICC	0.13				
$N_{\text{Sampling Site}}$	75				
Observations	150				
Marginal R^2/Conditional R^2	0.6 / 0.65				

Note: To control for the fact that multiple community types were characterized at the same sampling sites, we included sampling site as a random effect. Model performance is summarized by marginal and conditional R^2 values, reflecting the explanatory power of fixed effects alone and that of fixed and random effects together, respectively. Bold p-values indicate statistically significant effects ($p < 0.05$).

Abbreviations: Comm. type, community type; ICC, intraclass correlation coefficient; N, sampling size; NDVI, normalized difference vegetation index.

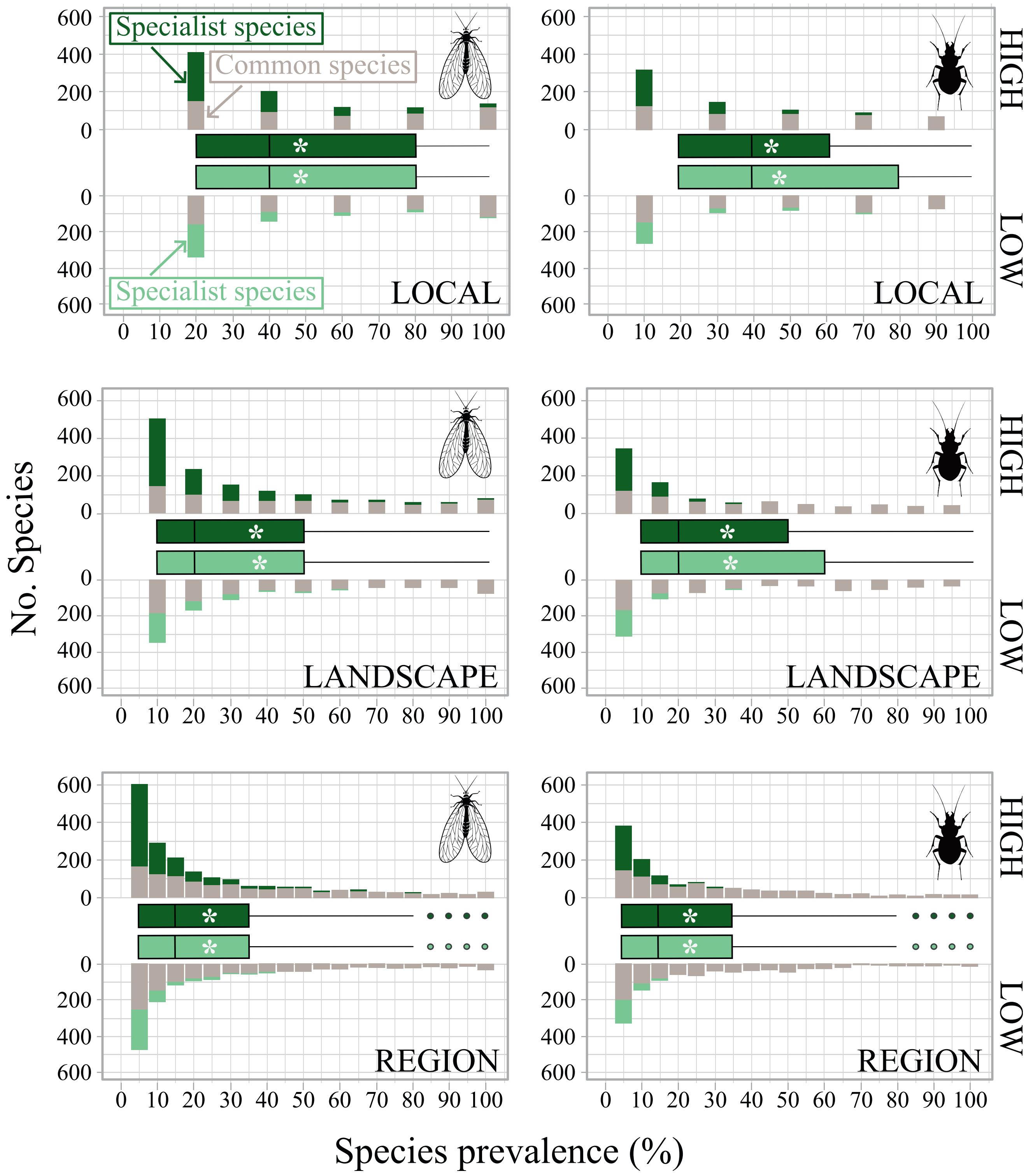

FIGURE 4 Species prevalence (%) of flying and ground-dwelling arthropods at low- and high-productivity sites across scales (local, landscape, and region). The community type is indicated by a silhouette in the upper-right corner of each panel (flying vs. ground-dwelling). Each panel contains two horizontal boxplots summarizing the distribution of prevalence values across all species at low- (light green) and high- (dark green) productivity sites. In each boxplot, the central line represents the median prevalence, box limits correspond to the first and third quartiles (interquartile range), whiskers extend to 1.5× the interquartile range, and individual points denote species with prevalence values outside this range. Within each box, mean values are shown with an asterisk. Above and below each boxplot, bar plots illustrate the proportion in numbers of *common* (gray colored) and *specialist* species of high- and low-productivity sites (dark and light green colored, respectively). Insect silhouettes credit: P. Peña-Aguilera.

was found at both ends of the productivity gradient (Appendix S1: Table S5). Thus, at both ends of the gradient, species pools were dominated by *common* rather than *specialist* species. This pattern was more pronounced in ground-dwelling communities compared to flying communities and more evident in low-productivity sites than in high-productivity sites (Figure 4).

For species occurrences, we found similar patterns. Both *common* and *specialist* species were dominated by singleton species, that is, species found at a single sampling site. This dominance was stronger at high-productivity sites and constant across community types and scales. The number of species scored at more than one sampling site notably decreased with increasing numbers of sites sampled, especially for *specialist* species (Figure 4).

