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RESEARCH ARTICLE

Warming effects on decomposition via trophic cascades vary across elevations in an alpine meadow ecosystem

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Abstract

1. Warming increases the foraging rates of ectothermic predators, potentially resulting in increased predation pressure on detritivores through top-down effects, thereby influencing decomposition. Trophic cascade effects under warming are shaped by many factors, including temperature, precipitation and trophic structure. Greater species diversity may weaken these cascades through intensified interspecific interactions and, in turn, shape how decomposition responds to warming (the vertical diversity hypothesis), but this process has seldom been examined in natural ecosystems.
2. Here, we experimentally increased warming at three elevations (4650, 4950 and 5200 m) in an alpine meadow ecosystem to test the predator-mediated effects of warming on decomposition, as well as the role of arthropod diversity in these processes.
3. Among the three elevations, arthropod diversity and predator abundance were significantly greater at 4950 m than at 4650 and 5200 m. Warming increased predator abundance at all three elevations, but decreased detritivore abundance only at 4650 and 5200 m. Detritivore abundances at 4650 and 5200 m, but not at 4950 m, were correlated negatively with predator abundance under experimental warming. Based on multigroup structural equation models, warming primarily reduced litter decomposition directly during the cold season when arthropod activity was limited. In contrast, during the warm season and over the whole year, both periods with greater arthropod activity, warming predominantly reduced litter decomposition via predator-driven top-down effects, rather than through direct effects. Although warming increased predator abundance across all elevations, the resulting trophic cascade was observed only at 4650 and 5200 m, where elevated predator abundance suppressed detritivores and reduced litter decomposition. In network analysis, indicators of arthropod diversity had the most correlations with indicators of ecosystem function, suggesting that the warming-driven decline in detritivore abundance could influence ecosystem functionality negatively.

4. Synthesis: We conclude that warming-induced increases in predator abundance can reduce detritivores and decomposition through strong top-down effects, but these effects appear confined to elevations with low arthropod diversity. Our study provides a novel perspective on the factors shaping decomposition responses to warming. Large-scale field studies and mesocosm-based experiments are warranted to assess the generality of this effect.

KEYWORDS
brown food web, ecosystem function, interspecific interaction, multi-trophic interactions, predation pressure, top-down effect, vertical diversity

1 | INTRODUCTION

Top-down and bottom-up processes have important effects on ecosystem functions and properties. These processes and their outcomes have been demonstrated in ecological studies (Knight et al., 2005), but most examined living food webs ('the green world'), in which predators increased plant growth indirectly by reducing the abundance and diversity of herbivores (Barnes et al., 2020). Considering the effects caused by predators expected from classical theories of trophic cascades, the top-down impacts of predators in detritus-based food webs ('the brown world') may operate in an opposite pattern to that in living food webs (Hawlena et al., 2012). In living food webs, the top-down effects of predators generally reduce abundance and foraging of herbivores, thus promoting plant growth. But in detritus-based food webs, the top-down effects of predators may reduce the decomposition rate by detritivores, decelerate nutrient cycling and, thus, restrict plant growth (Wu et al., 2011). The interaction between predators and detritivores in detrital food webs and the impact of this interaction on ecosystem functions have been largely ignored, while studies that examined these relationships have reported equivocal results (Hawlena et al., 2012; Melguizo-Ruiz et al., 2020). It is important to understand the cascading effects of the top predator on food web structure and decomposition because decomposition is a key link between above- and below-ground processes in terrestrial ecosystems (Freschet et al., 2013; Wardle et al., 2004). Abiotic conditions can modulate the strength of top-down effects in communities, and our experimental study was aimed at identifying such effects across communities differing in diversity.

Climate warming is a common driver of the strength and frequency of trophic interactions (Romero et al., 2018). Warming can enhance ectotherm rates of metabolism, food consumption, reproduction and foraging (Høye et al., 2020; O'Connor, 2009; Thakur et al., 2018). Predation pressure has been hypothesized to increase with warming due to increased predation activity (Romero et al., 2018), which can lead to stronger top-down effects of predators (Hoekman, 2010). This should ultimately affect the function of the lower prey trophic level (Figure 1a,b). It has been reported that increased predation pressure reduced decomposition by detritivores and, thus, limited nitrogen input and plant growth (Hawlena et al., 2012; Wu et al., 2011). However, an increase in predator abundance can also, intriguingly, promote the abundance of detritivores and their decomposition effects (Koltz et al., 2018; Melguizo-Ruiz et al., 2020). The effects of predator-driven trophic cascades on ecosystem functioning may depend on environmental context factors, such as water and resource availability, temperature, topography and the complexity of the food web (Bradford et al., 2016; Koltz et al., 2018; Melguizo-Ruiz et al., 2020; Romero et al., 2018; Wu et al., 2014). Identifying the key factors that regulate trophic cascade strength is, therefore, essential for improving our understanding of how climate warming influences biogeochemical cycling.

The relationship between biodiversity and ecosystem functioning depends on diversity both within trophic levels (horizontal diversity) and across trophic levels (vertical diversity, including predator and omnivore diversity). The vertical diversity hypothesis states that intraguild predation (IGP) can weaken the strength of trophic cascades and strengthen the relationship between biodiversity and ecosystem functions (Wang et al., 2019; Wang & Brose, 2018). In food webs with complex interspecific relationships (high vertical diversity), a change in environmental factors may not influence specific trophic groups and their functions in simple, unidirectional ways due to the complexity of food web pathways (Duffy et al., 2007; Polis & Strong, 1996). When the richness and abundance of predators and omnivores are high, IGP among predators and interspecific interactions between predators and omnivores can produce antagonistic effects that reduce net predation pressure on the low trophic levels (Holt & Polis, 1997; Melguizo-Ruiz et al., 2020; Polis et al., 1989; Wu et al., 2011). Therefore, species diversity at higher trophic levels may be one of the key factors regulating the strength of trophic cascades (Figure 1c,d). Biodiversity-ecosystem function experiments have typically demonstrated strong effects when varying low-diversity assemblages, but with saturation at high diversities (Hagan et al., 2021). Variation in species diversity could exhibit particularly strong effects in biomes with overall low species richness, such as alpine communities. Community structure in the alpine ecosystem is likely to be altered due to climate change, which can have consequences for ecosystem functions (Koltz et al., 2018).

O'Gorman et al. (2023) concluded that trophic cascades may be particularly strong under warming in ecosystems dominated by a single apex predator. We reasoned that cascades might be weak in diverse predator assemblages, which have a large range of antagonistic effects (e.g. IGP and interference) that can suppress the consumption of low trophic levels and decomposition (Figure 1). In this study, we examined the role of warming and arthropod diversity in driving decomposition at three sites along an elevational gradient between 4650 and 5200 m above sea level (a.s.l.). We chose an open rather than a caged design to enable the free movement of predators, and to allow avoidance responses of low trophic levels. We hypothesized that (1) warming affects the abundance of detritivores by influencing predator abundance and, thus, the strength of trophic cascades (Figure 1a,b); (2) the effects of warming on detritivores would cascade down to decomposition processes (Figure 1a,b); and (3) at high arthropod diversity, the top-down effect of predators on detritivores under warming would be weaker than at low arthropod diversity, and decomposition would remain unchanged or would even increase (Figure 1c,d).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted on the southern slope of the Nyanqing Tanggula Mountain, in the central part of the Qinghai–Tibetan Plateau. The average daily temperature in the region is 1.8°C, and the annual rainfall is 479 mm. Rainfall and temperature increase from May to September with distinct dry and wet seasons. The average daily temperature increased by 1.6°C over the past 50 years (Wang et al., 2013).

