



# Contribution of different predator guilds to tritrophic interactions along ecological clines

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The strengths of interactions between plants, herbivores, and predators are predicted to relax with elevation. Despite the fundamental role predators play in tritrophic interactions, high-resolution experimental evidence describing predation across habitat gradients is still scarce in the literature and varies by predator. With this opinion paper, we look at how tritrophic strength of systems including different vertebrate and invertebrate predator guilds changes with elevation. Specifically, we focus on how birds, ants, parasitoids, and nematodes exert top-down pressure as predators and propose ways, in which each group could be better understood through elevational gradient studies. We hope to enrich future perspectives for disentangling the different biotic and abiotic factors underlying predator-mediated trophic interactions in a diversity of habitats.

## Addresses

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## Introduction

Tritrophic interactions (TTIs) link the trophic chain from autotrophs, herbivores, and predators. The top-down cascading effect of predators attacking herbivores indirectly benefits plants, structuring biodiversity and community dynamics [1]. Plant traits mediate TTIs through constitutive or herbivore-induced chemical profiles that lure predators near the site where herbivory has occurred [2], and/or physical features such as plant structures, domatia and/or extrafloral nectaries, which provide habitat to support predators [3]. However, a plants' ability to

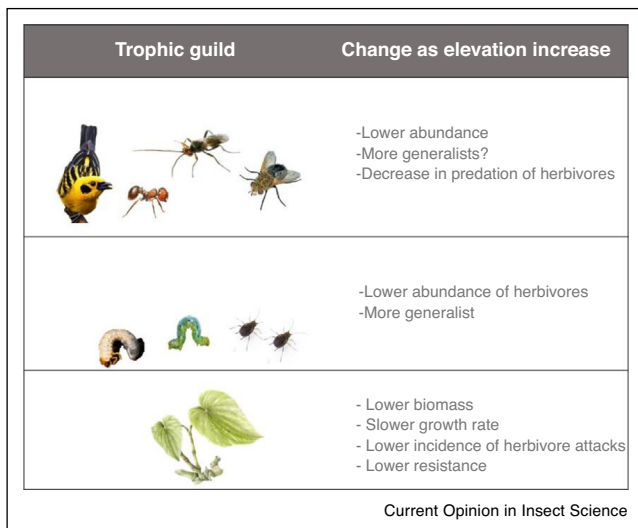
recruit predators varies [4,5]. Much of this variation might be explained through understanding the connection between the type of key predator driving the TTI and the variability in the ecological conditions that drive these interactions (i.e. varying abiotic and biotic factors) [6–8]. In this opinion paper, we aim to discuss how to disentangle the relative role of biotic versus abiotic factors dictating the variability of TTIs in four key predator guilds of vertebrates and invertebrates, for which there is extensive research. To do so, we will use elevational gradients as a conceptual model based on their intrinsic abiotic and biotic variation [9,10].

Using elevational gradients to address variation in biological interactions has several advantages. First, adaptation to habitat-specific abiotic and biotic factors can be studied along elevation transects regardless of biogeographic history, gene-flow barriers, and within homogenous macroclimatic conditions [10,11]. Second, for every 1000 m in elevation gain, temperatures drop roughly 5–6°C, with consequences for enzymatic activity at all trophic levels [12]. Therefore, elevational gradients could be used to address the effect of climate change on TTIs [13]. Third, along elevational gradients, plants and insects show wide variation in many functional and phenotypic traits, including physiological, growth-related, reproduction-related, and defense-related traits. Trait variation in divergent habitats should in turn influence the magnitude and direction of TTIs [14•]. By assembling patterns exposed by elevation-gradient research, we highlight the patterns of TTIs associated with several well-studied guilds of predators. For each predator example, we address how each-specific tritrophic system can be studied along elevational gradients to disentangle abiotic and biotic selection pressures. In doing so, we aim at stimulating future research that may address how different biotic and abiotic factors shape multitrophic interaction networks along ecological clines.