When examining the prevalence patterns of *common* species across the productivity gradients, we found generally moderate-to-high correlations between the low and high ends of each gradient. These correlations were particularly strong for ground-dwelling arthropods and increased in general with spatial scale, suggesting similar prevalence at both ends of the gradient (Appendix S1: Figure S3). Consequently, the higher occurrence of *specialist* species at high-productivity sites along with an even prevalence of *common* species across the productivity gradient explained the differences in overall species richness between low- and high- productivity sites.

Beta diversity is similar at both ends of the productivity gradient

At both ends of the productivity gradient, communities of flying and ground-dwelling arthropods showed greater total dissimilarity and turnover with increasing scale (Figure 5). Moreover, total dissimilarity and species turnover was slightly higher for ground-dwelling communities than for flying communities. Notably, overall community dissimilarity did not increase significantly with productivity across any of the scales or community types considered (Figure 5; Appendix S1: Table S3). For ground-dwelling communities, we found a slight difference in the relative contribution of different beta diversity components across scales, with high-productive sites showing higher species replacement and lower nestedness (Figure 5).

In general, post hoc comparisons of marginal means of beta diversity components confirmed the lack of significant differences between low- and high-productivity sites across scales (Appendix S1: Table S3). Only for the nestedness component of flying arthropods at the local and region scales, and for the turnover component of ground-dwelling arthropods at the local scale, did we find significant differences in the marginal means between low- and high-productivity sites ($p < 0.05$)—as still coupled to substantial overlap in distributions between the groups (Figure 6; Appendix S1: Table S3).

Similar increases in *shared* versus *unique* species maintain constant beta diversity

Communities of flying and ground-dwelling arthropods at each extreme of the productivity gradient showed similar patterns in terms of *unique* versus *shared* species. Within each productivity category (either low or high), there were noticeable differences in the mean number of species shared between sampling sites. On average, high-productivity sites shared more species than low-productivity sites, and the number of *shared* species decreased linearly with increasing scales (Figure 7). However, the numbers of *unique* species, which reached its peak at highly productive local sites, also matched those of *shared* species. Consequently, at any given scale, the average ratio of *unique*-to-*shared* species remained comparable between low- and high-productivity sites (see ratios in Figure 7).

