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Seasonal changes in arthropod diversity patterns along an Alpine elevation gradient

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Abstract. 1. Deciphering patterns in species distributions and species interactions along ecological gradients are fundamental topics in ecology. Theory holds that species diversity is greater and interactions are stronger under warmer and more stable environments, such as low elevations and latitudes. However, recent findings have shown conflicting evidence, potentially due to seasonal effects.

2. We aimed to address this gap by studying seasonal changes in arthropod communities over an elevation gradient in the Swiss Alps, as well as herbivore-predator interactions and their resulting consequences on plant herbivory levels.

3. Overall, we found hump-shaped patterns in arthropod abundance, richness and diversity with increasing elevation, with all factors peaking below the tree line. However, these patterns varied seasonally, with strong mid-elevation peaks at the beginning of the summer, shifting to a pattern of linear decrease at the beginning of the fall. In searching for mechanisms explaining these changes, we found that shifts in arthropod communities over elevation and seasons usually followed shifts in vegetation productivity estimates. Other factors, such as top-down control by natural enemies, which was generally stronger at low elevations, and plant species-specific resistance rates along elevation gradients were also implicated as drivers of diversity and herbivory rates.

4. These results highlight the complexity of arthropod communities' responses to environmental gradients, which vary during the season in response to relative changes in both bottom-up and top-down forces.

Key words. environmental gradients, herbivory, natural enemies, species distribution.

Introduction

Predicting species distributions and their interactions along climatic gradients is one of the main objectives for ecologists (Tylianakis *et al.*, 2008; de Sassi *et al.*, 2012; Rasmann *et al.*, 2014). Variation in temperature and precipitation along large scale ecological gradients, such as along elevation and latitude has been shown to impact the distribution of species and their range limits (Pauli *et al.*, 2007; Colwell *et al.*, 2008; Parmesan & Hanley, 2015). Furthermore, although species are connected by trophic links, individual species respond differently to climatic factors (Pincebourde *et al.*, 2017). Accordingly, environmental gradients are powerful tools for understanding how abiotic climatic conditions modify trophic interactions and species distributions (Schemske *et al.*, 2009; Sundqvist *et al.*, 2013; Rasmann *et al.*, 2014; Galmán *et al.*, 2018; Moreira *et al.*, 2018). Notably, elevation gradients have been useful for assessing the effect of climatic factors on community composition changes (Körner, 2007; Rasmann *et al.*, 2016), while simultaneously minimizing the confounding effects of historical and biogeographical differences in the species pools (Hodkinson, 2005; Beck & Kitching, 2009; Moreira *et al.*, 2018).

Plant and insect diversity is generally predicted to decline with increasing elevation (Rahbek, 1995; Rahbek, 2005; Nogués-Bravo *et al.*, 2008; Moreira *et al.*, 2015), likely due to decreases in the annual thermal budget for growth and development at high elevation (Hodkinson, 2005). Accordingly, a review of the distribution of 25 major plant and animal taxa along elevation gradients observed that, while single taxa show complex distribution patterns, scaling up diversity values at the community level leads to a general linear decline with elevation

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(Peters *et al.*, 2016). Plant productivity has also been shown to be a good predictor for arthropod biomass, diversity, and richness (Richardson *et al.*, 2002; Vinson & Hawkins, 2003; Sweet *et al.*, 2015; Beck *et al.*, 2017; but see Sanders *et al.*, 2007), and thus, a good predictor for elevational influences on arthropod communities. However, patterns between elevation and diversity indices are quite variable in both form (i.e. linear, hump-shaped, or more complex non-linear relationships, Peters *et al.*, 2016) and direction (i.e. positive vs. negative, McCain, 2009; McCain & Grytnes, 2010; Rasmann *et al.*, 2014; Peters *et al.*, 2016; Galmán *et al.*, 2018; Moreira *et al.*, 2018) across different groups of organisms. A positive, hump-shaped curve of species richness along elevation seems to be the pattern most frequently observed (Rahbek, 1995, 2005; Brehm *et al.*, 2007; Nogués-Bravo *et al.*, 2008; Kessler *et al.*, 2011; Beck *et al.*, 2017). This pattern could be generated by a mid-domain effect, in which mid-elevations accumulate species from both high and low elevation (Rahbek, 2005; Brehm *et al.*, 2007), or because mid-elevation zones are statistically more prone to accumulate a higher number of species than margins via random distribution events (Sanders, 2002; Colwell *et al.*, 2004).