The vegetation type between 4650 and 5210 m a.s.l. is alpine meadow, dominated by the sedge *Kobresia pygmaea*. The growth of *K. pygmaea* is limited mainly by drought at the low elevation (4650 m), and by low air temperature at the high elevation (5200 m) (Wang et al., 2013). In the growing season, vegetation coverage is usually greater than 75%, maximum plant height is less than 10 cm,

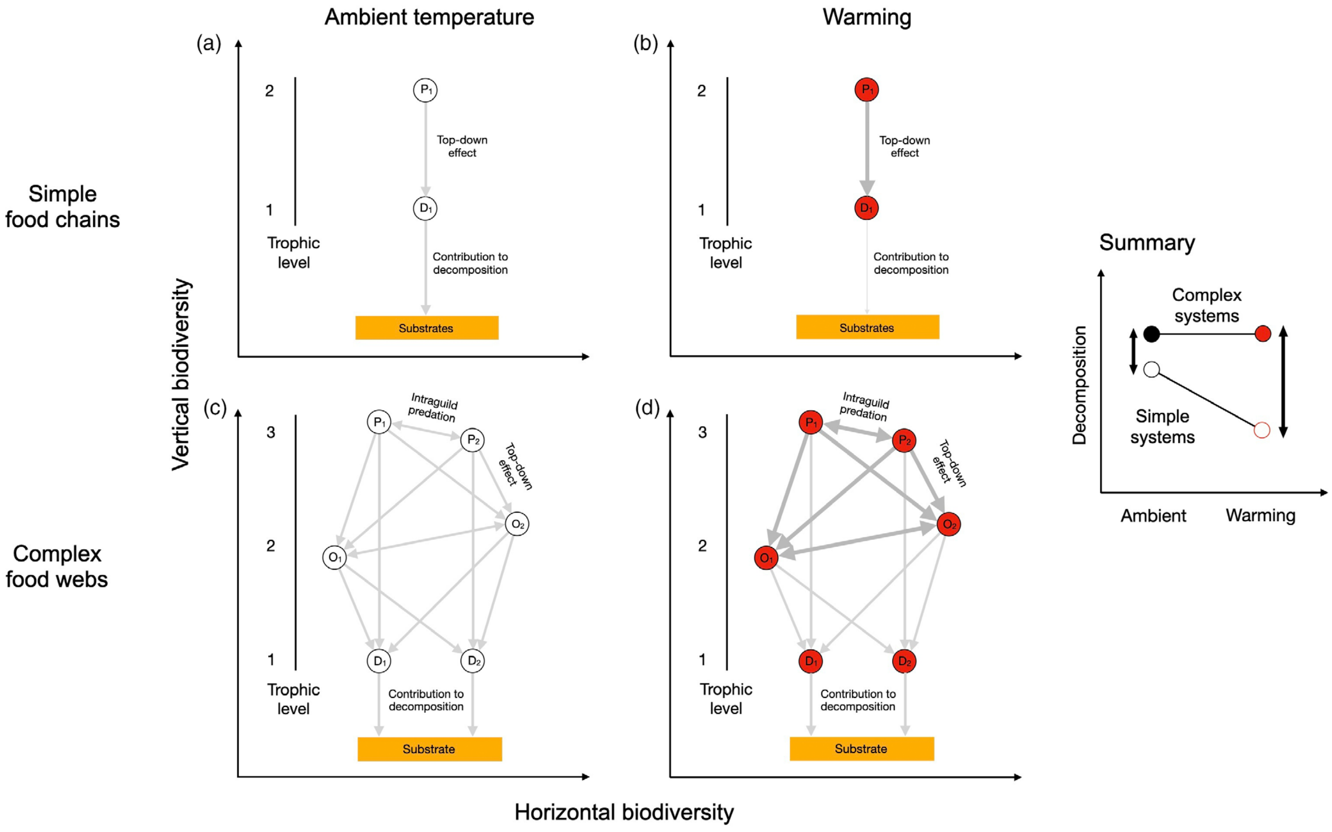


FIGURE 1 Conceptual framework illustrating how vertical diversity affects the response of low trophic levels and ecosystem functions to warming. Biodiversity can be characterized in two axes: Within a trophic level (horizontal diversity) and across trophic levels (vertical diversity). Higher diversity of predators and omnivores in complex food webs increases vertical diversity to a greater extent than simple food chains. In complex food webs, stronger intraguild predation and predator-omnivore interactions weaken the top-down effects of high trophic levels on detritivores under warming, maintaining decomposition. Simple food chains lack omnivory and intraguild predation under ambient temperature (a) and warming (b). Complex food webs with intraguild predation and omnivory are displayed under ambient temperature (c) and warming (d). In (a) and (b), the simple food chains include a predator species (P_1), a detritivore species (D_1), and substrates. In (c) and (d), the complex food webs include two predator species (P_1 and P_2), two omnivore species (O_1 and O_2), two detritivore species (D_1 and D_2), and substrates. The arrows indicate interspecific interactions, double-headed arrows indicate intraguild predation, and darker, wider arrows indicate stronger interactions.

and the height of the dominant species, *K. pygmaea*, is generally less than 6 cm. In 2006, three 20 m × 20 m areas were fenced around weather stations at 4650, 4950 and 5200 m to prevent damage from livestock.

2.2 | Experimental design

Because of the homogeneity of vegetation on the Qinghai–Tibetan Plateau, it is difficult to find sites with substantial biodiversity differences at local scales (Figure S1a). However, biodiversity usually changes with altitude (Zhao et al., 2018), and therefore, we examined the effect of biodiversity at different altitudes. To address the effects of temperature and moisture, we had an additional low-diversity area at the highest elevation (5200 m). As altitude increases (4650–5200 m), temperature and moisture changes are linear (Figure S2), while diversity changes are unimodal (Wang et al., 2013). We examined the effects of two temperature treatments (ambient temperature and warming) at three altitudes (4650, 4950 and 5200 m). In total, 30 experimental plots were established at three elevations: 2 temperature treatments × 3 elevations × 5 replicates = 30 plots. The distance between any two plots was at least 2 m so that each plot was independent. To closely mimic natural conditions, we did not fence the plots, which enabled us to examine emigration and immigration, including prey movement influenced by predators and predator movement driven by warming. By allowing for these natural processes to occur, our study differs from closed mesocosm experiments, enabling us to better understand the effects of trophic interactions in natural systems.

In December 2019, an open top chamber (OTC; top edge = 50 cm, bottom edge = 72.5 cm, height = 45 cm, coverage area = 1.37 m^2; Figure S1b) was used for warming, following the standard method described in the International Tundra Experiment (Marion et al., 1997). The gap between the bottom of the OTCs and the surface was 5 cm, and the activities of arthropods were not restricted by the edges of the OTCs (Figure S1b), at least in the detrital food webs. Weather stations (HOBO H21-USB Micro Station, Onset, Bourne, MA, USA) provided the near-surface air temperature and air humidity at 10 cm above-ground level and soil temperature at 5 cm depth at the three elevations. The experimental warming was maintained for 12 months, from the beginning to the end of the experiment. The OTCs increased the air temperature by 1.81°C, 1.87°C and 1.28°C and the soil temperature by 1.42°C, 1.37°C and 1.01°C at 4650, 4950 and 5200 m, respectively (Figure S2).