DISCUSSION

The relationships between productivity and community patterns have been the topic of much debate. Our study provides empirical evidence for how arthropod communities are organized across gradients of productivity at multiple scales. Across all scales examined, alpha diversity increased with productivity, whereas patterns of beta diversity showed little relationship with productivity. These patterns were repeated across communities of flying and ground-dwelling arthropods. When resolved at the species level, the biodiversity patterns were consistent with the scenario of no changes in species mean prevalence across the productivity gradient (scenario b in Figure 1), and suggest more complex processes of community assembly. Below, we will discuss each finding in turn.

Arthropod alpha diversity consistently increased with productivity across scales

Arthropod alpha diversity increased with productivity consistently across scales, suggesting a positive relationship between energy availability and species richness. This overall pattern aligns with our a priori hypothesis

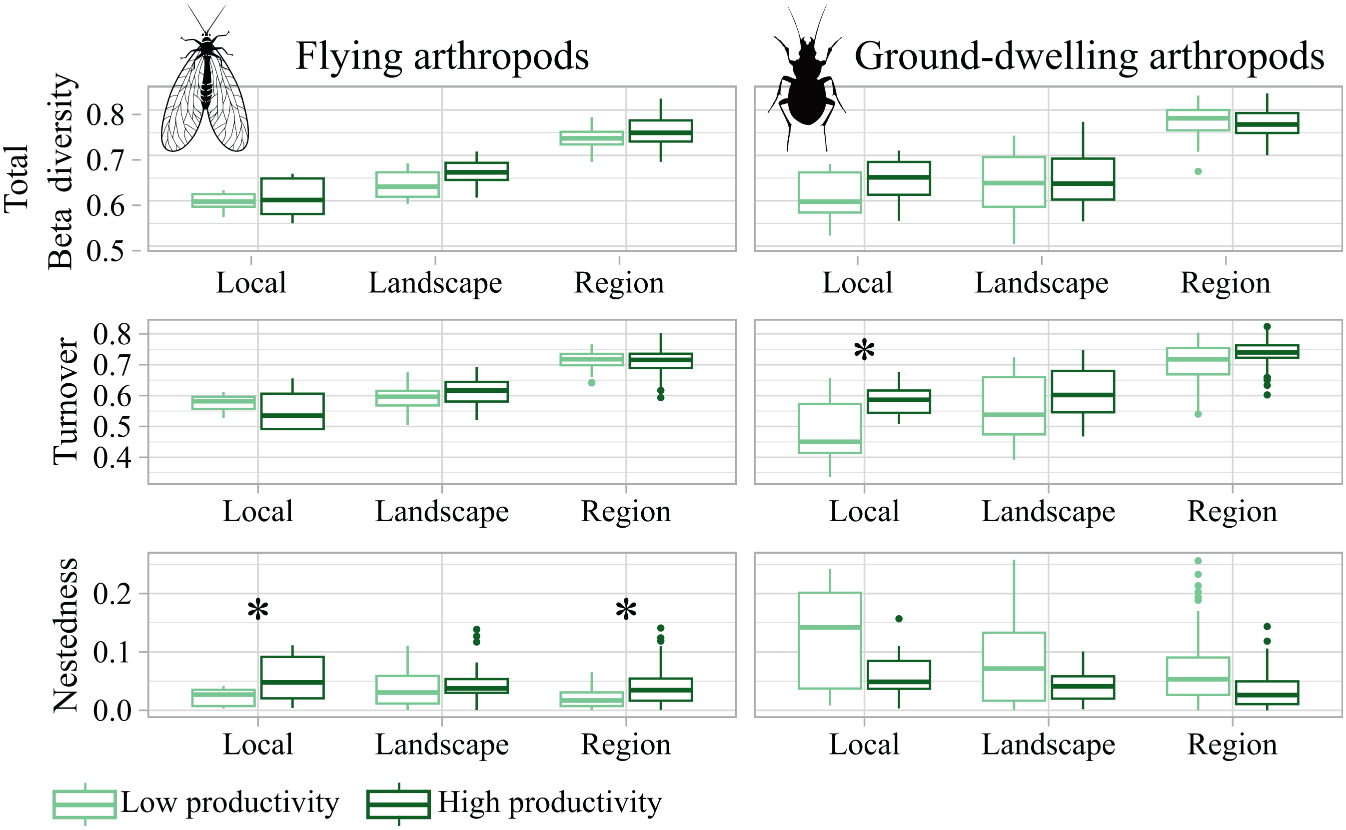

FIGURE 5 Community dissimilarity among community types at each of the scales addressed (local, landscape, and region). Following Baselga and Orme (2012), we partition overall dissimilarity into its turnover and nestedness components. Shown in each panel, box plots show the overall distribution of pairwise community dissimilarity values between each pair of sampling sites of either low- (light green) or high-productivity (dark green) sites. In each boxplot, the central line represents the median value, box limits correspond to the first and third quartiles (interquartile range), whiskers extend to 1.5× the interquartile range, and individual points denote species with dissimilarity values outside this range. Panels correspond to individual community types (flying vs. ground-dwelling communities). Note that while we see an increase in community dissimilarity across community types with increasing spatial scale, the differences in beta diversity values between low- and high-productivity areas remained low and generally statistically nonsignificant. We only detected significant differences (shown with asterisks) in nestedness between low- and high-productivity areas for flying communities (at both local and regional scales), and in turnover for ground-dwelling communities (at the local scale). Insect silhouettes credit: P. Peña-Aguilera.