In the case of arthropod herbivores, their response to climatic gradients may be derived from direct effects, with arthropods responding to changing environmental parameters (e.g. temperature), or indirectly, through interactions with other organisms like their host plants, competitor species, parasitoids, predators, or pathogens (Hodkinson, 2005; Sundqvist *et al.*, 2013; Mooney *et al.*, 2016). Accordingly, theory on elevation gradients holds that herbivore pressure decreases with elevation, as climate becomes more cold and unstable (Rasmann *et al.*, 2014). However, recent reviews found no evidence of the expected trends, or even increasing herbivory pressure with elevation, challenging the generality of this expectation (Moreira *et al.*, 2018). Therefore, the diversity and abundance of arthropod herbivores along elevation is not only mediated by temperature changes but also by bottom-up effects including plant quality and defenses, and top-down control from predators and pathogens (Sundqvist *et al.*, 2013; Moreira *et al.*, 2018).

Changes in abiotic conditions along elevation may influence herbivory pressure by modifying plant chemical and physical traits related to their resistance or nutritive quality to herbivores (Rodríguez-Castañeda *et al.*, 2010; Moles *et al.*, 2011; Pellissier *et al.*, 2012, 2016). Accordingly, if high-elevation plant species are less nutritive and more defended (either physically or chemically) than their low-elevation counterparts, it would drive a reduction in herbivore pressure at high elevation, as observed in oaks (Galmán *et al.*, 2019), pines (Moreira *et al.*, 2014), and *Cardamine* species (Defossez *et al.*, 2018). However, the reverse seems to be more common; high elevation plant communities tend to be more palatable, at least against generalist caterpillars (Callis-Duehl *et al.*, 2017; Descombes *et al.*, 2017), suggesting variable effects of plant defenses on herbivory along elevation depending on the system under investigation.

Shifts in the abundance or diversity of herbivores' natural enemies may also influence herbivory pressure on plants along elevation gradients (Hodkinson, 2005; Godschalx *et al.*, 2019). Higher trophic levels such as parasitoids and predators are important drivers of species interactions, and have been shown to be especially sensitive to abiotic change (Nelson *et al.*, 2019). This increase in sensitivity of higher trophic levels may be explained by their relatively smaller population size and greater metabolic demands (Petchey *et al.*, 1999; Voigt *et al.*, 2003). Previous studies exploring the distribution of natural enemies along elevation gradients have suggested a decline in predation and parasitism with increasing elevation (Brenner *et al.*, 2002; Hodkinson, 2005; Péré *et al.*, 2013; Morris *et al.*, 2015). Consequently, herbivore-predator interactions should be stronger at lower latitudes and elevations (Coley & Barone, 1996; Mooney *et al.*, 2016; Moreira *et al.*, 2018), and it is expected that predation risks for insect herbivores are higher at low elevations (Roslin *et al.*, 2017). However, recent research reports conflicting evidence about the generality of this paradigm (Moles *et al.*, 2011; Moles & Ollerton, 2016).

