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Effects of plant traits and community attributes on insect herbivory along elevation

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Emma Shih Mendez B.Sc.

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## **Abstract**

Mountains bear steep elevational gradients associated with large variations in biotic and abiotic conditions. How the interaction between plants and insects changes along these gradients, and by which factors the relationship is shaped, remains a complex topic. In this study, I investigated patterns of insect herbivory damage along an elevational gradient of 1600 m above the alpine tree line in the Stubai Alps in Austria, based on a comprehensive set of damage observations collected on 2693 individuals of 49 species. More precisely, I questioned how damage changes along elevation and how these changes are related with plant traits and features of the plant communities within which the target plants grow. I found that insect herbivory was generally low above the treeline and showed a steady decline along elevation. The relationship between insect herbivory and certain plant functional traits and community attributes imply that the decreasing trend is associated with plant species turn-over and corresponding changes in plant traits most likely associated with palatability and attractiveness to insect herbivores.

## **Abstract (Deutsch)**

Gebirge weisen steile Höhenunterschiede auf, die mit großen Schwankungen der biotischen und abiotischen Bedingungen einhergehen. Wie sich die Interaktion zwischen Pflanzen und Insekten entlang dieser Gradienten verändert und durch welche Faktoren die Beziehung geprägt wird, bleibt ein komplexes Thema. In dieser Studie untersuchte ich die Muster von Insekten-Fraßschäden entlang eines Höhengradienten von 1600 m über der alpinen Waldgrenze in den Stubai Alpen in Österreich, basierend auf einem umfassenden Satz von Schadensbeobachtungen, die an 2693 Individuen von 49 Arten gesammelt wurden. Insbesondere habe ich untersucht, wie sich die Schäden mit der Seehöhe verändern und wie diese Veränderungen mit den Pflanzenmerkmalen und den Merkmalen der Pflanzengemeinschaften, in denen die Zielpflanzen wachsen, zusammenhängen. Meine Ergebnisse zeigen, dass die Herbivorie von Insekten oberhalb der Baumgrenze im Allgemeinen gering war und mit zunehmender Höhe stetig abnahm. Die Beziehung zwischen der Insektenherbivorie und bestimmten funktionellen Eigenschaften der Pflanzen sowie den Merkmalen der Pflanzengemeinschaften lässt vermuten, dass der abnehmende Trend mit dem Wechsel der Pflanzenarten und den entsprechenden Veränderungen von Pflanzenmerkmalen zusammenhängt, die höchstwahrscheinlich mit der Attraktivität für Insektenherbivoren zusammenhängen.

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## Frame opening

Covering just over a tenth of all terrestrial land area outside Antarctica, mountains host around a third of global terrestrial species diversity and half of all diversity hotspots (Körner, Paulsen and Spehn, 2011; Körner *et al.*, 2017). The topographic complexity and large elevational amplitude over short geographical distances found on mountains result in a highly heterogeneous environment. Indeed, mountains' steep vertical gradients come with pronounced environmental variation, particularly changes in barometric pressure, atmospheric temperature, clear sky radiation, and UV radiation (Körner, 2012).

Along these gradients, mountains' vegetation can be classified into distinct zones, based on life form composition and the physiognomy of the species dominating the landscape (Nagy and Grabherr, 2009). At low elevations, the colline zone changes into the montane zone, characterized by deciduous and conifer forests, respectively. The forested zone ends at an imaginary line which corresponds to the upper limits of tree growth. At the tree line, what is left of the forest, patches of small-stature trees, give way to the alpine and nival zones. While the alpine zone is characterized by closed vegetation, including dwarf shrub communities and alpine grasslands; the nival zone is defined as having extensive rock cover and low vascular plants cover as the vegetation shifts to being dominated by bryophytes and lichens (Barry, 2008). However, the term 'alpine zone' is often used more broadly and refers to the whole mountain area above the natural tree line, including the nival zone.

Alpine ecosystems on Earth represent approximately 3% of land area and harbor about 4% of the Earth's flora (Heywood and UNEP, 1995; Körner, 1995). Common features of alpine climates include low atmospheric pressure and temperature, and high UV radiation and frequency of cloud cover (Körner, 2021). However, the way alpine plants encounter their climate does not necessarily reflect global or regional patterns, but rather ones of a much smaller scale. Alpine plants are known to be surrounded by a microclimate which can differ greatly from the ambient climate. The main determinants of the microclimate are related not only to the macroclimate and topography (solar radiation, slope and exposure), but also to the plant stature (Körner, 2021). Alpine plants are remarkably adapted to their environments by growth forms which buffer them against harsh physical conditions, especially low temperatures. Common growth forms for plants in alpine environments are low stature woody shrubs, herbaceous perennials, tussock-forming graminoids and cushion plants.

Despite alpine plants showing global trends in terms of growth form, their functional traits are largely variable (Körner, 1995). As plant functional traits illustrate the effects of the environment on the plants and of the plants on their ecosystem (Díaz *et al.*, 2016), they can influence other trophic levels, for example their primary invertebrate consumers, insect herbivores. The interaction between plants and insects is crucial for both parties. On the one hand, many plants, including the majority of alpine herbs, rely on the help of insects for reproduction. On the other hand, to insects, plants represent mating, egg-laying and feeding sites (Opp and Prokopy, 1986). To fulfill their nutritional requirements and optimize feeding and mating, herbivores meticulously choose their host plants. In turn, the feeding behavior of insect herbivores causes injuries which can reduce growth, delay flowering, and thus influence plants' performance and survival. Therefore, plants are thought to have developed specific mechanisms to help defending against herbivores and/or attracting mutualists, namely plant functional traits (Pellissier *et al.*, 2018).

These traits are generally related to plant morphology or primary chemistry. Morphological traits such as leaf thickness, leaf toughness or leaf area are associated with palatability and attractivity qualities of the

target plant. A plant that is difficult to chew, bite and/or digest may cause avoidance behavior in an herbivore. Elements related to a plant's primary chemistry have to do with the plant's nutritional content. Herbivorous insects acquire all their resources, whether for energy or for growth, through plants. Therefore, the nutritional value of plants is of particular interest to them and they are significantly affected by different food quality (Waring and Cobb, 1992). This is especially true for nitrogen (Coley and Barone, 1996; Leingärtner *et al.*, 2014; Kristensen, Michelsen and Metcalfe, 2020), because insects need proteins as basic structural materials despite nitrogen being in an extremely short supply in a usable form (Schoonhoven, Jermy and Loon, 1998). Water is another crucial element for insect nutrition, largely contributing to growth performance (Schoonhoven, Jermy and Loon, 1998). Thus, plant traits such as leaf water content, leaf dry matter content, or leaf contents of specific nutrients, may well predict the attractiveness of plants to insect herbivores.

Herbivory has also been linked to features from the community within which an observed plant is found. Vegetation density, composition, and host plant availability affect how the dietary regime of herbivorous insects evolve (Rasmann, Alvarez and Pellissier, 2014). Herbivory levels were, for example, found to be positively correlated to local plant species richness and host species abundance (Hülber *et al.*, 2015), maybe because the availability of alternative host plants is advantageous to generalist herbivores. As such, attributes from the vegetation neighboring the host plant may contribute to patterns of herbivory damage.