and with previous studies in various ecosystems (Cusens et al., 2012; Gillman & Wright, 2006). Such relationships have typically been attributed to more productive environments supporting larger species pools, possibly due to increased resource availability and habitat complexity (Eriksson et al., 2006). Across subarctic landscapes, habitat heterogeneity and productivity are usually tightly coupled. At our sites, this connection was evident as we found higher species counts at more complex and productive sites. The pattern of higher richness at more productive areas was repeated across scales, indicating that the mechanisms driving alpha diversity remain stable regardless of spatial extent. Moreover, we found the strength of the productivity–richness relationship to be similar among flying and ground-dwelling arthropod groups, despite a difference in average species richness (Figure 3). This consistency in patterns suggests that similar processes drive community assembly not only across scales, but also across taxa in subarctic landscapes.

In terms of the identity of potential drivers, high-productivity sites are characterized by denser and more structurally complex vegetation than low-productivity sites in subarctic landscapes. This connection is particularly evident at the tree line, which marks a transition from more productive and heterogeneous mountain birch forest to less diverse and productive mountain tundra. Variation in vegetation structure likely contributes to the differences in species richness observed between the two arthropod communities. Ground-dwelling arthropods are predominantly predators whose distribution and abundance are strongly influenced by habitat complexity. For these species, vegetation structure can determine access to hunting grounds (Bowden & Buddle, 2010) and mediate predator–prey interactions (Brose et al., 2003;