In order to shed further light on how arthropod communities vary along elevation gradients, and how they could in turn influence plant communities, we performed arthropod capture surveys and common garden experiments along an elevation transect from 440 to 2050 m in the Swiss Alps. We explored elevational patterns in abundance, richness and diversity of arthropod communities, including herbivore, predator and parasitoid communities, and their resulting impacts on herbivory pressure. We hypothesised the following: (i) total arthropod diversity and abundance should show hump-shaped patterns with increasing elevation; and (ii) these patterns should hold when we focus only on herbivore arthropods. As natural enemies are supposedly more sensitive than herbivores to environmental factors such as decreasing temperatures (Voigt *et al.*, 2003), (iii) the ratio between natural enemies and herbivores should decrease with elevation; and (iv) this should result in higher overall herbivore damage at low-elevation. By addressing these hypotheses our study builds towards a better understanding of how arthropod communities and their impacts on host plants are affected by environmental gradients.

Materials and methods

Arthropod sampling and classification

In summer 2018, we investigated changes in arthropod communities along an elevation gradient in the Western Swiss Alps (municipality of 'Lavey-Morcles'; 46°12′0″N; 07°02′0″E). Arthropods were collected at 440, 1520, 1760 and 2050 m above sea level (asl). At each elevation, arthropod captures were performed along five three-meter long transects, oriented westward, by regularly sweeping the net (50 cm in diameter) from one side of the middle of the transect to the other, 5–10 cm below the vegetation canopy height. Changes in temperature and precipitation experienced during the season may differentially affect arthropods at different elevations. For this reason, samplings were performed four times over the whole vegetation season: on 4 July, 7 August, 28 August, and 18 September 2018, only on sunny days. For each site, we calculated normalised difference vegetation index (NDVI) within a maximum of 2 weeks around the four sampling times. NDVI values, based on high-resolution hyperspectral satellite imagery from Landsat7, and calculated as a ratio between the red (R) and near-infrared (NIR) values with the formula NDVI = (NIR − R)/(NIR + R), are related to the local plant photosynthetic activity.

Arthropod diversity was estimated according to the *Rapid Biodiversity Assesment* (RBA) method, which is based on the morphospecies classification of the sampled individuals (Oliver & Beattie, 1993, 1996; Bolger *et al.*, 2000; Kerr *et al.*, 2000; Obrist & Duelli, 2010). Specifically, two or more specimens were considered to belong to the same morphospecies if we could not detect any external morphological difference between them (Obrist & Duelli, 2010). The functional guild of morphospecies was then extrapolated based on their taxonomic group following Obrist and Duelli (2010), Balzan *et al.* (2014) and Dubuc (2007), see Table S1. When multiple functional types per taxonomic group were present, assignment was done according to the species identification whenever possible, or to the most dominant feeding habit in that group, either as juvenile or adult stage. For instance, if an observed species is known to spend most of its lifetime in juvenile stage, and as a herbivore, it was categorised as “herbivore”.

Herbivory assay

To address the effect of entire arthropod communities on plant damage along elevation gradients, eleven different plant species were transplanted to two common gardens at low elevation (‘Lavey’, Switzerland, elevation: 437 m asl; lat./long.: 46°11055.13″N/7°1031.47E) and mid-elevation (‘Morcles’, Switzerland, elevation: 1519 m asl; lat./long.:46°12054.97″N/7°2036.81″E). We omitted the high-elevation level from this analysis, as early snowfall impeded plant installation above 2000 m asl. Each common garden consisted of 20 replicates per species, with each plant grown individually in 13 cm diameter pots to avoid confounding effects of plant–plant competition on plant growth. Plant species were selected based on two criteria: their high abundance in the study area, and their wide distributional range along elevational gradients in the Alps. We therefore selected: the yarrow (*Achilea millefolium L.*), brown knapweed (*Centaurea jacea L.)*, orchard grass (*Dactylis glomerata L.*), Volga *fescue* (*Festuca valesiaca aggr*.), bird’s-foot trefoil (*Lotus corniculatus L.*), bristly hawkbit (*Leontodon hispidus L.*), narrowleaf plantain (*Plantago lanceolate L.*), mouse-ear hawkweed (*Pilosella officinarum L.*), bladder campion (*Silene vulgaris*, *Moench Garck*, *s.str*.), red clover (*Trifolium pretense L.*), and the tufted vetch (*Vicia cracca L.*). Plants were germinated in standard potting soil composed of turf-like organic matter, compost, coconut fibre, and soil (30%:30%:20%:10%; Ricoter, Switzerland), and grown for two months under controlled conditions before being placed in the field on 27 June 2018.