Both plant community structures and insect populations change with elevation (Körner, 2004; Descombes *et al.*, 2017; Fernandez-Conradi *et al.*, 2020; Pitteloud *et al.*, 2020), therefore the interaction between plants and insect inevitably changes too. Although the research on herbivory along elevation is extensive, the results are diverse. The most observed pattern is that herbivory decreases as elevation increases (Shizuo, 1998; Pellissier *et al.*, 2014; Rasmann, Buri, *et al.*, 2014; Rasmann, Pellissier, *et al.*, 2014; Hülber *et al.*, 2015; Buckley *et al.*, 2019). However, some studies found no effect of elevation on herbivory (Leingärtner *et al.*, 2014; Berardi *et al.*, 2016), while others found even an increase at higher altitudes (Kristensen, Michelsen and Metcalfe, 2020; Paudel *et al.*, 2021; Zvereva, Zverev and Kozlov, 2022). The disparity of results suggests that herbivory is not only affected by elevation alone but perhaps by numerous factors acting in concert, including the above-mentioned plant traits (Moreira *et al.*, 2018) and community attributes. As the effects of plant traits on herbivory along elevation remains relatively unexplored, it is unclear to which extent the relationship between the two is co-determined by the simultaneous species turn-over in plant assemblages and the associated change in traits related to plant morphology and primary chemistry.

The current study is part of a broader project, MICROCLIM (<https://www.mountainresearch.at/microclim/>) which investigates the future of alpine flora under climate change by evaluating predictive models with monitoring data. More precisely, the project aims at understanding the effect of microclimatic variations in alpine environments, in order to simulate plant population dynamics on European mountain summits. The European Alps extend over 1200km from the Mediterranean Sea to the Vienna basin, with approximately 8% of its total surface area being above the treeline (Ozenda and Borel, 2003). In Austria, the Alps represent approximately 63% of the country's area (Moser *et al.*, 2005) and harbor close to 3000 vascular plant species (Niklfeld, 1999). Sedges (Cyperaceae) and rushes (Juncaceae) are characteristic of the alpine grasslands (Nagy and Grabherr, 2009), while the vegetation in the nival zone is dominated by only four plant families (Asteraceae, Brassicaceae, Caryophyllaceae and Poaceae) (Ozenda and Borel, 2003). Although the knowledge on insect diversity is still incomplete, the elevational distribution limits of different orders of invertebrates in the Austrian Central Alps has been studied. To name a few orders which

include surface-dwelling herbivorous invertebrates: Caelifera (grasshoppers) and Hemiptera (true bugs) reach their upper limit of distribution within the alpine zone; while most Coleoptera (beetles), Hymenoptera (eg. ants), Diptera (flies) and Lepidoptera (butterflies) can get as far as the nival zone (Meyer and Thaler, 1995).

In this paper, I looked at how insect herbivory varies along an elevational gradient of 1600 m above the alpine tree line, and whether these changes are correlated with plant traits and features of the plant communities surrounding the observed plants. For this, I used a comprehensive set of damage observations collected on 2693 individuals of 49 species. I chose plant traits associated with plant palatability and with plant water and nutrient contents, namely leaf thickness, leaf area, leaf dry matter content, leaf carbon content and leaf nitrogen content. To account for the surrounding plant community, I included three features: species richness, total plant cover and target plant cover. I investigated whether the variation of herbivory along elevation is, at least partly, due to plant species turn-over and the corresponding changes in plant traits and community features.

# Manuscript

## Introduction

Alpine regions are facing warming temperatures, changing precipitation patterns, and decreasing snow covers (Kotlarski *et al.*, 2022), which alter alpine plant community structures (Jurasinski and Kreyling, 2007; Amagai, Kudo and Sato, 2018) and insect populations (Illich and Zuna-Kratky, 2022). These changes come with an upward shift of species along elevation, which has been documented for plants (Grabherr, Gottfried and Pauli, 1994; Walther, Beißner and Burga, 2005) and insects (Panza and Gobbi, 2022). Elevational gradients are characterized by changes in temperature, precipitation, atmospheric composition, wind speed, and radiation (Hodkinson, 2005). These factors shape the environment in which insect and plant species live and interact, thus the plant-insect herbivore relationship also varies along an altitudinal gradient.

The literature on herbivory along elevational gradients is diverse. The most frequently reported pattern is a decrease of herbivory damage with increasing elevation (Shizuo, 1998; Pellissier *et al.*, 2014; Rasmann, Buri, *et al.*, 2014; Rasmann, Pellissier, *et al.*, 2014; Hülber *et al.*, 2015; Buckley *et al.*, 2019), usually explained with the elevational changes in insect traits and activity. Higher elevations, and the associated stress generated by the shift in climatic conditions, have been shown to affect insect features such as wing size, color, body size, thermal tolerance, and fecundity (Shizuo, 1998; Hodkinson, 2005). These elevational variations of insect traits shape insect abundance, richness, and activity. As a consequence, arthropod species richness and abundance linearly decline with increasing elevation, at least above the tree line (Descombes *et al.*, 2017; Fernandez-Conradi *et al.*, 2020; Pitteloud *et al.*, 2020).

A decrease of herbivory with elevation is the most frequent, but not the only pattern reported. Indeed, some studies found no change of herbivory with elevation (Leingärtner *et al.*, 2014; Berardi *et al.*, 2016), while others found even an increase at higher altitudes (Kristensen, Michelsen and Metcalfe, 2020; Paudel *et al.*, 2021; Zvereva, Zverev and Kozlov, 2022). The variation of herbivory along elevation hence remains a complex topic which is simultaneously affected by numerous factors, including plant defense traits (Moreira *et al.*, 2018).

Plant secondary metabolites have been referred to as a primary defense mechanism (Coley, Bryant and Chapin, 1985) which is associated with elevational gradients in herbivory (Rasmann, Buri, *et al.*, 2014; Buckley *et al.*, 2019; Fernandez-Conradi *et al.*, 2022). However, resistance to herbivory is not always well predicted by secondary metabolites (Carmona, Lajeunesse and Johnson, 2011; Berardi *et al.*, 2016). On the other hand, plant traits related to morphology and primary chemistry, such as leaf toughness, silica content, C/N ratio, can play an important additional role in defense against or attractiveness to herbivores. Among these attributes, several are associated to traits of the leaf economic spectrum (LDMC, SLA) (Pellissier *et al.*, 2018). While their variation along elevation has been studied (Callis-Duehl *et al.*, 2017; Kergunteuil *et al.*, 2018), their relationship to herbivory damage is insufficiently explored. Hence, it is unclear whether and to which extent the variation of herbivory along elevation is co-determined by the simultaneous species turn-over in plant assemblages and the associated change in traits related to plant morphology and primary chemistry.