## Elevation-driven patterns of species interactions

Predator communities and predation risk decline with elevation [12,15•] (Figure 1). As a result, fewer herbivores die from enemy-caused mortality with increasing elevation [16]. If the herbivore populations do not perfectly parallel the physiological constraints limiting predators at high elevation, elevation could release herbivore populations from predation (enemy-free hypothesis) and thus

Figure 1



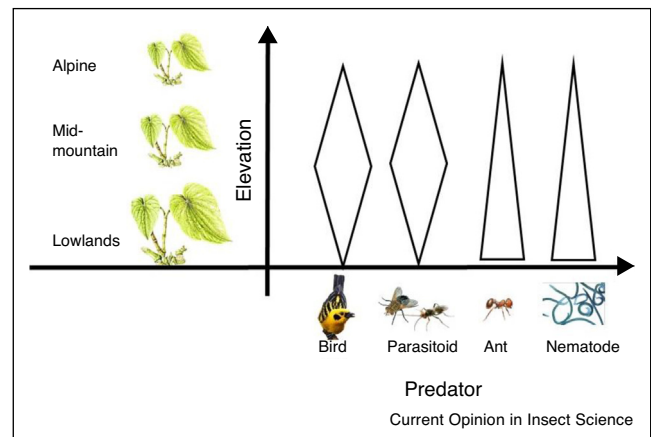
Tritrophic interaction changes along elevational gradients. Shown are different tritrophic systems including different herbivore guilds and different predators guilds discussed in the text.

increase herbivore pressure. Indeed, arthropod predator attack rates on global average drop 9.6% with every 100 m of increasing elevation [15<sup>o</sup>]. However, herbivore populations do not necessarily boom at higher elevations, being similarly constrained by temperature effects on enzymatic rates [12]. Herbivores along elevational gradients tend to feed with a more generalist approach [10,17], responding to lower concentrations of direct chemical defenses [18,19] and other plant trait patterns following the elevational gradient but mostly due to the reduced availability of primary productivity. In line with Oksanen [20], reduced predator communities at higher elevations may be a symptom of trophic biomass availability, limited at the base by plant trait allocation differences between elevation-specific habitats. While predator–prey interactions in elevation-specific habitats have been of interest for a long time to understand trophic ecology, the mechanisms underlying predator effects in tritrophic interactions have not been well characterized. To elucidate patterns based on well-studied guilds of predators, here we describe how elevation influences plant-mediated TTIs for several distinct predator types (Figure 2): birds (vertebrate, second-order predator), ants (invertebrate predator with aggressive behaviour for plant defence), parasitoids (invertebrate predator with specific host-finding behaviour for plant defence), and belowground predatory nematodes (microfauna, belowground predator) in order to outline current advances and propose-specific future venues of research for each.

#### Plant–herbivore–bird interactions

As abundant and efficient insectivores, all trophic levels are affected by the presence of birds, and plants benefit

Figure 2



Trends in predator abundance/diversity along elevational gradients. Overall, predators tend to decline sharply at high elevation. Nonetheless, some groups, such as insectivorous birds and parasitoids seems to display peak abundance at mid-elevation. Stronger predation/parasitism is designated by a width of the figure.

from the presence of insectivorous birds across habitats (tropical, temperate, boreal), land-use type (agroecosystem or natural forests) and development (saplings and mature trees) [21,22]. Further, the more diverse the bird community, which also depends on the plant community diversity, the stronger the TTI strength [23]. However, bird predation has less of an influence compared to arthropod predators on worldwide elevational patterns of attack rates [15<sup>o</sup>]. Several elevation-specific factors may contribute to structuring how birds may not emerge in the elevational meta-analysis, yet serve to strengthen positive effects on plants through TTIs. First, elevation-driven conditions alter habitat structure, and second, different elevations support various migratory paths for specific groups of birds. Bird predation pressure often depends on appropriate habitat, structured by the plant communities including tree diversity and canopy density [22,23]. Elevation-driven changes in plant communities, with a shift from deciduous to coniferous forests to above the treeline influence the role of birds as top-down tritrophic interactions, and as a result, their effects on plant growth [24]. A general trend is that insectivorous bird species number and abundance decreases with increasing elevation, although at mid-elevation, bird diversity spikes, and the burst in diversity is entirely driven by insectivores [25–27]. A study along a tropical elevational gradient found higher bird predation in tropical montane habitats [28]. In temperate forests, Schwenk *et al.* [24] found that bird exclusions increased arthropod abundance in low and mid elevations but had little effect at high elevations. Insectivorous birds selecting for particular plant indirect defense characteristics to further facilitate their predation efficiency has not been