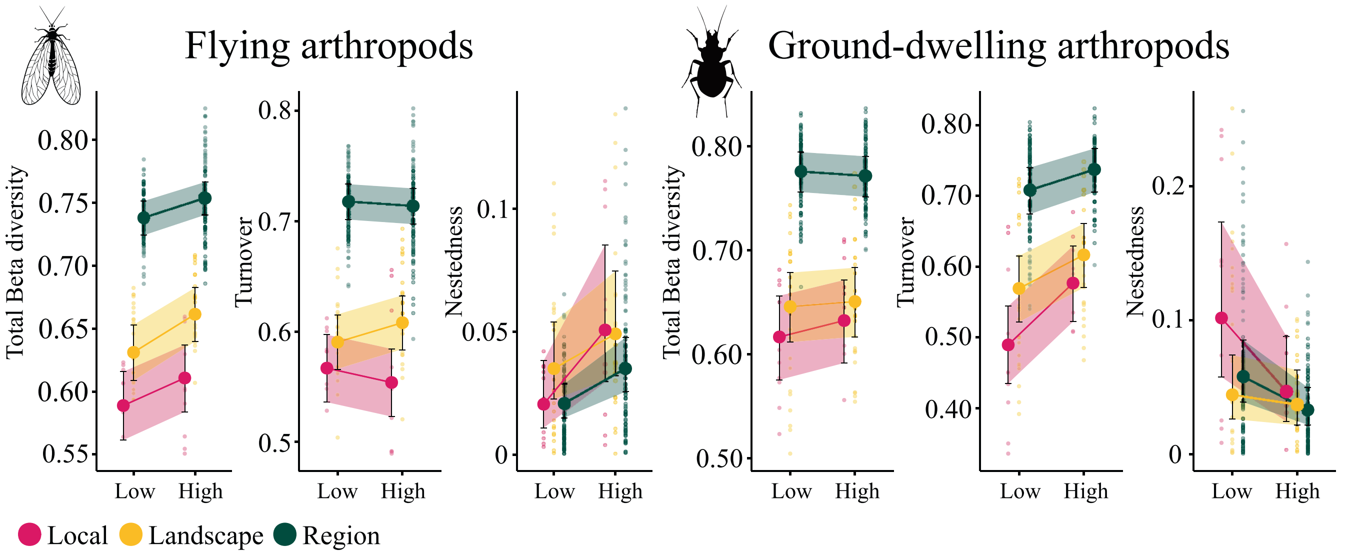

FIGURE 6 Beta diversity components between low- and high-productivity areas for each of the three scales assessed (Local in pink, Landscape in yellow, and Region in green). Shown in each panel are the fitted slopes between mean pairwise Jaccard dissimilarity, turnover and nestedness at low- and high-productivity sites for flying and ground-dwelling arthropods. Small points represent raw pairwise community dissimilarity values between each pair of sampling sites within each specific scale. Large opaque points show fitted means with 95% CIs (whiskers) from the generalized linear mixed-effect model of each beta diversity component as a function of productivity and scale. Insect silhouettes credit: P. Peña-Aguilera.

Jiménez-Valverde & Lobo, 2007). In contrast, flying arthropod communities comprise a diverse array of species with varied life cycles, dispersal abilities, and feeding strategies. For these organisms, vegetation structure primarily influences larval development and feeding opportunities across multiple microhabitats. Furthermore, the high mobility of flying insects allows them to exploit a wider range of productive sites, contributing to their overall higher species richness compared to ground-dwelling species. As a result, the relationship between vegetation and arthropod richness appears to be driven more by physical habitat complexity than by plant species richness per se. Consistently, Peña-Aguilera et al. (2023) reported only a weak correlation between plant and arthropod species richness in the same region.

Diversity patterns reflect a proportional increase of all community components along the productivity gradient

At none of the scales evaluated did mean species prevalence (i.e., average prevalence of species across sites) differ between low- and high-productivity sites for either community type (Figure 4). This result matches neither greater (Figure 1a) nor diminished (Figure 1c) distributional overlap towards high-productivity sites. If high-productivity sites with higher species richness showed greater mean species prevalence (Figure 1a), then we would anticipate higher species overlap at the productive end, where food resources sustain greater species diversity—a phenomenon well documented elsewhere (Cusens et al., 2012; Gillman & Wright, 2006; Mittelbach et al., 2001; Waide et al., 1999). Conversely, a decline in mean prevalence at high-productivity sites (Figure 1c) would suggest that richness gains were primarily driven by rare or specialized species restricted to fewer sites, as observed in other ecological systems (Baastrup-Spohr et al., 2015; Sánchez González et al., 2023). Instead, the current outcome aligns with our second scenario, which predicts that mean species prevalence does not change substantially in areas of high productivity. Consistent with this prediction, our results show that increased productivity boosts overall alpha diversity by proportionally adding both *common* and *specialist* species, without affecting species-specific prevalence or turnover. In other words, while more species can persist locally, prevalence across sites remains similar, as resources and habitat heterogeneity also increase proportionally from low- to high-productivity areas.