Whether an insect herbivore is attracted to a plant depends not only on the host plant itself but also on the properties of the surrounding plant community. Herbivory levels were, for example, found to be

positively correlated to local plant species richness and host species abundance (Hülber *et al.*, 2015), maybe because the availability of alternative host plants is advantageous to generalist herbivores. Such context-dependency might additionally contribute to patterns of herbivory damage along elevation, as species composition and species richness of plant assemblages vary with elevation (Theurillat *et al.*, 2003; Pellissier *et al.*, 2012).

In this study, we explored patterns of herbivory damage along an elevational gradient of 1600 m above the alpine tree line, based on a comprehensive set of damage observations collected on 2693 individuals of 49 species. In particular, we studied how damage changes along elevation and how these changes are correlated with plant traits and features of the plant communities within which the target plants grow. Among traits, we selected leaf thickness, leaf area, leaf dry matter content, leaf carbon content and leaf nitrogen content. These traits were thought to be related to herbivore preferences as they are linked to plant palatability and to water and nutrient contents of host plants (Callis-Duehl *et al.*, 2017; Li *et al.*, 2021). Among features of the surrounding plant community, we included species richness, total plant cover and target plant cover. Based on these data, we evaluated the idea that changes in herbivory damage across elevation are not only attributable to decreasing herbivore activity but at least partly also to plant species turn-over and associated changes in predominating plant traits and plant community contexts. We tested the following hypotheses: (1) herbivory damage decreases with increasing elevation; (2) herbivory damage is related to plant traits and community context; (3) the change of plant traits and community context with elevation explains the decrease of herbivory damage at high altitudes.

## Methods

### *Study area*

The present study covered an area of approximately 490 hectares including the treeless vegetation from 1845 m to the summit at 3497 m a.s.l. on Mount Schrankogel in the Stubai Alps, Tyrol, Austria (11°05'58"E, 47°02'41" N) (Figure 1). The chosen elevational gradient covered the upper subalpine, the alpine and sub-nival to nival zones. The plots corresponded to a range of eight habitats, especially dwarf shrub heaths, various types of grasslands, snow beds and scree areas (Table 1, Appendix). Mount Schrankogel is characterized by a siliceous bedrock. The growing season usually starts between the end of May and the beginning of July, depending on elevation, and lasts until mid-September.

Field work for the data presented in this paper was carried out during the summer of 2021. As part of a larger research project, vascular plant surveys were conducted on 900 1 m x 1 m quadrats distributed across all accessible areas of the mountain and the south-facing slope of the adjacent Sulztal valley. Sampling sites were selected based on a stratified random-sampling design which considered elevation, slope (derived from both 3 m x 3 m and 99 m x 99 m windows), a multiscale topographic position index (Gallant & Wilson 2000, Conrad *et al.* 2015; derived with both 10 m and 100 m maximum radius), Potential Incoming Solar Radiation (May–September sum), and the Normalized Difference Vegetation Index (NDVI; calculated from Sentinel-2 images at 10 m resolution as summer maximum of the year 2020). The surveys included a complete list of all vascular plant species growing within the 1 m<sup>2</sup> plots together with an estimate of their cover-abundance value according to a modified Braun-Blanquet scale ( $r = <0.1\%$ ,  $+ <1\%$ ,  $1 <5\%$ ,  $2a <15\%$ ,  $2b <25\%$ ,  $3 <50\%$ ,  $4 <75\%$  and  $5 >75\%$ ). Out of these 900 plots, 444 with target species (see below) were randomly selected in a way to minimize the number of plots and to have an average

minimum distance between two plots of around 50 m. Although the area is not impacted by agricultural practices like mowing, certain plots had to be discarded because of damage from grazing by domestic or wild animals.

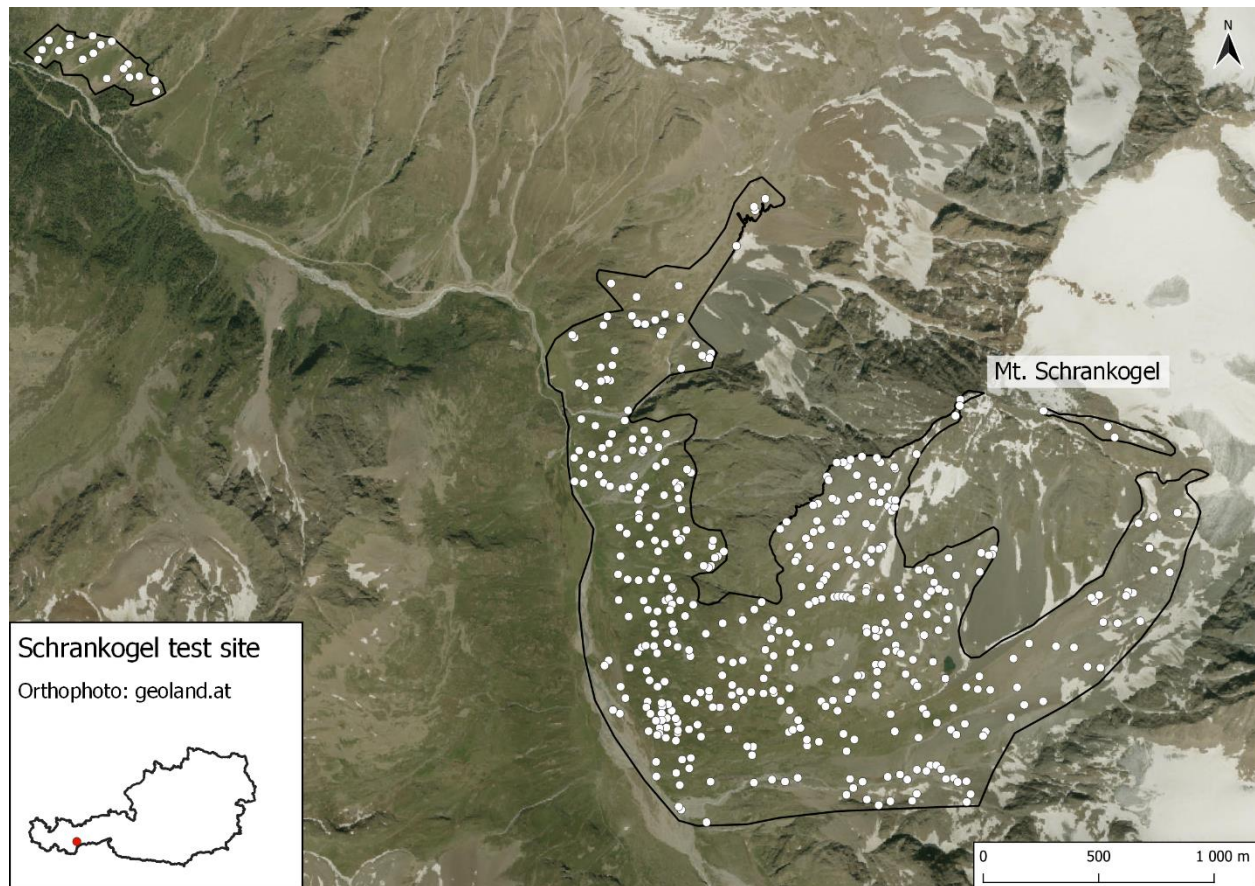


Figure 1 The distribution of plots for herbivory surveys on Mount Schrankogel.