recorded, nor tested along a gradient of habitats with elevation. Nonetheless, recent evidence suggests that birds use plant-derived and herbivore-derived olfactory cues to find insect prey [29,30]. Bird versus insect physiology (endotherm versus ectotherm) and temporal patterns (i.e. migration, growing season length), and insect apparency from a birds-eye view (darker color morphs and sun-soaking behavior at higher elevations with lower temps) could be important factors to consider in studies along elevational gradients. Such studies could also resolve some of the context-dependent conclusions from testing birds as keystone or top-down impacts on food webs [24].

### Plant–herbivore–parasitoid interactions

Parasitoid wasps and flies contribute to the top-down impacts on the trophic structure of communities and control herbivorous insect populations differently depending on elevational habitat. The elevation-specific factors determining the strength of parasitoid pressure in TTIs will depend on how easy it is to find a host and how safe will the parasitoids' progeny be once the herbivore is parasitized. Factors that influence the ability of parasitoids to find a host have to do with plant indirect defense traits such as investment in emitting volatile recruitment cues, and how cold temperatures may limit the ability to search and find hosts. Exposure to the cool and short-lived productivity peaks that occur at high elevations may limit parasitism, by allowing adult parasitoids a short window to find a suitable host for its' progeny [31]. The safety of the parasitoid will have to do with how palatable the host is to other predators and how likely it is for the host to get hyperparasitized. Plants in high-elevation sites show more inducible patterns of herbivory-associated volatile cues to recruit parasitoids, and secretion of extrafloral nectar [32], which is typically associated with ants but can also be important for sustaining parasitoids [33]. Higher elevation extrafloral nectaries had higher visitation by parasitoid wasps and flies [5]. However, parasitism in many temperate examples disappears above a peak parasitism rate at mid-elevations [12,34]. A macroecological approach via meta-analysis of known plant–herbivore–parasitoid interactions has shown parasitism rates decreasing with elevation, and functional types of parasitoids to be differentially influenced by elevation, depending on the external or internal nature of the herbivorous host insect [35]. Indeed, host specificity is a key feature of parasitoids in TTIs; unlike herbivores becoming more polyphagous with increasing elevation, parasitoids become more specialized, decreasing their host breadth from several species at lower elevations and tend to attack single host species at higher elevations [36]. This suggests that elevation patterns in parasitism rates we have observed so far are biased because of a sub sampling effect since it takes more effort to find unique interactions than generalized ones [37].

Taking together known elevational patterns of plant diversification, insect enzymatic rates, and parasitism rates, we could speculate that the increased host specificity of parasitoids under more extreme abiotic stress may result from the additional physiological costs in responding to their host insects' sequestered toxins, immune responses, and increased diet breadth. Limited host adaptation is evident through translocating a leaf-mining weevil species from high elevation, where it escapes parasitoid attack, to lower elevation, where leaf miner parasitism rates are higher, and yet the weevil remained parasitoid-free [36]. The implications for parasitoid-specific TTIs in varying habitats on food web structure and plant success are beginning to emerge, but require the simultaneous understanding of plant volatile cues mediating recruitment, abiotic limitations on in-host development, and intraguild predation from hyperparasitoids and other second-order consumers.