Herbivore damage on each plant was scored by visually assessing the percentage of leaf area removed by herbivore arthropods, and according to seven defoliation classes: 0%, 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, and >76%, as suggested by Kozlov *et al.* (2015). The midpoint of each leaf damage class was used to calculate the average defoliation percent per plant. Herbivory estimations were performed at three time points (9 July, 7 August, and 12 September 2018).

Statistical analysis

All analyses were conducted in of R v3.6.1 (R Core Team 2019), using the packages ‘lme4’ (Bates *et al.*, 2015), ‘car’ (Fox & Weisberg, 2019) and ‘multicomp’ (Hothorn *et al.*, 2008).

We used linear models to test the effects of elevation, season and their interaction on arthropod abundance (total number of individuals), richness (number of unique morphospecies), and diversity (estimated by calculating Shannon’s index with the ‘diversity’ function from the package ‘vegan’; Oksanen *et al.*, 2010). Fixed effects were elevation (four levels), and the sampling times during the season (four levels). The shape of the relationship between elevation and abundance, richness, and diversity parameters was estimated by comparing three competitive models: a null model with no effect, a linear model of elevation and a quadratic model of elevation. Model selection was carried out by using the Aikake information criterion, with lower values indicating better models (Burnham & Anderson, 2004). Response variables were log-transformed to improve the distribution of model residuals. To estimate changes in arthropod communities (i.e. beta diversity) over space (elevation) and time (season), we next performed permutational analysis of variance (PERMANOVA). Beta diversity between samples was computed using Bray-Curtis dissimilarities. The same procedure was applied to a subset of the data with only the herbivore arthropod functional group in order to estimate the effects of elevation, season and their interaction on herbivore communities.

The RBA index for biocontrol was calculated by dividing the number of natural enemy morphospecies (i.e. parasitoids and predators) by the number of herbivorous morphospecies (Obrist & Duelli, 2010). The effect of elevation and season on the biocontrol index was assessed by performing linear models as described above.

Finally, linear models were performed as described above, to analyse the effects of elevation, season and plant species identity on arthropod herbivory for potted plants. We tested all two- and three-way interactions between elevation, season and species identity. The herbivory response variable was log-transformed to improve the distribution of model residuals.

Results

Shifts in arthropod communities along elevation gradients

Overall, the sampling yielded 1292 arthropod individuals, which were classified into 275 morphospecies belonging to 12 different orders (Table S1). The most abundant functional guild was herbivores (38% of total abundance), followed by predators (15%) and parasitoids (12%), with pollinators being the least common (3%). The remaining arthropods (31%) had more than one or other functional guilds.

Total arthropod abundance, richness and diversity varied with the elevation and the season (Table 1; Fig. 1). Global elevation patterns exhibited a hump-shaped distribution, with a maximum at mid-elevation (Fig. 1; Table S2). However, this pattern varied during the season, with significantly higher values of arthropod abundance, richness and diversity at the beginning of the

Table 1. Summary of linear models evaluating the effects of elevation, season, and their interactions on arthropod abundance, richness and diversity.