### **Study taxa**

Out of 253 plant species recorded across the 900 plots, 57 target species were selected to include the most common species while representing different growth forms, families, habitats, and elevations. This selection process randomly picked out species while preserving the highest variation in traits and in ecological indicators values (Landolt *et al.*, 2010). Eight species were then removed to fit the smaller species list used in the plant traits measurements (see below), resulting in 49 species. The number of observations and plots was thus reduced to 2693 and 425, respectively. The final species list represented 19 families and consisted of 27 herbs, 16 graminoids, 5 shrubs, and 1 cushion plant. The complete species list with corresponding families and growth forms can be found in Table 2 (Appendix).

### **Plant traits measurements**

For functional traits analysis, species were sampled at vicinities of a subset of 17 plots which were located within each species' elevational optimum. This was the mean altitude of species' occurrences in the 900 plots. The selected 17 plots covered elevations ranging from 2125 m to 3100 m a.s.l. For each species, five

mature individuals were collected at one of the 17 plots and measured for five traits: leaf thickness, leaf area, leaf dry matter content (LDMC), leaf carbon content (C) and leaf nitrogen content (N). Leaf thickness (in mm) was measured with a thickness gauge. Three measurements, taken at different locations close to the lamina, provided a mean leaf thickness for each individual. Leaf thickness could not be measured for certain species with too small or succulent leaves. Leaf area (in cm<sup>2</sup>) was calculated from leaf scans using the software ImageJ (imagej.nih.gov). Leaf dry matter content (in g dry weight g<sup>-1</sup> fresh weight) was calculated as

$$LDMC = \frac{dw(g)}{fw(g)}$$

with oven-dry weight (dw) and saturated fresh weight (fw) of single leaf samples. Nutrient analysis, namely leaf nitrogen content (in % dry mass) and leaf carbon content (in % dry mass) was done with oven-dried leaf material in an EA-IsoLink machine (EA IsoLink™ IRMS System; Thermo Scientific™). For each plant trait, the values of different samples were averaged to provide one value per species.

### ***Community attributes and plant traits community means***

For calculating community traits, alpha-numeric cover values were converted into percentages using the midpoint of the interval covered by the respective alpha-numeric value (see above). These covers were then used to calculate plant traits community means of each assemblage at each 1 m<sup>2</sup> cell given that the total cover of all species for which trait data had been measured reached at least 75% of the total cover of all species recorded on the plot. In this paper, total cover refers to the sum of covers of all herbs and shrubs per quadrat, while target cover refers to the cover of the target plant species. Species richness was calculated as the sum of the number of taxa identified in each quadrat.

### ***Herbivory surveys***

At each plot, two individuals of each of three or four target plant species were selected, visually inspected, and leaf damage caused by insect herbivory was assessed on a three-level scale (0%: no damage; 1-10% of the plant damaged; >10% of the plant damaged). The variation in damage levels across our sites was low, thus the ordinal scale was turned into an incidence scale of presence and absence of herbivory signs. Leaf damage caused by insects was defined as marks of precisely chewed or pierced leaves. Herbivory from vertebrates, considered when the plant was missing larger parts and showed wide chewing marks, was excluded.

### ***Analysis***

We undertook a step-wise analysis starting with a binomial generalized linear model (GLM) to assess the effects of elevation on insect herbivory within the context of community attributes (species richness, total cover, target cover). Each observed individual was considered an independent unit in this model. Second, to explore whether the variation in herbivory-levels among species could modify the apparent impact of elevation, we introduced a random intercept of species to this model by fitting a generalized linear mixed-effects model (GLMM). Third, we used a GLM to assess the effects of plant species traits (leaf thickness, leaf area, LDMC, C, N) on herbivory without considering elevation nor community context. In this model, the means of the five measurements per trait taken from each species were used as the predictor variables and the incidence of herbivory damage as the response variable. Then, we assessed how community means of each plant trait change along elevation by visualizing simple linear regression models using

scatter plots separately for each trait. Lastly, we fitted a combined GLMM by including the plant traits as additional predictors to the mixed model described above. All variables were scaled before being integrated into the models, and certain plant traits were log transformed. Generalized linear models and generalized linear mixed models were computed with the functions `glm` in the base package of R (R Core Team, 2021) and `glmer` in the R package `lme4` (Bates *et al.*, 2015), with family specified as 'binomial'. Regression lines were plotted using `ggscatter` from the `ggpubr` package (Kassambara, 2020). All analysis was run with R (R Core Team, 2021).

## Results

Overall, our results showed low levels of herbivory. Out of 2693 individuals, 525 displayed signs of herbivory damage (20%). Four species had a percentage herbivory among individuals higher than 50% (*Trifolium badium*, *Vaccinium gaultherioides*, *Salix herbacea*, and *Vaccinium myrtillus*), with the highest percentage detected in *Trifolium badium* (70%). In contrast, seven species showed no herbivory at all (**Error! Reference source not found.**). When visualizing herbivory percentages among individuals along 100 m elevational groups, herbivory was highest in the lowest elevation groups (Figure , Appendix). Even then, the highest herbivory percentage among individuals, found between 1800 m and 1900 m, was below 30% when considering all species together (Figure , Appendix).

### *Elevation and community attributes*

When fitting a generalized linear model on the relationship between herbivory and elevation and community attributes (Table 1, a), we found significant effects of elevation and target cover, with coefficient estimates of -0.25 and 0.10, respectively. These results hence suggest an elevational decrease of herbivory, while higher cover of the host plant is linked to higher chances of herbivory. Although these two variables could predict herbivory in the initial model, after including species-specific random effects, results changed drastically (Table 1, b). The random intercept of species identity let both the elevational trend and the significance of target cover disappear. However, total cover became a significant predictor, indicating that a denser vegetation is associated with lower likelihood of herbivory. No significance was found for species richness in either of the two models.

### *Plant traits*

When testing the relation between herbivory and plant traits, we found significant positive correlations with leaf area, leaf carbon content and leaf nitrogen content, with coefficients of 0.74, 1.08 and 0.56, respectively (Table 1, c). No significant relationships were found with leaf thickness nor leaf dry matter content (Table 1, c). Community means of each individual plant trait showed that leaf area, leaf dry matter content, leaf carbon and leaf nitrogen content were all decreasing with elevation, while leaf thickness remained approximately constant (Figure 3).

### *Combined mixed model*

A mixed model combining all traits showed significant relationships between herbivory damage and total cover, leaf area, leaf carbon content and leaf nitrogen content. For the community traits, results were in line with the ones from the first GLM, with total cover being the only significant variable in predicting herbivory damage; while elevation, species richness, and abundance showed no significant relation to

herbivory. Regarding the plant traits, leaf area, leaf carbon and leaf nitrogen content remained significant variables.