2.3 | Decomposition measurements

To minimize potential confounding effects from substrate quality variation when measuring trophic cascades, we selected a single plant species, *K. pygmaea* as the decomposition substrate. *Kobresia pygmaea* is the most widespread species in alpine meadow ecosystems, making it a suitable representative for generalizing decomposition processes across alpine meadow ecosystems (Miehe et al., 2019). Leaf litter and roots of *K. pygmaea* were collected in December 2019, cleaned with water, oven-dried at 65°C to a constant weight and stored at −20°C until decomposition measurements. Nylon mesh bags (10 cm × 15 cm) with three different mesh sizes (Figure S1c) enabled us to distinguish three-sized decomposer communities (small, medium and large), and quantify the arthropod contribution to decomposition (Handa et al., 2014). Nylon mesh bags of 0.05 mm allowed only microorganisms and a very few microfauna, mesh bags of 1.0 mm allowed mesofauna, and mesh bags of 5.0 mm allowed most fauna access to the decomposition station. Eight grams of leaf litter and roots was placed in nylon mesh bags and was spread out above the ground to measure litter decomposition (Figure S1c), and nylon mesh bags containing roots were buried 0–5 cm below the surface to measure root decomposition (Figure S1d). The litter bags were surrounded by PVC pipes to reduce the effect of wind, and three holes at the bottom of the PVC pipes allowed arthropod access (Figure S1c). The PVC pipes were placed vertically on the ground surface without being inserted into the soil, and thus did not interfere with subsurface water flow or rainfall infiltration. Additionally, the openings at the bottom facilitated air circulation, minimizing any potential effects on temperature and moisture conditions inside the pipes.

Nylon mesh bags were placed in the fields during three distinct incubation periods: Period 1 (cold season): 20 December 2019–20 June 2020; Period 2 (warm season): 20 June 2020–20 December 2020; and Period 3 (one whole year): 20 December 2019–20 December 2020. The same substrate, 8 g of leaf litter and roots, was used in all three incubation periods to measure decomposition. After the bags containing the substrate were collected, the leaf litter and roots were cleaned, oven-dried at 65°C and weighed. A total of 540 samples (3 elevations × 2 temperature treatments × 3 mesh sizes × 2 leaf litter and root × 3 incubation periods × 5 replicates) were weighed.

2.4 | Arthropod sampling and identification

We collected arthropods using substrate sifting and pitfall traps in late June 2020, a time of rising air temperature, greening of vegetation and peak arthropod activity on the Qinghai–Tibetan Plateau (Yin et al., 2023). After the litter bags were collected, the arthropods in the 5-mm mesh-sized decomposition bags were collected using Tullgren funnels for 72 h, preserved in alcohol, and brought to the laboratory for identification (Macfadyen, 1961; Wise & Lensing, 2019). In the alpine meadow, arthropods generally hibernate in the soil with eggs or larvae in the cold season, so we did not sample arthropods in the cold season. A pitfall trap, with a diameter of 10 cm, was placed in the centre of each treatment plot with the lip of the cup flush with the soil surface for 10 days. Each cup had a side hole to prevent excessive rainfall from washing out the arthropods with overflow. Due to the limited height of the canopy in alpine meadows that is typically less than 10 cm, there was minimal accumulation of litter on the soil surface. Pitfall trap sampling is consistent, passive, repeatable, causes little disturbance to the environment and is commonly used to assess arthropod diversity (Lange et al., 2011), especially for ground-dwelling species such as beetles and spiders. In this study, since the canopy height of the plant community was very low (<10 cm), there was little accumulation of litter. Most arthropods, except for adult Lepidoptera, Diptera and Hymenoptera, foraged on the soil surface. Therefore, pitfall traps were highly suitable for sampling arthropods at the study site.

Most arthropods were identified to the genus or species level using a microscope. For taxa that were difficult to identify, we consulted experts who specialized in different arthropod groups. The identified taxa were categorized into four trophic guilds (Table S1), namely predators (e.g. spiders, centipedes and ground beetles), omnivores (e.g. ants and darkling beetles), detritivores (e.g. millipedes) and herbivores (e.g. leaf beetles and true bugs).

2.5 | Plant community survey and soil property measurement

We surveyed the plant community at the end of August 2020 according to the standard field vegetation survey method (Luo et al., 2023), which included the number of plant species, plant coverage and plant height. Three random quadrats (0.25 m × 0.25 m) were examined in each plot, and the three quadrats were combined for statistical analysis.

Following the vegetation sampling, three topsoil (0–10 cm) and three subsoil (10–20 cm) samples were collected in each treatment plot, and samples in each soil layer were combined in one sample for soil property measurements. Soil total carbon and total nitrogen were determined using an elemental analyser (Vario EL III, Elementar, Langenselbold, Germany), and soil ammonium nitrogen (NH_4^+-N) was measured with a flow analyser (Auto Analyzer 3, Evisa, Ludwigshafen, Germany).

2.6 | Data analysis

The effects of mesofauna and macrofauna on decomposition were calculated as:

$$ES_{mesofauna} = \left(M_{1mm} - M_{0.05mm}\right) / M_{1mm}, \quad ES_{macrofauna} = \left(M_{5mm} - M_{1mm}\right) / M_{5mm},$$

where $M_{0.05mm}$ is the mass loss of leaf litter or roots in a nylon mesh bag of 0.05 mm, M_{1mm} is the mass loss of leaf litter or root in a nylon mesh bag of 1 mm, M_{5mm} is the mass loss of leaf litter or root in a nylon mesh bag of 5 mm.

Linear mixed models tested the effects of warming, elevation and their interaction on arthropod communities, as well as the effects of arthropods on leaf litter and root decomposition across different time periods (Bates et al., 2015). In these models, elevation, warming and their interactions were fixed effects, and plot was a random effect. Tukey's test was used for multiple comparisons (Lenth, 2016). Where necessary, data were log-transformed for normality and to improve the degree of fit of models. Linear regressions tested the relationships between predator and detritivore abundances. The predator and detritivore abundances were log-transformed. Non-metric multidimensional scaling (NMDS) analysed the differences in species composition of arthropod communities among the three elevations and the effect of warming on arthropod composition at different elevations. Permutational multivariate analysis of variance tested for the effects of elevation and warming on any significant dissimilarity in species composition of arthropods.

We used piecewise multigroup structural equation models (SEMs) to test whether the relationships between predictor and response variables varied across elevations (Lefcheck, 2016). This approach can be viewed as an extension of analysis of covariance (Siqueira et al., 2024), as, for example, it enables us to examine whether the effect of warming on trophic cascades differs with elevation. Specifically, we examined whether warming drives decomposition directly or indirectly by influencing the structure of the food web. An a priori conceptual model for the SEM was developed based on our hypothesized causal relationships and was supported by results from the linear mixed models and correlation analyses (Figure S7). The model included pathways from the warming treatment to arthropod community structure and ultimately to decomposition. Specifically, we hypothesized that warming would increase predator abundance, which would, in turn, reduce detritivore abundance. This would lower the contribution of detritivores to litter decomposition and, ultimately, reduce the overall decomposition rates. We also included a direct path from warming to decomposition in the model to distinguish the direct effects of warming from its indirect effects mediated through trophic interactions. In the piecewise SEM, plots were used as a random effect to fit multiple linear mixed models. A χ^2-value of Fisher's C above the significant level indicated the model was consistent with the data and could be accepted.