Response variable	Explanatory variables	d.f.	*F*-value	*P*-value
Arthropod abundance	Elevation (E)	3	20.29	<0.001
	Season (S)	3	7.56	<0.001
	E × S	9	9.50	<0.001
	Residuals	64		
Arthropod richness	E	3	24.40	<0.001
	S	3	3.53	0.02
	E × S	9	6.48	<0.001
	Residuals	64		
Arthropod diversity (Shannon's H)	E	3	17.49	<0.001
	S	3	3.09	0.03
	E × S	9	3.47	0.01
	Residuals	64		

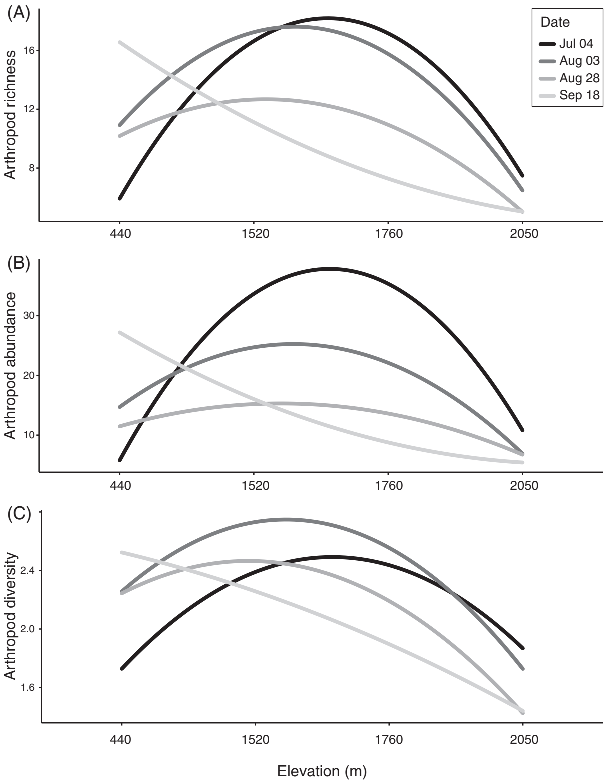

Fig. 1. Model predictions for total arthropod richness (A), abundance (B) and diversity (C) along the altitudinal gradient at the four dates sampled. Richness was estimated as the number of different arthropod morphospecies found in each sample. Arthropod abundance refers to the total number of morphospecies per sample. Diversity was measured as the Shannon's index value for each sample based on morphospecies richness and abundance.

season, shifting to a linear decrease by the end of the season (Fig. 1; Table S2). Moreover, the overall community composition of arthropods also varied with the elevation (Fig. 2; PERMANOVA; $F_{3,64} = 3.959$; $R^2 = 0.115$; $P < 0.001$), the season ($F_{3,64} = 2.790$; $R^2 = 0.08$; $P < 0.001$; Fig. 2) and their interaction ($F_{9,64} = 2.151$; $R^2 = 0.187$; $P < 0.001$).

Shifts in herbivore communities along elevation gradients

In total, we found 509 herbivore arthropods, classified into 91 morphospecies from 13 taxa belonging to 6 different orders. Hemipteran insects were the most abundant, representing almost the half the total herbivore number (22% Auchenorryncha and 25% Sternorrhyncha), followed by Diptera (22%) and Coleoptera (17%). Herbivore abundance, richness, and diversity varied with elevation and season (Table S3; Figure S1). As observed in the total arthropod dataset results, global elevation patterns exhibited a hump-shaped distribution, with a peak for the mid-elevation (Figure S1; Table S4). Again, this pattern shifted during the season with significantly higher values of arthropod abundance, richness, and diversity at the beginning of the season, shifting to linear decrease at the end (Figure S1; Table S4).

Shifts in biocontrol index along elevation gradients

The average biocontrol index was 0.91 and ranged between 0.00 and 4.00, which means that we found on average almost one predator or parasitoid species for each herbivore species in each of our samples. The biocontrol index was dependent on the elevation ($F_{3,64} = 4.00$; $P = 0.011$; Fig. 3), but remained constant during four dates sampled ($F_{3,64} = 0.63$; $P = 0.596$) along the whole elevation gradient ($F_{9,64} = 3.83$; $P = 0.159$). Finally, biocontrol rates were significantly higher at 440 and 1760 m compared with 1520 and 2050 m (Fig. 3).