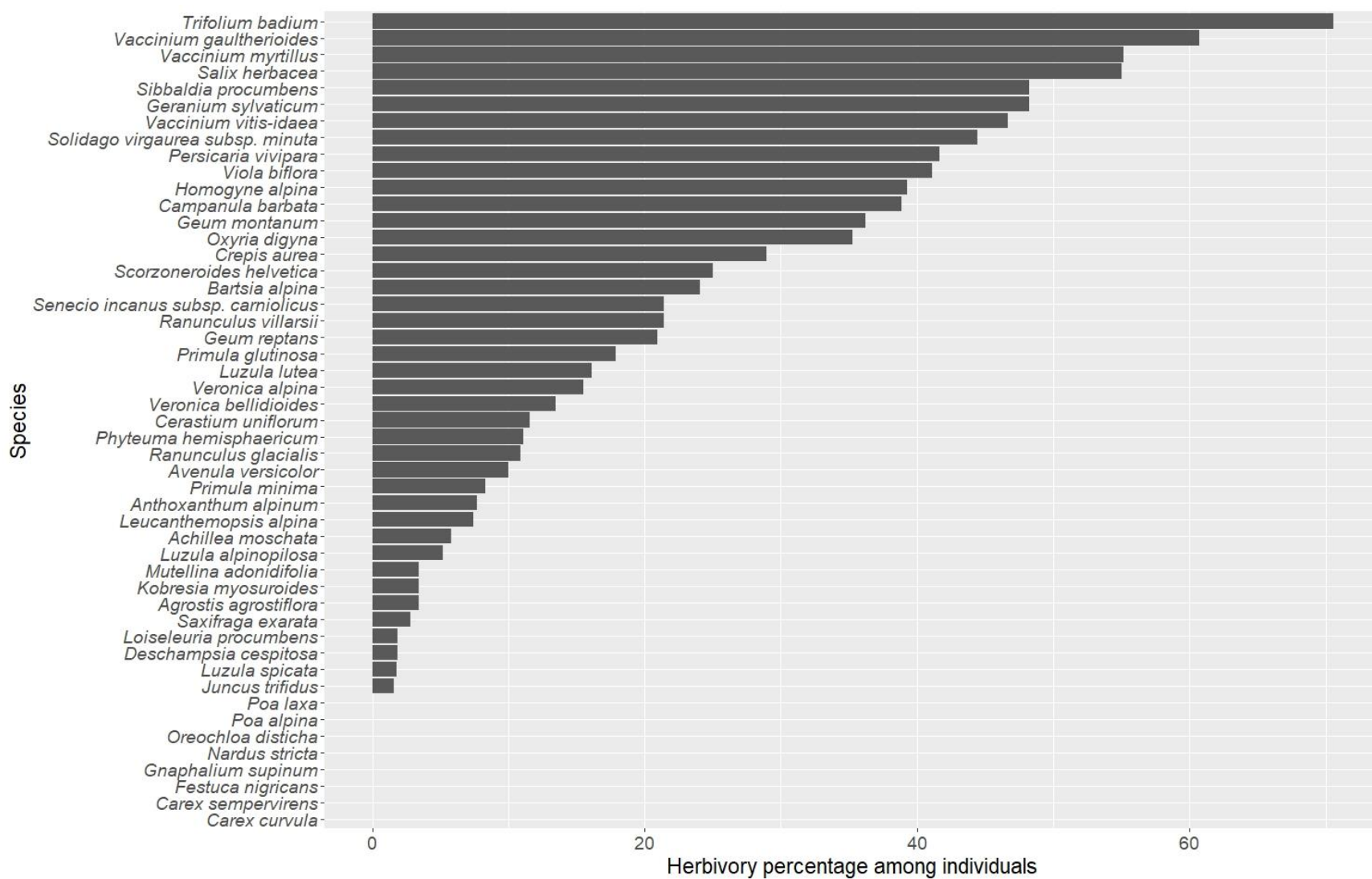


Figure 2 Herbivory percentage among individuals for each of 49 alpine plant species.

Table 1 Results from generalized linear models (GLM) and generalized linear mixed-effects models (GLMM) testing the effect of elevation, community traits and plant traits on insect herbivory damage in 49 alpine plant species on Mount Schrankogel (Austria). Plant species identity was used as the random factor in the GLMMs.

Variables	Estimate	Std. Error	z value	Pr(> z )	R <sup>2</sup>
<b>(a) Elevation + community attributes GLM</b>					0.011
(Intercept)	-1.44	0.05	-29.07	<0.0001	
Elevation	-0.25	0.06	-4.18	<0.0001	0.006
Species richness	0.08	0.06	1.17	0.2421	0.000
Total cover	-0.09	0.07	-1.27	0.2042	0.001
Target cover	0.10	0.05	2.10	0.0360	0.002
<b>(b) Elevation + community attributes GLMM</b>					0.006
(Intercept)	-2.16	0.28	-7.83	<0.0001	
Elevation	0.04	0.08	0.45	0.6548	0.000
Species richness	0.03	0.08	0.37	0.7110	0.000
Total cover	-0.28	0.08	-3.36	0.0008	0.003
Target cover	0.09	0.07	1.23	0.2184	0.001
<b>(c) Plant traits GLM</b>					0.124
(Intercept)	-1.73	0.06	-27.45	<0.0001	
Leaf thickness	-0.06	0.07	-0.83	0.4069	0.000
Leaf area	0.74	0.07	10.88	<0.0001	0.053
Leaf dry matter content	-0.12	0.09	-1.35	0.1755	-0.000
Leaf carbon content	1.08	0.08	14.05	<0.0001	0.088
Leaf nitrogen content	0.56	0.09	6.17	<0.0001	0.017
<b>(d) Elevation + community attributes + plant traits GLMM</b>					0.115
(Intercept)	-2.14	0.19	-10.99	<0.0001	
Altitude	0.07	0.08	0.78	0.4375	0.000
Species richness	0.03	0.08	0.40	0.6899	0.000
Total cover	-0.29	0.08	-3.46	0.0005	0.003
Target cover	0.08	0.07	1.07	0.2835	0.000
Leaf thickness	-0.01	0.23	-0.03	0.9778	0.000
Leaf area	1.08	0.23	4.70	<0.0001	0.045
Leaf dry matter content	-0.30	0.28	-1.07	0.2844	0.003
Leaf carbon content	1.30	0.25	5.21	<0.0001	0.069
Leaf nitrogen content	0.59	0.28	2.12	0.0343	0.011