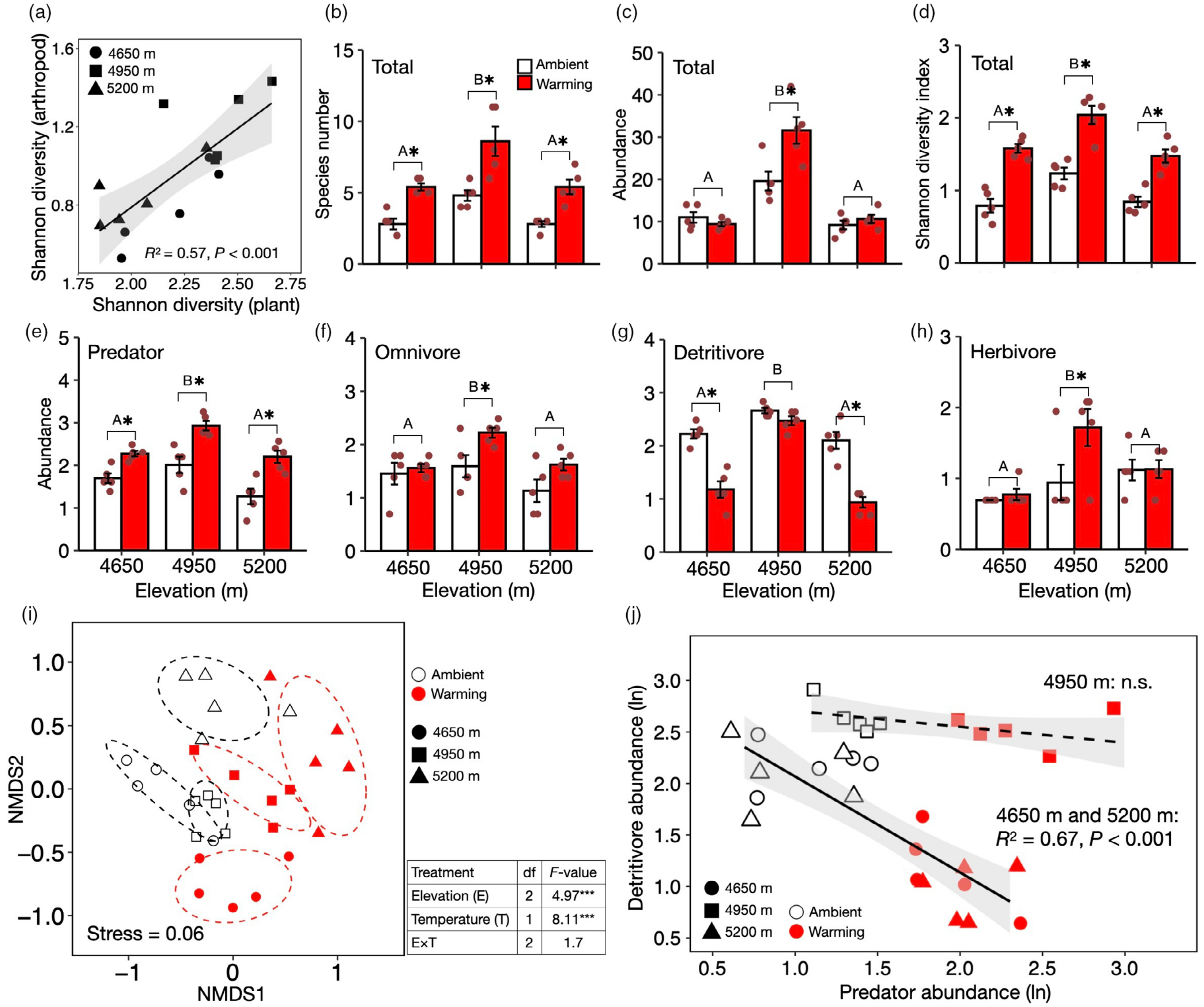
We determined the correlation network by Pearson pairwise correlations among arthropod diversity, trophic structure, litter decomposition, and soil and vegetation properties under ambient temperature and warming treatment. We calculated pairwise correlations and network metrics each time by randomly resampling 80% of the dataset 10,000 times and determined the 95% confidence intervals for edge weights and expected influence. Only significant correlations (i.e. those with 95% confidence intervals not overlapping zero) were retained in the network. The 'network' and 'bootnet' packages assessed connections among indicators (Epskamp et al., 2018; Jones, 2020). The expected influence of a target indicator was the sum of the correlations between the indicator and the remaining indicators. The edge weights and expected influence were estimated from 10,000 bootstraps of the empirical network, and the bootstraps were used to calculate the 95% confidence intervals for these indicators. All statistical analyses used the R Statistical Software v. 4.1.2.

3 | RESULTS

3.1 | Arthropod diversity and trophic groups

In the unmanipulated system, arthropod taxonomy diversity was correlated positively and strongly with plant species diversity across the entire altitudinal gradient (Figure 2a). The number of species, abundance and Shannon diversity index of arthropods were greatest at 4950 m, with no difference between 4650 and 5200 m (Figure 2b–d). The abundance of predators, omnivores, detritivores and herbivores was also greater at 4950 m than at either 4650 or 5200 m (Figure 2e–h). These results suggest the greatest vertical diversity (more abundant predators and omnivores) occurred at 4950 m with high arthropod diversity.

Experimental warming increased predator abundance at all three elevations and omnivore abundance at 4950 m (Figure 2e,f) but decreased detritivore abundance at 4650 and 5200 m (Figure 2g). At elevations of 4650 and 5200 m, warming significantly reduced the abundance of dominant detritivores (millipedes), with some at zero abundance (Figure S3). According to the NMDS analysis, the species composition of arthropod species separated clearly among elevations and between temperature treatments (Figure 2i).



Treatment	df	*F*-value
Elevation (E)	2	4.97***
Temperature (T)	1	8.11***
ExT	2	1.7

FIGURE 2 Changes in food web structure during the experiment. (a) Linear relationships between Shannon diversity of plant species and Shannon diversity of arthropod species. Effects of warming and elevation on (b) total number of arthropod species, (c) total abundance of arthropod, (d) Shannon diversity index, (e) predator abundance, (f) omnivore abundance, (g) detritivore abundance and (h) herbivore abundance. Bars represent mean ± SE. Means with different capital letters among elevations differ from each other ($p < 0.05$); *$p < 0.05$ between warming levels at each elevation differ from each other. (i) Non-metric multidimensional scaling (plot) of arthropod composition under ambient temperature and warming among elevations. The table presents the results of permutational multivariate analysis of variance examining the effects of elevation and temperature, and their interaction on arthropod composition. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. (j) Linear relationships between predator and detritivore abundances at different elevations. Solid lines represent significant ($p < 0.05$) relationships; dashed lines represent non-significant relationships (ns = $p > 0.05$).