Arthropod herbivory at different elevations

Herbivores removed 2.2% of total leaf area on average, varying between 0% and 37.5%. Herbivore damage depended on the plant species studied (species effect: $F_{10,87} = 8.02$, $P < 0.001$; Figure S2), and herbivory within plant species varied across elevation ($F_{10,87} = 0.85$, $P = 0.03$; Figure S2), indicating that while some species were more eaten at low elevation, others were more eaten at mid elevation. Specifically, herbivory damage was higher at mid-elevation for *P. lanceolata* and *D. glomerata*, and at low elevation for *L. corniculatus* and *V.*

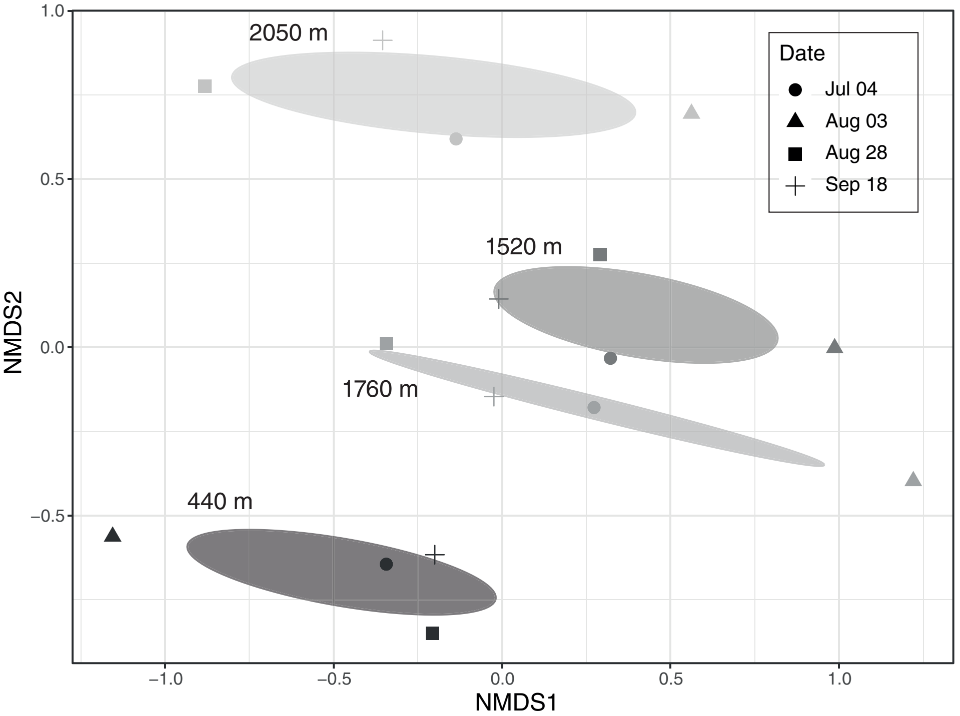

Fig. 2. Non-Metric Multidimensional Scaling representation for arthropods communities' beta diversity. Dissimilarities between samples were computed with the Bray-Curtis index, averaged over 1000 random permutations. Points represent mean dissimilarity values for each elevation at each sampling date. The stress value associated with this representation was 0.15. Ellipses represent 95% CIs around each elevation group.

cracca. For the remaining seven species studied, herbivory remained constant across low and mid-elevations (Figure S2). Overall, the total amount of herbivory appears stable along the elevation gradient (elevation effect: $F_{1,87} = 0.247$, $P = 0.62$).

Discussion

Here, we highlighted elevational patterns in diversity and interactions among herbivorous and predatory arthropod communities, and the effects of shifts in these communities on herbivory rates in eleven widely distributed plant species. First, we showed that the elevational patterns in arthropod abundance, richness, diversity, and community composition changed over the course of the growing season. Second, we observed that the proportion of herbivores and natural enemies remained constant within each elevation during the entire season, but was generally greater at low elevation. Finally, herbivory in our common gardens was dependent on plant species identity. Taken together, these results suggest that elevation patterns in plant-herbivore-predator interaction are strongly dependent on the seasonal variability and the identity of plant species involved.