### Plant–herbivore–ant interactions

Plant–ant symbioses, often mediated by nectaries or domatia, are ubiquitous in both tropical [38] and temperate [39] habitats. Yet, the resulting strength of ant-driven TTIs depends on the ant species and behavior, as well as the environmental conditions [40,41]. Ant abundance and diversity steadily decline with increasing elevation [32,42]. We confirmed elevational declines in ants along the Swiss Alps by gathering more than 4000 occurrence data points for over 100 years (source: infofauna.ch). Overall, ant diversity steadily declines at a pace of about 1.8 species lost per 100 m gain in elevation, covering a range of roughly 49 ant species at 300 m to practically zero ant species around 3000 m (Pearson correlation,  $r = -0.89$ ,  $p < 0.001$ ). Even in cases where ant communities remain consistent across elevation sites, trophic interactions can depend on environmentally driven changes in behavior. Ant foraging and aphid-tending behavior are more intense at lower elevations [43], confirming earlier observations that ants take up less of plant-provided extrafloral nectar at higher elevations, and serve less of a defensive service [5]. Given that the aggressiveness of ants depends on their protein:carbohydrate ratios [44], behavioral differences across elevation in relation to aphid-tending or plant-protecting may be connected to foraging requirements for meeting insect physiological demands under different temperatures associated with elevation. When plants are less protected by ants at higher elevations in the tropics, plants respond by shifting defense investment away from ant-attracting traits towards direct defense and herbivory tolerance [45]. In the Alps, *Vicia sepium* plants switch from a constitutive production of ant-attracting volatile organic compounds at low elevation to only induce the volatiles upon herbivore damage at high elevation [32].

Connecting ant-driven trophic structures to the top-down role of other predators and the plant traits that

mediate TTIs in different habitats could have major implications, given the role of ants as ecosystem engineers, connected to biogeochemical cycling and below-ground processes. For instance, one avenue for understanding ant–plant interactions and how they change across elevation there could be to work with stable isotopes for measuring the transfer of carbon and nitrogen between plants and ants [43,46].

#### Plant–herbivore–nematode interactions

Soil-dwelling predators can also shape TTIs from below-ground, where roots are also subjected herbivory [47,48]. As with shoots, herbivore-damaged roots release information-rich volatile cues into the soil to recruit predators, including not only many arthropod predators [49], but also entomopathogenic nematodes [50,51]. To date, very few examples exist that explored the effect of elevation (or any other ecological gradient) on belowground TTIs. Recently, Kergunteuil *et al.* [52] showed that the entomopathogenic nematode-based biocontrol potential of high-elevation soils was lower than for low-elevation soils. We hypothesized plants relax indirect defenses at high elevation. We tested this hypothesis using reciprocal transplant common-garden experiments of high and low elevation ecotypes *Festuca rubra* and factorially manipulated herbivore and predator presence. We found that only low-elevation ecotypes survived better when in the presence of root herbivores and entomopathogenic nematodes [53]. Future experiments will need to quantify root herbivory at different elevations and quantify plant fitness *in situ* when root herbivores are added to the different soils. Belowground TTIs in varying environmental conditions have potential to unveil major ecosystem processes since soil-based predators also intersect with detritivore food webs [54], and, therefore, have potential to have a top-down impact (from below) on geochemical cycles and nutrient availability. If higher elevation soil-dwelling predators are prey-limited, we would expect this to contribute to the slowed enzymatic rates, which are hypothesized to cause the lower decomposition rates observed at higher elevations.

#### Future outlooks for tritrophic interactions and elevation

There have been two general approaches to studying trophic cascades along elevational gradients. The first approach is to study plants, herbivores, and predators/parasitoids, and report changes across elevational gradients in diversity, herbivory, parasitism rates, diet breadth, and food-web structure [17,55]. In general, these studies build on previous knowledge on distributions of plant and herbivore species, thus contributing to the partial knowledge on the parasitoid and predator communities. A second approach is to characterize detailed plant defense profiles across elevational gradients and associates these profiles to the response in herbivores and predators/parasitoids [53,56\*]. Future research would

preferentially integrate the two approaches. For instance, this could be achieved by conducting reciprocal transplants of plant species with known plant direct and indirect defense mechanisms, and analyzing plant resistance to herbivory through studies of the changes in concentrations and the allocation of plant resources across the gradient. In concomitance, the distribution of the herbivore community, herbivory rates, and parasitism/predation rates should be analyzed. Finally, macroecological studies such as these ones can be now combined with recently available techniques such as DNA fingerprinting of plant genus–herbivore communities and parasitoids across the entire elevation distribution. Such a food-web structure could then be analyzed in relation to plant metabolomics profiling, which then can be integrated to herbivore and parasitoid food webs [57]. Given the intensified effects of environmental conditions on predators in a trophic system [58], understanding the contribution of the separate and interacting TTIs across environmental gradients is essential for understanding food web stability across different habitats around the world.

#### Conflict of interest statement

Nothing declared.

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