While overall species richness increased with productivity, the majority of the individual species contributing to local arthropod communities were widely distributed across the landscape (i.e., the *common* species) and thereby largely independent of productivity patterns. This pattern contrasts with studies reporting higher spatial turnover and endemism across alpine–arctic gradients (e.g., Hein et al., 2024) or strong habitat-specific

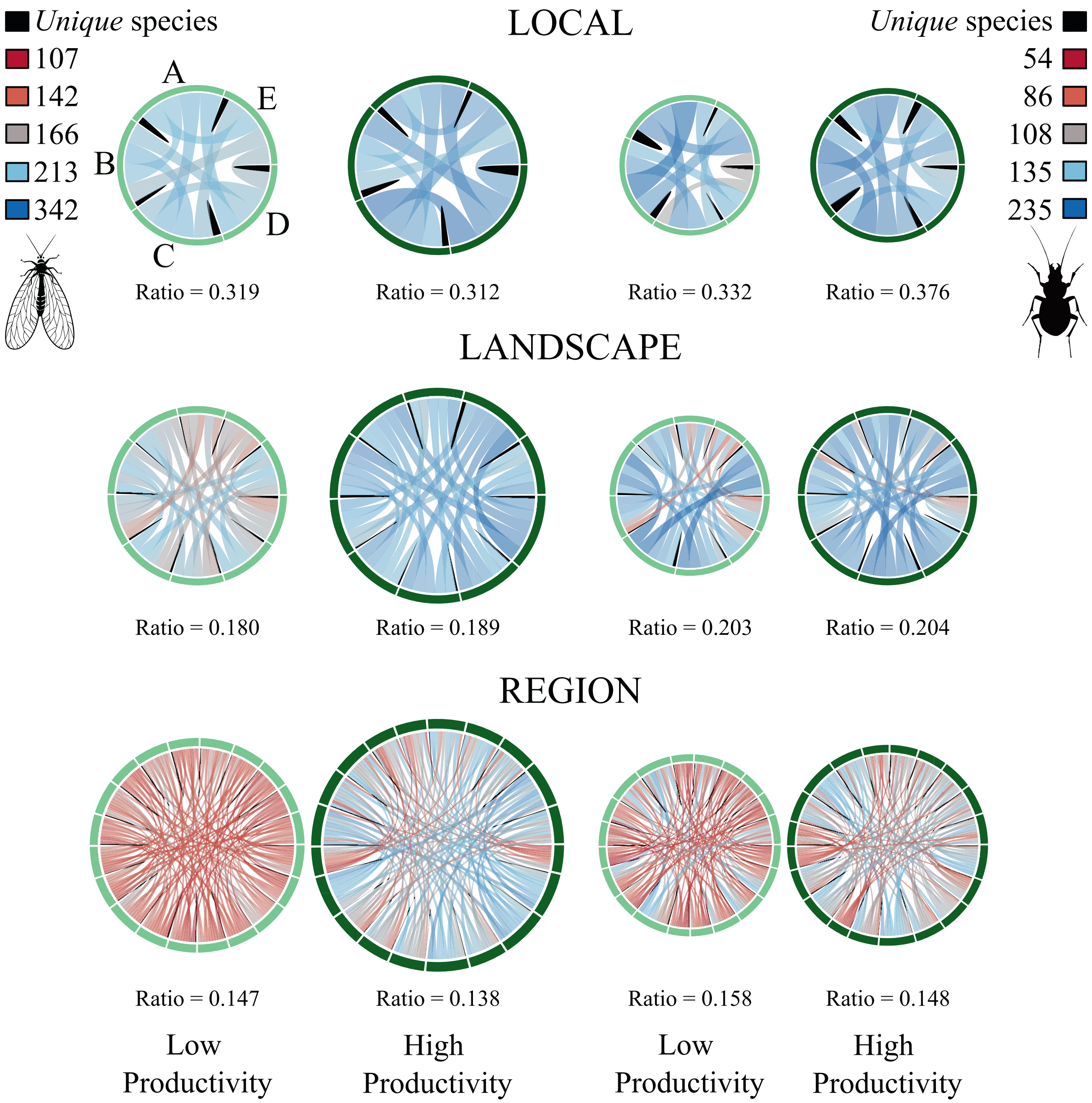

FIGURE 7 Chord diagrams illustrating the proportion of species *unique to* and *shared between* sampling sites within the same productivity category for flying arthropods (left diagrams) and ground-dwelling arthropods (right diagrams) at each scale assessed. The color of the connections shows the number of species shared between each pair of sampling sites, with red indicating a lower proportion and blue, a higher proportion. Species *unique to* a sampling site are shown in black. The ratio between mean *unique* species to mean *shared* species is shown below each chord diagram. The size of each diagram is proportional to the number of species included. Color gradients are scaled separately for each taxon. Note remarkably similar patterns of species sharing among individual sites (e.g., A–E in the top left diagram), despite variation in the overall species pool. Insect silhouettes credit: P. Peña-Aguilera.