Overall, we found that arthropod species abundance, richness, and diversity followed a hump-shaped elevation pattern, as suggested by previous research (Rahbek, 2005; Brehm *et al.*, 2007; McCain, 2009; McCain & Grytnes, 2010; Beck *et al.*, 2017). However, this pattern varied during the season (Beck *et al.*, 2010). By early July, there was a hump-shaped pattern in arthropod abundance, richness, and diversity. However, the mid-elevation peak decreased by the beginning of August, became very small by the end of the month, and finally, the hump-shaped pattern changed to a linear decline by mid-September. Elevational changes in arthropods diversity patterns along the season could be explained by changes in the NVDI (Tucker, 1979; Tucker & Sellers, 1986): at the beginning of the season NDVI increased at higher elevations, while at the end of the season it was higher at low elevations (Figure S3).

The observed changes in arthropod diversity along elevation during the season could be mediated by two mechanisms. Either (i) some arthropod groups migrate from higher elevations downwards at the end of the season, or (ii) communities change independently from each other over the course of the season. Our beta-diversity analyses indicated that local arthropod community composition and structure, while slightly varying during the season, were more homogenous within each elevation. These results suggest that arthropods do not migrate from high or mid elevations to low elevation following patterns of plant productivity (NDVI). Rather, arthropod communities change within elevation bands through changes in local arthropod community composition and relative abundance. Therefore, while small migrations and slightly different phenological events likely occur over the course of the season (Hodkinson, 2005), we suggest that habitat heterogeneity and distribution of host plants along elevation gradients strongly contributes to observed differences in arthropod communities across elevations (Hodkinson, 2005; Rahbek *et al.*, 2007; Pellissier *et al.*, 2013).

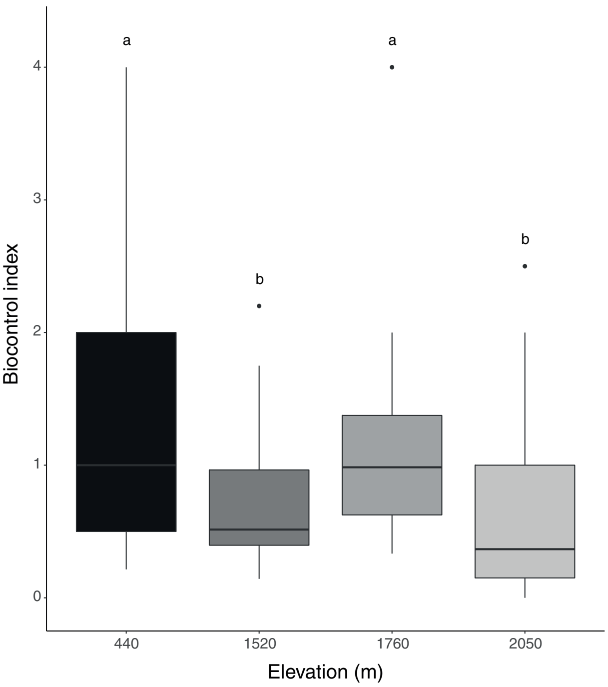

Fig. 3. Biocontrol index values at the four elevations sampled. For all elevations ($n = 20$, five repetitions at each four dates sampled), biocontrol index values were calculated by dividing the number of natural enemy morphospecies (i.e. parasitoids and predators) by the number of herbivorous morphospecies by following the rapid biodiversity assessment method (RBA). Boxes represent first and third quartiles and horizontal line represents the median. Letters above bars indicate statistical differences between elevations.