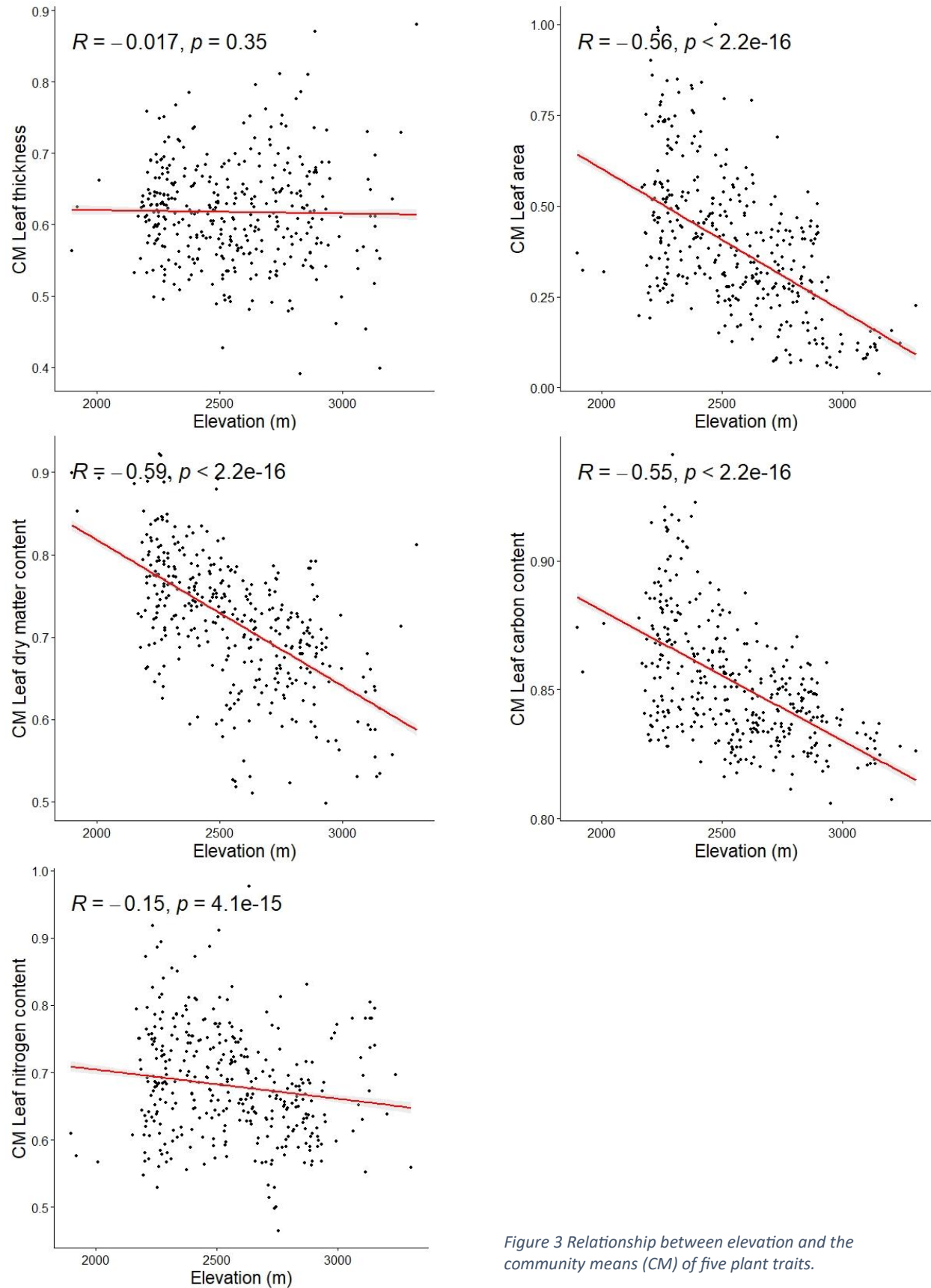


Figure 3 Relationship between elevation and the community means (CM) of five plant traits.

## Discussion

### *Overall levels of herbivory*

We documented 20% of observations exhibiting signs of herbivory, which reflects relatively low levels compared to reports of 57% across five European alpine plant species (Hülber *et al.*, 2015). In the latter work, however, the authors focused on species with high known or expected palatability while our selection was independent of plant attractiveness and included several species which are obviously not used by insect herbivores at all. Our results are in line with those from Diemer (1996), who found, along an altitudinal transect in alpine environment, 15-26% of individuals of *Ranunculus glacialis* showing signs of herbivory damage. With this range, Diemer (1996) concluded that herbivory is widespread in alpine environments. Whether a percentage value is depicted as high or low is hence obviously subject to interpretation. However, the author hypothesizes snow mice to be the primary herbivore of this species, revealing for the current study a doubt on whether the damages we observed were only due to insect herbivory.

Results of herbivory damage can be interpreted in two ways: by looking either at the percentage of individuals affected or the percentage of plant biomass damaged. Before changing herbivory damage from an ordinal to an incidence scale, our data showed that only five plant individuals (out of 2693) had > 10% leaf herbivory damage, 20% of individuals had 1-10 % leaf damage, and 83% had no signs of herbivory at all. In the field, it was clear that plants which suffered from herbivory (marked within the large 1-10% range) showed damage closer to 1% than to 10%. The global average of arthropod herbivory was found to be 5.3% of the leaf tissue across all vascular plants (Turcotte *et al.*, 2014) and 7.6% for woody plants (Kozlov *et al.*, 2015). Although these results give a general image on herbivory rates, they are not directly comparable to ours due to differences in the elevations of the study areas. We are not aware of any publications on global insect herbivory rates in alpine environments. However, between 600 m and 1800 m, Pellissier *et al.* (2014) found herbivory rates of 6% damage in lowland populations and 0.2% in high elevation populations of *Plantago lanceolata*. If we assume that the average individual where we observed signs of herbivory has 1% of its biomass damaged, the numbers found in our study would actually match those reported by Pellissier *et al.* (2014) for *Plantago lanceolata* well.

The low herbivory rates found may partially be due to limitations in our study design. As we focused on holes and chewing marks, our sampling technique was insensitive to types of herbivory damage which removes entire leaves, such as grasshoppers that chew off whole leaves of their host plants. Blumer and Diemer (1996) found, at 2470m in the Swiss Alps, that grasshoppers removed 19 to 30% of aboveground plant biomass in *Carex curvula* and *Carex foetida* communities, respectively; and relied to 80-90% on *Carex* species as food sources. We may have overlooked herbivory in our two sedges, *Carex curvula* and *Carex sempervirens*, as no signs of damage were documented on either species. However, grasshopper populations vary geographically. In the field, we hardly saw or heard any grasshoppers. Similarly, the data of Descombes *et al.* (2017) from the western Swiss Alps suggest very low grasshopper abundance at elevations above c. 2300 m a.s.l. , i.e. for about two thirds of the elevational gradient covered by our data. Moreover, underestimation due to technical boundaries cannot explain the low levels of herbivory found in other species. Even if we account for underestimation in the *Carex* species, the overall herbivory rate would remain low. A more plausible explanation for the fact that the herbivory levels differ from those found in other studies in alpine environments, is the size of our species list. Unlike other studies which

selected one or few species prone to herbivory, we studied a comprehensive list of 49 species. By doing so, we provide a mean herbivory rate across plant communities.