In the linear models, there were decreases in detritivore abundances at 4650 and 5200 m with an increasing abundance of predators, but not at 4950 m (Figure 2j). The decrease in the abundance of detritivores with an increase in the abundance of predators ($R^2 = 0.24$, $p = 0.08$) emerged marginally only with the warming treatment (Figure S4), but not without warming ($p = 0.99$) at 4650 and 5200 m (Figure S4).

3.2 | Substrate decomposition

Our assessment of how arthropods influence decomposition was based on the magnitude of decomposition at different mesh sizes (see Section 2.6). The faunal effect on leaf litter and root decomposition at 4950 m was greater than at 4650 and 5200 m, and this difference was greater in Periods 2 and 3, which included the peak period of arthropod activity, than in Period 1 (Figure 3a,b). There was a significant ($p < 0.05$) or marginally significant ($p < 0.1$) interaction between elevation and warming on the faunal effects of leaf decomposition (Figure 3a,b). Specifically, warming did not influence the faunal effect at 4950 m in Periods 2 and 3 but decreased the faunal effects at 4650 and 5200 m (Figure 3a,b). Root decomposition was not affected by warming (Figure 3c,d).

3.3 | Relationship between arthropods and decomposition

We constructed multigroup SEMs for three distinct periods (cold season, warm season and one whole year) to examine how warming affects leaf litter and root decomposition across three elevations via predator-mediated top-down trophic cascades (Figure 4). Given the absence of established statistical approaches for comparing multigroup path coefficients in piecewise SEMs with random effects, we interpreted the differences qualitatively across elevations.

During the period of low arthropod activity (Period 1), warming influenced primarily litter decomposition through direct effects (Figure 4a). During Periods 2 and 3, which encompassed the peak arthropod activity, the direct effects of warming on litter decomposition were not significant (Figure 4b,c). Instead, warming affected decomposition indirectly through a trophic cascade. By increasing predator abundance, warming suppressed the abundance of detritivores and consequently reduced detritivore-mediated decomposition (Figure 4b,c). However, this trophic cascade occurred only at 4650 and 5200 m, where the pathways through which warming influenced decomposition were consistent (Figure 4b,c). At 4950 m, although warming also increased predator abundance, it did not further suppress detritivore abundance or their contribution to litter decomposition

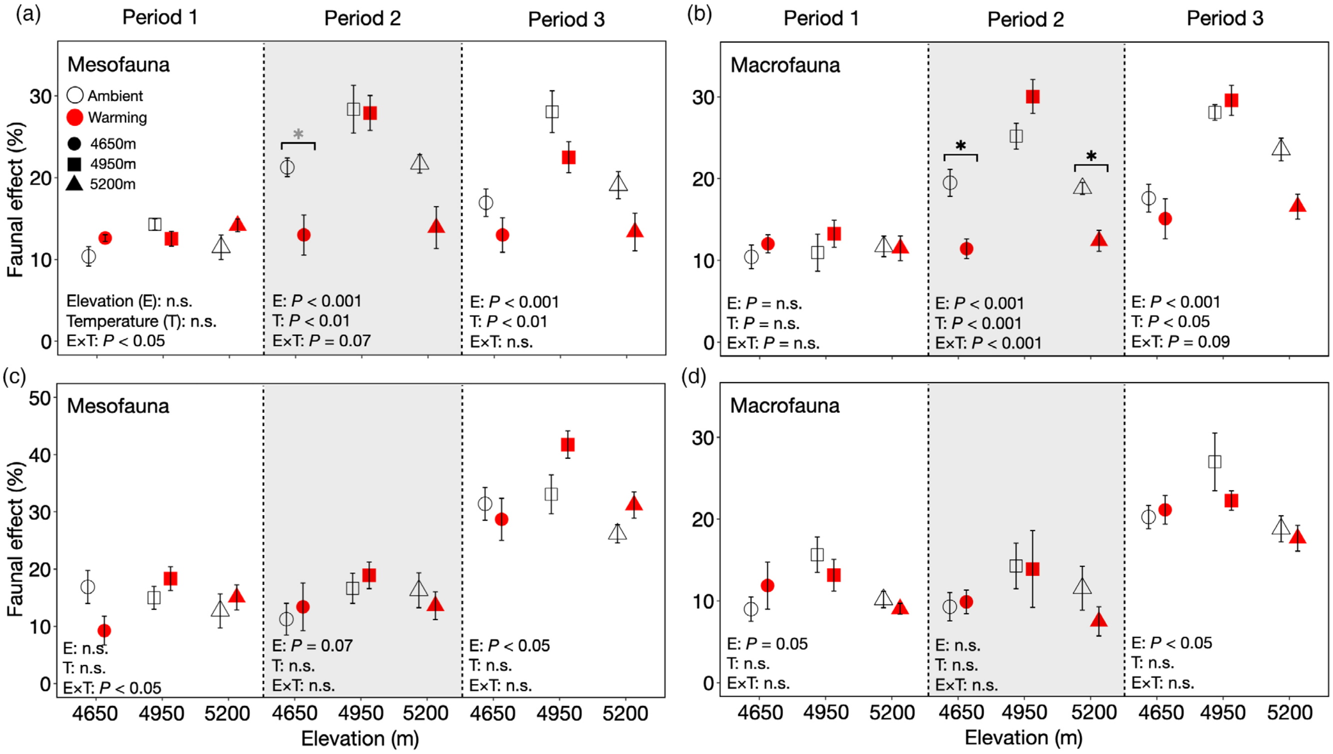
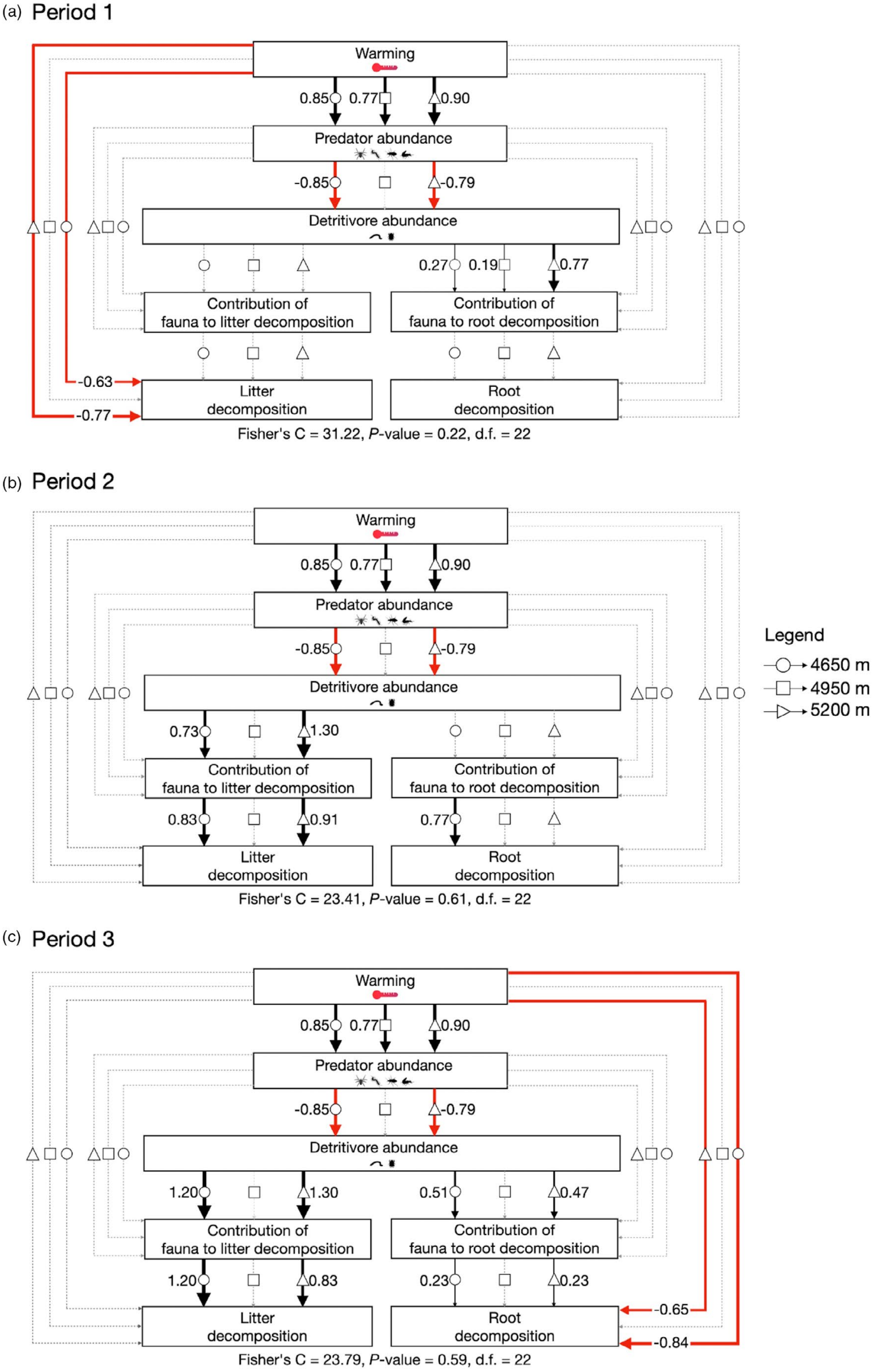