niche differentiation in particular groups (e.g., Beckers et al., 2018 for Carabidae). Instead, our results indicate a system dominated by a basal set of *common* and widely distributed species whose prevalence is similar across the gradient (i.e., highly correlated; Appendix S1: Figure S3).

Despite the evident stability in the core assemblage of *common* species, species richness still increased with productivity. The key contribution came from *specialist* species (i.e., species only appearing at one end of the productivity gradient), which, although individually rare, accumulated in disproportionate numbers at high-productivity sites. When partitioning the community, we found that *specialist* occurrence was on average 2.29 times higher in flying communities and 1.87 times higher in ground-dwelling communities at high- compared with low-productivity sites. While modest in ratio, these differences translated into substantial richness gains: 2076 versus 905 species for flying taxa and 1020 versus 544 species for ground-dwelling taxa at high- and low-productivity sites, respectively. Thus, although *specialists* often appeared as singletons and their prevalence declined when more sites were pooled, their overall contribution to richness was markedly greater in high-productive habitats. Considering the total species found at these locations, the substantial number of *specialist* species in high-productivity sites suggests that these habitats may harbor unique ecological conditions and provide other resources lacking from less productive environments. At the same time, it is worth mentioning that at the low-productivity end, we found a non-negligible proportion of *specialist* species for both community types.

Overall, our findings support the hypothesis that productivity increases biodiversity not by reshaping the distribution of widespread *common* species, but by creating ecological opportunities for *specialists* to persist alongside them. Therefore, insect communities at high latitudinal areas consist of a basal set of *common* species, with similar prevalence at both ends of the productivity gradient, and two distinct sets of *specialist* species, with a more diverse set preferring high-productivity sites over low-productivity sites.

Beta diversity varies with scale but not with productivity

Across the productivity gradient, dissimilarity between insect communities increased with spatial scale. As predicted, mass effects dominated local community patterns at the smallest spatial scale. At the largest spatial scale, turnover proved the highest. This is consistent with a scenario where low dispersal rates prevent arthropods from efficiently sampling for optimal habitat across the whole extent of our study area (Figure 5; Appendix S1: Figure S1). Supporting this idea, turnover was higher at the regional scale in the least dispersive group, the ground-dwelling arthropods. Nonetheless, we did not find support for the hypothesis put forward by Heino et al. (2015), where a difference in beta diversity between low- and high-productivity sites is expected at the landscape (intermediate) scale. In our study, we found no significant differences in community dissimilarity between low- and high-productivity sites for any of the scales assessed.

Species turnover is generally understood as the outcome of both environmental filtering and dispersal processes (da Silva et al., 2018; Soininen et al., 2018). Our results support this notion, as turnover increased with spatial scale in both community types and across both ends of the productivity gradient. Nevertheless, the similarity in turnover between opposing ends of the productivity gradient at the landscape scale rules out this extent as the potential "sweet-spot" where dispersal limitation and environmental filtering balance to maximize species sorting. One possible explanation is that the productivity gradients encompassed in our study are not broad enough to reveal such a pattern, which may only become apparent at larger spatial extents, for instance, across the entire Scandinavian Peninsula. This limitation is further reinforced by the dispersal abilities of high-latitude insect communities. Since they are composed largely of efficient dispersers with broad environmental tolerance, differences in turnover between low- and high-productivity sites are likely to remain small. At the landscape scale, the absence of a further increase in beta diversity at high-productivity areas may therefore reflect the coexistence of multiple species pools with different habitat affinities, yet dominated by species capable of dispersing widely—a scenario which we discuss in more detail below.