The observed diversity patterns for the whole arthropod communities were similar, but not identical when focusing only on herbivores, suggesting that climatic conditions influenced elevation and seasonal changes to arthropod communities in a functional guild-dependent manner (Peters *et al.*, 2016). Indeed, the biocontrol ratios remained relatively constant during the season, and decreased with elevation. At low elevation, the abundance of natural enemies was generally higher than herbivore abundance, with a mean biological control index of 1.42. Conversely, mean herbivore abundance was higher than the abundance of natural enemies at high elevation, with mean rates of 0.62, while at mid-elevation herbivore and predator abundances were balanced. These results agree with general elevational patterns found across several studies (Coley & Barone, 1996; Péré *et al.*, 2013; Mooney *et al.*, 2016; Moreira *et al.*, 2018), and suggest than higher trophic levels are more influenced by environmental changes than herbivores (Nelson *et al.*, 2019). Predator attack rates have been shown to drop about 9.6% for each 100 m of increase in elevation (Roslin *et al.*, 2017). This decrease with elevation is less pronounced for parasitism rates, which have been estimated to decrease ca. 0.44% every 100 m in a global meta-analysis (Péré *et al.*, 2013). In this study, we found a decrease of ca. 7.17% of potential biocontrol by both predators and parasitoids for every 100 m, which agrees with classic theory suggesting a steady decrease in biotic interactions with elevation (Brenner *et al.*, 2002; Hodkinson, 2005; Péré *et al.*, 2013; Morris *et al.*, 2015).

Based on general theory, we would expect higher herbivory at low elevation (Rasmann *et al.*, 2014). However, we found no general decline in the total herbivory along our elevation gradient. Instead, herbivory was strongly dependent on plant species identity, with only two out of the eleven plant species studied suffering higher herbivory at low elevation. Although our altitudinal gradient used for plant herbivory was incomplete for high elevation, the strong variability of effect signs we observed supports the general trend that among non-woody plants, herbivory patterns are highly variable between species (Galmán *et al.*, 2018). Moreover, because we used the same set of plants at two elevations to measure herbivory, our results suggest that the generally accepted pattern of declining herbivore damage with increasing elevation (Galmán *et al.*, 2018) might be driven by the unique composition of plant communities at different elevations. Our results therefore highlight the importance of interactions between arthropod herbivore abundance and plant defenses within each elevation level (Descombes *et al.*, 2017).

We acknowledge that these results are preliminary in many ways. For instance, our data represent a single altitudinal gradient in the Swiss Alps, sampled over one year. Conducting similar studies in other regions of the world, over the course of the whole vegetation season, and across several years could confirm the generality of the patterns we reported. Moreover, our classification of functional groups based on morphospecies allowed us to rapidly describe variations for each feeding guild independently, but the oversimplification of some taxonomic groups with respect to their diet likely added noise to our results. A rigorous taxonomic treatment with a more precise delimitation of functional groups would further improve the accuracy of our conclusions. However, in spite of these limitations, our results still demonstrate the importance of accounting for seasonal effects to better understand the ecological factors underlying species distributions and interactions along geographical gradients.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

SR conceived the idea, LM collected the data, PF-C and ED analysed the data, PF-C wrote the first draft of the manuscript and all authors contributed critically to the writing.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

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

Figure S1. Model predictions for total herbivore richness, abundance and diversity along the altitudinal gradient at the four dates sampled.

Figure S2. Mean herbivory (as percent of leaf area removed) for the eleven plant species at low and mid elevation.

Figure S3. Normalized difference vegetation index (NDVI) evolution during the vegetation season at different elevations.

Table S1. Functional groups into which sets of arthropods were classified according to the taxonomic level shown.

Table S2. AIC table of model selection for best fitting model explaining arthropod abundance, richness and diversity along elevation gradients in Swiss Alps at the different sampling dates.

Table S3. Summary of linear models evaluating the effects of elevation, season and their interactions on herbivore abundance, richness and diversity.

Table S4. AIC table of model selection for best fitting model explaining herbivore abundance, richness and diversity along elevation gradients in Swiss Alps at the different sampling dates.

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