FIGURE 3 Effects of elevation and temperature, and their interactions on the effects of mesofauna (a, c) and macrofauna (b, d) on litter (a, b) and root decomposition (c, d) at different periods (Period 1: Cold season; Period 2: Warm season; Period 3: One whole year). Bars represent means ± SE. Asterisk represents significant (black: $p < 0.05$) or marginally significant (grey: $p < 0.10$) differences between warming and ambient temperature at each elevation. The lower left position of each facet presents the results of the linear mixed model on the effects of elevation and temperature, and their interaction on faunal effect, ns = $p > 0.10$.


(a) Period 1

Fisher's C = 31.22, *P*-value = 0.22, d.f. = 22

(b) Period 2

Fisher's C = 23.41, *P*-value = 0.61, d.f. = 22

(c) Period 3

Fisher's C = 23.79, *P*-value = 0.59, d.f. = 22

FIGURE 4 Multigroup structural equation models illustrating how warming affects leaf litter and root decomposition across three elevations (4650, 4950, and 5200 m; $n = 30$). Panel (a) represents Period 1 (cold season), panel (b) represents Period 2 (warm season), and panel (c) represents Period 3 (one whole year). Black lines indicate positive effects, and red lines indicate negative effects. Solid lines denote significant pathways ($p < 0.05$), whereas dashed lines indicate non-significant pathways ($p > 0.05$). Different shapes represent different elevations, circles for 4650 m, squares for 4950 m, and triangles for 5200 m. Numbers along the paths represent standardized path coefficients. The p-value >0.05 for Fisher's C indicates that the model is consistent with the data.

(Figure 4b,c). Furthermore, over one whole year, warming affected root decomposition via both direct pathways and indirect trophic cascade effects, but only at 4650 and 5200 m.

3.4 | Connection between arthropods with multiple indicators

In the network, the lines indicate the significant correlation between the two indicators, independent from others, and the expected influence is the sum of the correlations between the target indicators and other indicators. Indicators related to faunal diversity had the greatest expected influence (many and strong links with other indicators) under both temperature treatments (Figure 5b,d). The expected influence of the number of arthropod species was greatest with no warming (Figure 5b); faunal abundance had the greatest expected influence with warming (Figure 5d); while the expected influences of detritivore and omnivore abundances increased greatly under warming when compared with ambient temperature (Figure 5d).

4 | DISCUSSION

Arthropod abundance and richness and abundance of each trophic guild were greater at 4950 m than at both lower (4650 m) and higher (5200 m) altitudes. This pattern in arthropod species richness was consistent with the distribution of plant diversity along the elevation gradient (Figure 2a). We interpret this pattern in species diversity in the plant community and its arthropod assemblage as reflecting two contrasting abiotic factors. Due to the low temperature at 5200 m and the low water availability at 4650 m, the plant diversity (species richness) at 4950 m was greatest (Wang et al., 2013). Greater plant species diversity likely provides more 'niches' (e.g. food resources, micro-habitats) for arthropods through a bottom-up effect and, thus, a plant community with high species diversity supports high arthropod species diversity (Barnes et al., 2020; Santonja et al., 2017; Scherber et al., 2010). In the present study, changes in arthropod diversity were caused by plant diversity; however, we focussed on the effects of vertical diversity on cascading effects and decomposition under warming. Additionally, we discussed the potential effects of plant diversity on trophic cascades.

4.1 | Effects of warming on arthropod communities

The present study demonstrated shifts in predator and prey abundances over relatively short timescales. Population sizes can change due to births, deaths or movement. The first two demographic processes require long timescales and, therefore, it is likely that our study was too short to detect changes due to births and deaths. Our findings suggest that the increased abundance of predators in the warming treatments resulted from immigration from the surrounding area. As noted in Section 1, warming could increase the ability of ectothermic predators to capture prey, and/or translate consumption into population growth. Consequently, our warming treatments could have been attractive targets for predators, drawn from the surrounding landscape, leading to an increase in predator numbers (Holt & Kotler, 1987).

Elucidating the mechanisms for the observed correlations is challenging, but we can make some suggestions. Higher temperatures can promote the development, reproduction and activities of predaceous ectotherms, thus increasing predation pressure on lower trophic levels (Romero et al., 2018), while greater predator densities can alter food web structure via top-down trophic cascades (Antiqueira et al., 2018; Barnes et al., 2017). In the present study, the timescale of warming was within a single year, which might represent just one generation for some taxa. A behavioural effect influencing local predator abundance can operate over short timescales via predator migration. The open system in this study permitted aggregative numerical responses by predators, which were likely attracted to warming plots because foraging rates are faster there. This short-term behavioural effect can match longer term population responses requiring multiple generations (Holt & Kotler, 1987). Prey resources can affect predator abundance through bottom-up effects, and predator abundance is usually correlated positively with detritivore abundance (Barnes et al., 2017; Santonja et al., 2017; Tumolo et al., 2023). Thus, the negative correlation between predator and detritivore abundances is consistent with stronger top-down processes under warming (Tumolo et al., 2023), particularly under low diversities. This result supported *Hypothesis 1*.