### ***Herbivory and elevation***

The elevational decrease of herbivory damage found in our first model validates our first hypothesis and results from other studies (Shizuo, 1998; Pellissier *et al.*, 2014; Rasmann, Buri, *et al.*, 2014; Rasmann, Pellissier, *et al.*, 2014; Hülber *et al.*, 2015; Buckley *et al.*, 2019). However, after adding a random intercept for species identity in our initial model, elevation was no longer a significant predictor. This change suggests that the elevational trend in herbivory has to do with a turnover of plant species along elevation. It is impossible, however, to distinguish whether the lower level of herbivory in species at higher elevations is due to a decrease of herbivory activity or in attractiveness and palatability of the plants growing at these higher elevations. Nevertheless, we visually found no consistent trend of herbivory damage when analyzing elevational trends for each species separately (Figure , Appendix). This goes in line with Rasmann, Pellissier, *et al.* (2014), who documented that herbivory patterns in seedlings of natural tree communities along elevation were not found at the species level and highlighted the importance of the succession of species along the elevation gradient in shaping the pattern of herbivory variation at the community level. Both of these results support the idea that herbivory rates do not solely depend on a decrease in insect activity and abundance with elevation but at least partly on which plant species are available at each elevation. They complement reports that climate does not fully account for the elevational gradient in herbivory (Galmán *et al.*, 2018); and accentuate the importance of plant assemblage variations in determining changes in herbivory.

In this mixed model, target cover, which showed a slight positive significant relationship with herbivory in the first model, loses its significance, while total cover revealed a significant negative correlation with herbivory damage. The effect of the target cover gets lost perhaps because different species intrinsically have different cover values. The negative relationship between herbivory and total cover may be explained by a delusion effect, as plants more easily hide from predators when the neighboring vegetation is denser. *Brachypodium* sp., for example, was found to be negatively affected by herbivory, but only when neighboring vegetation was removed (Corcket, Callaway and Michalet, 2003).

### ***Herbivory and plant traits***

We found a significant positive relationship between leaf area and herbivory damage. This may simply imply that the larger the leaf, the more easily a plant can be sensed, and thus the higher chance it has of becoming the target food source of an herbivorous insect. Plant attractivity for insects is also reflected by the nutritional quality of a plant. Several studies found a positive relationship between herbivory levels and leaf nitrogen content (Coley and Barone, 1996; Leingärtner *et al.*, 2014; Kristensen, Michelsen and Metcalfe, 2020). However, the relationship between herbivory and leaf carbon content remains unexplored. We found positive relationships between herbivory and leaf carbon content and leaf nitrogen content. Both proteins and carbohydrates are crucial requirements for insect herbivores' growth, survival and reproduction (Le Gall and Behmer, 2014; Roeder and Behmer, 2014), since carbohydrates act as the energy source needed to fuel the processes which use proteins and amino acids as building blocks (Mattson, 1980). A number of alpine plants are known to store relatively high concentrations of non-structural carbohydrates such as sugars, starch and lipids, probably due to photosynthesis being less limited by cold temperatures than downstream processes, which use the assimilated carbohydrates, such

as growth (Körner, 2021). However, as with nitrogen, there is considerable variation among species. To obtain adequate amounts of carbon and nitrogen to meet their dietary needs, insect herbivores seem to carefully select their food sources.

### ***Plant traits community means***

Regarding community means of plant traits, we found linear elevational decreases for leaf area, leaf carbon content and leaf nitrogen content, which partially contradict results from other studies. The decline of leaf area is not strictly comparable to the well-known reduction of specific leaf area (leaf area per leaf mass) along elevation (Callis-Duehl *et al.*, 2017; Defossez, Pellissier and Rasmann, 2018; Körner, 2021), but likely contributes to this latter pattern. For leaf carbon content, there is no conclusive trend in the literature. As discussed above, the allocation of carbon to long-term storage is not uncommon in high elevation plants (Reyes-Bahamonde, Piper and Cavieres, 2021) and provides an advantage in easing the strains caused by harsh environmental conditions (Mooney and Billings, 1960; Wyka, 1999). However, although higher non-structural carbohydrates have been associated with colder climates in trees (Hoch and Körner, 2009; Fajardo, Piper and Cavieres, 2011), they were not found to be significantly different between comparable lowland (500 m) and alpine (2500 m) herbaceous plant species (Körner, 2021). Most clearly, the elevational decrease of leaf nitrogen content opposes results from other studies (Körner, 1989; Shizuo, 1998). In an analysis of different mountain areas in all major climatic zones, Körner (1989) found a global trend of altitudinal increase of nitrogen content per unit leaf area. In the Austrian Alps more specifically, nitrogen content per unit leaf area of alpine plants (2850-3200 m) was 34% higher than of lowland plants (600 m) (Körner, 1989).

There are two possible explanations for the disparity between our results and those from the literature. The first is the difference in elevational ranges, which, in other studies usually covered lowland to alpine habitats while we only focused on a truncated gradient above the treeline. The altitudinal gradient of the current study was thus narrower and different from those in other studies. The second is that the trend of increasing nitrogen content is valid for individual species or coherent sets of species of a particular life form but may not fit means for whole communities which include species of different life forms, as the abundance of these life forms changes with altitude (Körner, 2021). Differences in plant identity within communities may thus explain why community level means of CN ratios were found to show no elevational trend in one study (Kergunteuil *et al.*, 2018), while another reports a decrease with elevation (Callis-Duehl *et al.*, 2017). In any case, the monotonical decrease for leaf area, leaf carbon content and leaf nitrogen content found in our study fit with the elevational decrease of herbivory, as these three factors were positively correlated to herbivory damage in the plant traits model.

### ***Elevation, community attributes, plant traits, and herbivory***

When combining elevation, community variables and plant traits variables in a single comprehensive model with species identity as a random factor, herbivory levels were found to be significantly correlated to one community trait and to four plant traits, while elevation remained an insignificant variable. We interpret these results as an indication that the elevational turnover of species towards those less attractive to insects at least contributes to the decrease of herbivory at higher altitudes. In other words, the decrease in herbivory is co-determined by the systematic elevational variation of traits related to plant morphology and primary chemistry. This interpretation is generally in line with results of Pellissier *et al.* (2013) who found that plant phylogenetic beta diversity correlated with butterfly phylogenetic beta

diversity, and suggested that the turnover of host-plant lineages structures herbivore assembly in space. Moreover, arthropod abundances was found to be highly correlated with plant community composition, but not with plant species richness, in montane European grasslands (Perner *et al.*, 2005). Plant identity and community conditions may mutually contribute to herbivore assembly and together modulate herbivory rates.

### ***Herbivory facing climate change***

Over the recent decades, reported rates of upslope shifts have been almost an order of magnitude faster for insects than for alpine plants in the European Alps (Vitasse *et al.*, 2021). These divergent rates of range shifts might put plants from high elevations under increasing herbivore pressure when climate warms (Rasmann, Pellissier, *et al.*, 2014). However, in contrast to studies focusing on trends over montane and subalpine to alpine gradients, our results suggest a decreasing attractiveness of species from those highest elevations. These trends appear due to a change in their primary chemistry and may compensate for a decrease in chemical defense traits in species of higher elevations (Descombes *et al.* 2017) to a certain extent. How interactions of plants with insect herbivores will actually develop when climate warms remains thus difficult to predict.