Constant proportions of *shared* versus *unique* species maintain dissimilarity patterns

At the landscape level, we expected to see significant differences in community dissimilarity between sites with low- and high-productivity levels (Figure 2). Contrary to these expectations, we found community dissimilarity to be similar at the opposite ends of the productivity gradient (Figure 5). Surprisingly, despite differences in species richness between low- and high-productivity sites (Figure 3), the ratios of turnover (i.e., the number of species which *were* replaced: $2\min(b,c)$) out of the species that *could* potentially be replaced ($a + 2\min(b,c)$) remained strikingly similar at both productivity ends (Figures 5 and 6). The same consistency is revealed by the chord diagrams (Figure 7), showing similar proportions of *shared* species between sampling sites within each productivity category. This unexpected finding suggests that the increase in numbers at high-productivity sites is consistently similar for both *shared* and *unique* species, accounting for the similarity in the ratio.

When examining how the dispersal capacity of each community type may influence the relationship between beta diversity and productivity at the landscape scale, we observed greater variability in turnover and nestedness values for ground-dwelling arthropods, particularly at low-productivity sites (Figure 5). This pattern suggests higher variability in the composition of ground-dwelling arthropods communities at each sampling site within the same productivity category (see Figure 7: notice the greater differences in color intensity between connections representing *shared* ground-dwelling species than *shared* flying arthropods). Our finding was also supported by patterns of nestedness-resultant dissimilarity (i.e., species richness differences) in ground-dwelling arthropods, which was higher at low-productivity sites compared to high-productivity sites.

As a plausible explanation for this pattern, low-productivity sites are generally located in the high tundra, while high-productivity sites are generally located at lower elevations below the tree line. Here, the high tundra is characterized by a topographically more heterogeneous landscape, harboring different conditions in terms of moisture run-off, snow deposition, and heat exposure (Kemppinen et al., 2018). These contrasting conditions will likely lead to stronger species filtering across low-productivity sites as compared to high-productivity sites for ground-dwelling species. When dispersal capacity is limited, as is the case for ground-dwelling arthropods, greater dissimilarity in species richness between communities at low-productivity sites is therefore to be expected.

Implications for communities in space and time

Across scales, our results reveal consistent relationships between productivity and community structure. Specifically, alpha diversity increased with productivity at local, landscape, and regional scales, while mean species prevalence remained stable, supporting a proportional yet constrained increase in diversity as habitat heterogeneity increased. Together, these patterns indicate that *common* species form a widespread, scale-independent backbone of communities, whereas richness gains in productive sites are primarily driven by singleton *specialists*.

We also found similar turnover patterns between low- and high-productivity sites separated by tens to hundreds of kilometers. Importantly, this turnover was independent of the overall size of the species pool. As richness increased, so did the absolute number of *unique* species per site pair, resulting in proportional turnover that remained constant across scales. The scale-independence of these patterns is encouraging, as it suggests that local biodiversity–productivity relationships can be extrapolated to broader spatial extents without being confounded by context dependence.

At the same time, we may not have reached the "sweet spot" where stronger species sorting along productivity gradients becomes evident. This is likely because the ecosystem is not yet saturated following the last glaciation, and many species are still colonizing these habitats (Nekola et al., 2024; Svenning & Skov, 2007). These colonizers are—by definition—generally strong dispersers with broad environmental tolerances, which may dampen productivity-driven sorting. Together, these findings indicate that productivity is a robust driver of arthropod diversity, but its effects unfold within a dynamic postglacial landscape still undergoing ecological assembly.

AUTHOR CONTRIBUTIONS

Pablo Peña-Aguilera conceived the idea with inputs from all co-authors. Pablo Peña-Aguilera planned, supervised, and conducted the fieldwork. Pablo Peña-Aguilera analyzed the data with inputs from Tomas Roslin, interpreted the results, and wrote the manuscript. All authors read the final version of the manuscript and contributed to its preparation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw sequences for the insect community data generated during the current study are available from the European Nucleotide Archive (https://www.ebi.ac.uk/ena/browser/home) within Project PRJEB63601. The code and data (Peña-Aguilera et al., 2026) are available from Figshare: https://doi.org/10.6084/m9.figshare.27878418.

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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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