The top-down effects of predators could be influenced by temperature, while the magnitude and direction of these effects often depend on environmental variables such as resource availability and the presence of refuges from predation (Tylianakis et al., 2008). Greater overall arthropod diversity can correlate with more prey resources for predators, but it also provides opportunities for a greater array of negative interactions between predators, as well as with omnivores (Koltz et al., 2018). Strong IGP and interference among predators have been shown to weaken top-down effects, particularly in systems with diverse predator guilds (Holt & Polis, 1997). Therefore, not all trophic cascades can propagate to low trophic levels, and some mechanisms can relieve or even reverse the trophic cascades with a high diversity among predators (Duffy et al., 2007). In the present study, warming increased predator abundance at the elevation with high arthropod diversity, but this was not accompanied by a decrease in the abundance

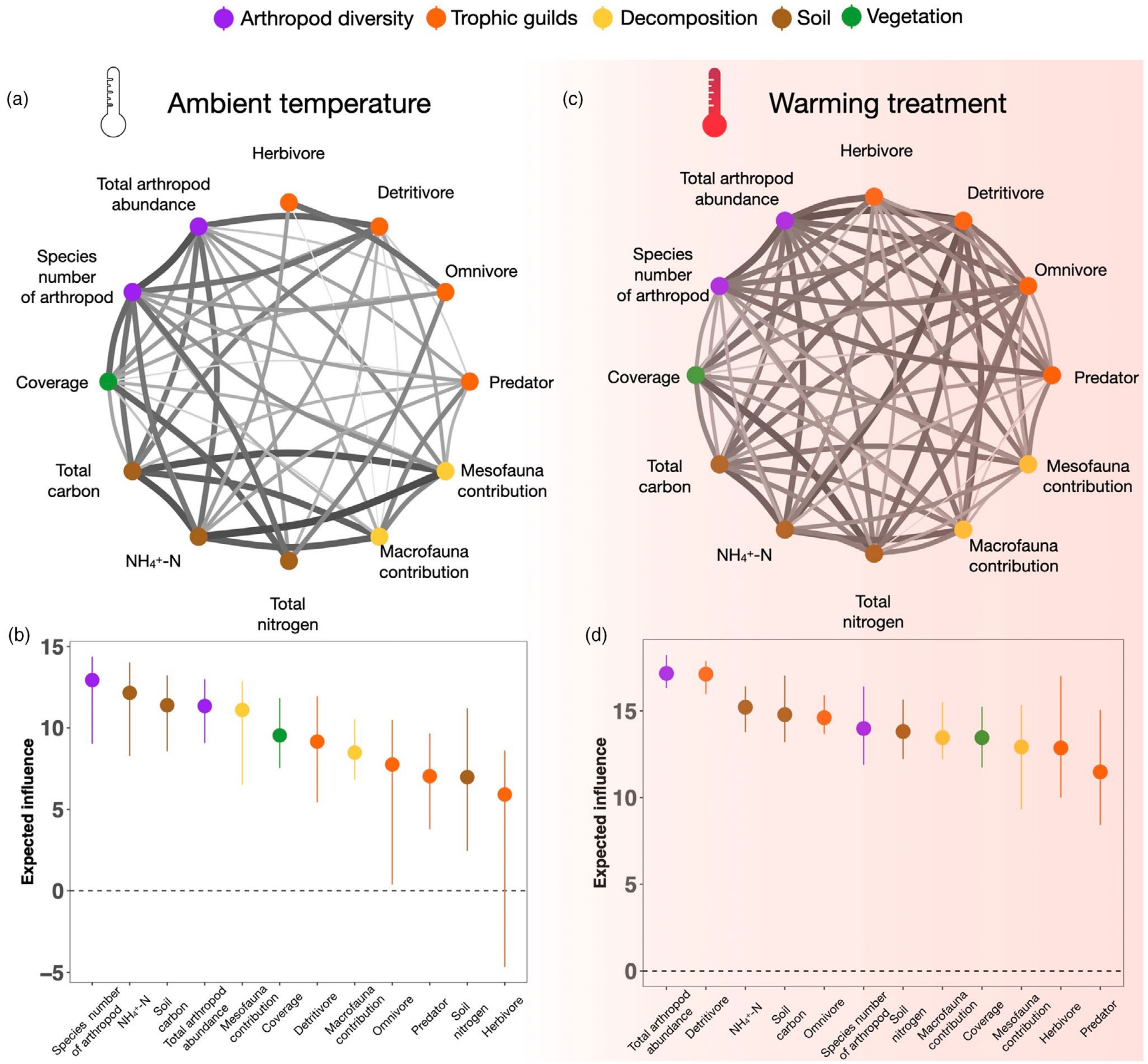


FIGURE 5 The networks for arthropod diversity (species number of arthropod and arthropod abundance), trophic guilds (abundance of predators, omnivores, detritivores, and herbivores), and ecosystem functions (decomposition, vegetation, and soil). (a) and (c) exhibit connectivity among arthropod diversity, trophic guilds, decomposition, soil, and vegetation under ambient temperature and warming treatment. (b) and (d) present the expected influence of each indicator on the network under ambient temperature and warming treatment. In (a) and (c), the lines indicate significant pairwise correlations between the indicators (95% confidence intervals do not overlap with zero); darker and wider lines indicate stronger correlations.

of lower trophic guilds. More abundant predators and omnivores were associated with higher vertical diversity (Duffy et al., 2007; Wang et al., 2019; Wang & Brose, 2018). Since the abundances of omnivores and predators were greater at an elevation with high than low arthropod diversity, IGP between predators (Wang & Brose, 2018; Wu et al., 2011), or stronger antagonistic interactions between predators and omnivores, might reduce total predation at the low trophic levels (Sitvarin & Rypstra, 2014). These antagonistic effects complicate the top-down effects expected when predator abundance is increased and can even reduce the negative effects of increased predators on lower trophic levels (Duffy et al., 2007). Moderate predation can increase the opportunities of coexistence of competing species at low trophic levels (Karakoç et al., 2020).

4.2 | Relationship between predators and decomposition under warming

We tested the vertical diversity hypothesis in brown food webs under warming. During periods of peak arthropod activity, the direct negative effect of warming on decomposition became non-significant. Instead, warming increased predator abundance significantly, which indirectly reduced detritivore abundance and subsequently decreased litter decomposition. These results supported *Hypothesis 2*. This indirect cascade effect was observed at both 4650 and 5200 m, sites with low arthropod diversity. The path structures at these two elevations were nearly identical and clearly differed from those at the mid-elevation site (4950 m), where arthropod diversity was greater and the cascade effect was not significant. These findings support *Hypothesis 3*, that top-down control by predators would be weakened at sites with high arthropod diversity, resulting in unchanged decomposition under warming. Given the relatively small sample size ($n=30$), the SEM could have been overfitted, and a larger dataset is needed to test these relationships more rigorously. Nevertheless, findings in the present study offer an initial indication that warming-driven changes in predator abundance can influence decomposition processes.

Warming affects decomposition by altering the magnitude and direction of effects of predators on low trophic levels (Romero et al., 2018; Tylianakis et al., 2008). In the current study, with low arthropod diversity, the cascading effects of increased predator abundance under warming on ecosystem function were substantial (Barnes et al., 2020), as they reduced the faunal effects on litter decomposition in the warm season to the same level as in the cold season with little fauna activity. Under ambient temperature conditions at elevations with low arthropod diversity, millipedes, the dominant detritivores, were observed in all plots. However, with warming, millipedes were present in only three plots, and their abundances were reduced (Figure S3). It is important to note that millipedes are the primary prey for predators such as ground beetles, spiders, centipedes and rove beetles (Melguizo-Ruiz et al., 2020). Given the high homogeneity of vegetation types (alpine meadow) on the Qinghai–Tibetan Plateau (Miehe et al., 2019), these effects could scale across the region.

When predicting decomposition rates as a consequence of climate change, the local climate temperature and precipitation are usually considered (Bradford et al., 2014, 2016). For example, when low temperature or moisture are limiting factors, warming or increased precipitation can promote litter decomposition by mitigating these constraints on microbial activity (Thakur et al., 2018). In the present study, the temperature at 5200 m was the lowest and the humidity was the highest of the three elevations (Figure S2); however, the faunal effects on litter decomposition at 4650 and 5200 m did not differ with warming, as both were affected negatively. Thus, at the local scale, biodiversity may potentially be one of the key factors determining how climate change influences decomposition, beyond the direct effects of climate alone (Joly et al., 2023). However, we emphasize that identifying arthropod diversity as a key modulating factor of warming effects in the present study is based on observed patterns and causal inference. Further research across multiple replicated sites, combined with controlled manipulative experiments, is needed to test the role of arthropod diversity and species interactions in shaping decomposition responses to climate warming.

4.3 | Relationship between arthropods and ecosystem functions

Based on the network analysis, species diversity played an important role, while diversity indicators of arthropods exhibited the strongest influence on ecosystem functions in both ambient temperature and warming treatments. It should be noted that in the warming treatment, the greatest expected influence was the total arthropod abundance and not the number of species. This may be related to the decrease in detritivore abundance and the contribution of arthropods to decomposition at elevations with low arthropod diversity, and the increase in total arthropod abundance and the contribution of arthropods to decomposition at the elevation with high arthropod diversity under warming. The expected influence of omnivore abundance increased greatly under warming compared to ambient temperature. Omnivores can contribute to ecosystem stability by increasing interspecific interactions and food chain length (McCann & Hastings, 1997). Additionally, we observed strong correlations between soil nutrient indicators and contributions of arthropods to decomposition, which suggests that reduced arthropod contributions to decomposition, driven by stronger top-down predator effects, may influence soil nutrient dynamics over longer timescales by altering biogeochemical cycling (Freschet et al., 2013). These potential effects may become more evident over extended periods, as the consequences of altered decomposition rates accumulate.

4.4 | Potential mechanisms

Plant diversity and biomass can influence the strength of trophic interactions. Furthermore, plant species diversity could (1) influence total plant biomass, which can alter the strength of predator–prey interactions (Holt & Barfield, 2013); and (2) diminish the impact of herbivores (Civitello et al., 2015; Keesing & Ostfeld, 2024). It is plausible that plant species diversity weakens the impact of predators on herbivores by providing a greater variety of microhabitats enabling an escape from predation. This would represent a bottom-up ‘dilution effect’ of plant diversity on interaction strengths across the food web. To our knowledge, this potential effect of plant species diversity on trophic interactions among species at higher trophic levels has not been reported. In the present study, we focussed on how diversity in predatory arthropods can influence top-down effects. However, there could also be complementary bottom-up effects of diversity on trophic interactions, as suggested in the present study.

The relationship between biodiversity and ecosystem functions has been studied extensively (Fanin et al., 2018). These studies tended to focus on only one trophic level (horizontal diversity), such as the relationship between plant diversity and primary productivity. However, how biodiversity influences ecosystem functions across multiple trophic levels in detritus-based food webs (vertical diversity) and shapes ecosystem responses to climate change is complex and remains poorly understood. Our findings provide support for the vertical diversity hypothesis, suggesting that vertical diversity may play a role in mediating ecosystem responses to climate warming, potentially by buffering detritivores from increased predator pressure under warming conditions. Our study offers new preliminary insights into how environmental factors may regulate decomposition responses to warming. Future research should employ more mesocosm-based manipulative experiments and large-scale field studies to test the generality of these findings.

AUTHOR CONTRIBUTIONS

Binyu Luo conceptualized the study, designed the methodology, conducted the investigation, prepared the visualizations, drafted the manuscript and revised it. Jingxue Zhao conducted the investigation and contributed to the methodology. A. Allan Degen and Robert D. Holt contributed to the methodology and revised the manuscript. Lauchlan H. Fraser revised the manuscript. Mei Huang, Wenyin Wang, Tianyun Qi, Zhen Peng and Lingyan Qi conducted the investigation. Peipei Liu conducted the investigation and revised the manuscript. Zhanhuan Shang conceptualized the study, designed the methodology, performed the formal analysis, revised the manuscript, administered the project, acquired funding and supervised the study.

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CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are available in Figshare: https://doi.org/10.6084/m9.figshare.30082258 (Luo et al., 2025).

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SUPPORTING INFORMATION

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

Figure S1. Study sites in alpine meadow (a); warming treatment (b); litter decomposition with different mesh sizes and windproof PVC pipes (c); root decomposition with different mesh sizes (d).

Figure S2. The average daily air temperature, soil temperature and air humidity at three elevations. The insets are annual averages.

Figure S3. Effect of warming on millipede abundance at three elevations.

Figure S4. Linear relationships between predator and detritivore abundances at elevations with low arthropod diversity under ambient temperature and warming.

Figure S5. Effects of mesh size and elevation on litter (a) and root (b) decomposition. * represents significant ($p < 0.05$) differences among mesh sizes at each elevation. Means with different lowercase letters differ significantly among elevations in the same mesh size. (c) Effects of decomposition period and mesh sizes on root and litter (left) and root (right) decomposition.

Figure S6. Linear correlations between predator abundance and decomposition under ambient temperature (a, b) and warming treatments (c, d) at three elevations and three periods.

Figure S7. A priori conceptual model illustrating how warming can influence decomposition through both direct and indirect effects mediated by trophic cascades.

Table S1. The taxa and trophic guilds of the arthropods. To enhance clarity, specific species names and their distribution are provided for some arthropod.

Table S2. Statistics of the linear mixed-effects models testing the effects of temperature, elevation, and their interaction (temperature × elevation) on the contribution of mesofauna to litter decomposition across three periods (Period 1 = cold season, Period 2 = warm season, Period 3 = whole year).

Table S3. Statistics of the linear mixed-effects models testing the effects of temperature, elevation and their interaction (temperature × elevation) on the contribution of macrofauna to litter decomposition across three periods (Period 1 = cold season, Period 2 = warm season, Period 3 = whole year).

Table S4. Statistics of the linear mixed-effects models testing the effects of temperature, elevation, and their interaction (temperature × elevation) on the contribution of mesofauna to root decomposition across three periods (Period 1 = cold season, Period 2 = warm season, Period 3 = whole year).

Table S5. Statistics of the linear mixed-effects models testing the effects of temperature, elevation, and their interaction (temperature × elevation) on the contribution of macrofauna to root decomposition across three periods (Period 1 = cold season, Period 2 = warm season, Period 3 = whole year).

Table S6. Statistics of the multigroup structural equation models for Period 1 (cold season), presenting the path coefficients that differ significantly across elevation groups.

Table S7. Statistics of the multigroup structural equation models for Period 2 (warm season), presenting the path coefficients that differ significantly across elevation groups.

Table S8. Statistics of the multigroup structural equation models for Period 3 (one whole year), presenting the path coefficients that differ significantly across elevation groups.

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