### **Conclusion**

Looking at both herbivory incidence and magnitude of damage within a comprehensive set of alpine plant species, we conclude that insect herbivory is generally low above the treeline in the European Alps. The still detectable decrease of herbivory with increasing elevation was found to relate to plant species turnover and changes in plant community traits that are most likely associated with palatability and attractiveness to insect herbivores. In particular, the average nutritional quality of plant species within communities appears to decrease with elevation. This might, to a certain extent, mitigate increasing levels of insect activity at high elevations when the climate warms.

## Frame closing

With observational data from a comprehensive set of alpine plants, the current study aimed at understanding the factors shaping insect herbivory in alpine environments. In general, I found low levels of herbivory damage, which does not necessarily mean that herbivory is negligible above the tree line. The amount of biomass affected by herbivory was low, while the percentage of individuals showing signs of herbivorous injuries was around 20%. Knowing to which extent plants can deal with small scratches and bites and how much biomass damage starts becoming detrimental for a plant's growth, would help understanding how herbivory influences plant health, especially in naturally harsh environments.

Although I found a strict decrease of insect herbivory levels with increasing elevation, this decline appears not only to be due to lower insect activity in the colder climates at high elevations. Rather, herbivory damage seems to at least co-depend on which plant species grows at which elevation, and is shaped by the succession of species along the elevation gradient (Rasmann, Pellissier, *et al.*, 2014). My results show that herbivory is related to specific functional traits from the host plant and to certain features from the neighboring plant community, which both change with elevation in a way that decrease the attractivity for insect herbivores.

While the current study was focused on plants, another way of approaching the topic of herbivory is evidently through the perspective of insects. Elevational changes in insect features have been associated with the stress generated by shifts in climatic conditions along elevation (Shizuo, 1998; Hodkinson, 2005). Whether, and to which extent, insect traits and plant traits are related to each other and simultaneously contribute to herbivory patterns remain open questions. Combining both plant and insect data may provide a more thorough understanding of herbivory dynamics along elevation.

Herbivore abundance at higher elevations is expected to increase (Rasmann, Pellissier, *et al.*, 2014) and result in stronger herbivory pressure for plants, especially because the rates of upslope shifts are much slower for plants than for insects (Vitasse *et al.*, 2021). However, our results suggest that high elevation plants are less attractive to herbivores, which may help the plants to mitigate the expected increase in herbivory pressure. Thus, climate warming may indirectly affect herbivory patterns through a change in plant communities and their functional traits with elevation.

The interaction between alpine plants and insects contributes to the richness of mountain biota and how it is affected by climate change will determine the faith of mountain biodiversity. Apart from ethical or cultural arguments which give importance to mountain preservation, mountain biodiversity sustains essential ecological and economical functions, such as ecosystem integrity, slope stability, and the provision of food, fodder and clean water (Körner, 2004). Giving attention to mountains is thus in the interest of all.

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## Appendix

Table 1 Habitat types, with corresponding number of plots, spanning across an elevational gradient of approx. 1600 m on Mount Schrankogel. The total number of plots is 425.

Habitat type	Number of plots
Alpine grasslands with <i>Carex curvula</i>	114
Alpine to nival transition	21
Dry scree with <i>Geum reptans</i>	44
Nival vegetation	29
Subalpine meadows	20
<i>Vaccinium</i> and <i>Rhododendron</i> shrubs	107
Wet scree with <i>Oxyria digyna</i>	9
Wet tall grass-herb grasslands	81

Table 2 Plant species names with corresponding growth form and family. The total number of species is 49.

Taxon	Growth form	Family
<i>Achillea moschata</i>	herb	Asteraceae
<i>Agrostis agrostiflora</i>	graminoid	Poaceae
<i>Anthoxanthum alpinum</i>	graminoid	Poaceae
<i>Avenula versicolor</i>	graminoid	Poaceae
<i>Bartsia alpina</i>	herb	Orobanchaceae
<i>Campanula barbata</i>	herb	Campanulaceae
<i>Carex curvula</i>	graminoid	Cyperaceae
<i>Carex sempervirens</i>	graminoid	Cyperaceae
<i>Cerastium uniflorum</i>	herb	Caryophyllaceae
<i>Crepis aurea</i>	herb	Asteraceae
<i>Deschampsia cespitosa</i>	graminoid	Poaceae
<i>Festuca nigricans</i>	graminoid	Poaceae
<i>Geranium sylvaticum</i>	herb	Geraniaceae
<i>Geum montanum</i>	herb	Rosaceae
<i>Geum reptans</i>	herb	Rosaceae
<i>Gnaphalium supinum</i>	herb	Asteraceae
<i>Homogyne alpina</i>	herb	Asteraceae
<i>Juncus trifidus</i>	graminoid	Juncaceae
<i>Kobresia myosuroides</i>	graminoid	Cyperaceae
<i>Leucanthemopsis alpina</i>	herb	Asteraceae
<i>Loiseleuria procumbens</i>	shrub	Ericaceae
<i>Luzula alpinopilosa</i>	graminoid	Juncaceae
<i>Luzula lutea</i>	graminoid	Juncaceae
<i>Luzula spicata</i>	graminoid	Juncaceae
<i>Mutellina adonidifolia</i>	herb	Apiaceae
<i>Nardus stricta</i>	graminoid	Poaceae
<i>Oreochloa disticha</i>	graminoid	Poaceae
<i>Oxyria digyna</i>	herb	Polygonaceae

<i>Persicaria vivipara</i>	herb	Polygonaceae
<i>Phyteuma hemisphaericum</i>	herb	Campanulaceae
<i>Poa alpina</i>	graminoid	Poaceae
<i>Poa laxa</i>	graminoid	Poaceae
<i>Primula glutinosa</i>	herb	Primulaceae
<i>Primula minima</i>	herb	Primulaceae
<i>Ranunculus glacialis</i>	herb	Ranunculaceae
<i>Ranunculus villarsii</i>	herb	Ranunculaceae
<i>Salix herbacea</i>	shrub	Salicaceae
<i>Saxifraga exarata</i>	cushion	Saxifragaceae
<i>Scorzoneroidea helvetica</i>	herb	Asteraceae
<i>Senecio incanus subsp. carniolicus</i>	herb	Asteraceae
<i>Sibbaldia procumbens</i>	herb	Rosaceae
<i>Solidago virgaurea subsp. minuta</i>	herb	Asteraceae
<i>Trifolium badium</i>	herb	Fabaceae
<i>Vaccinium gaultherioides</i>	shrub	Ericaceae
<i>Vaccinium myrtillus</i>	shrub	Ericaceae
<i>Vaccinium vitis-idaea</i>	shrub	Ericaceae
<i>Veronica alpina</i>	herb	Plantaginaceae
<i>Veronica bellidioides</i>	herb	Plantaginaceae
<i>Viola biflora</i>	herb	Violaceae

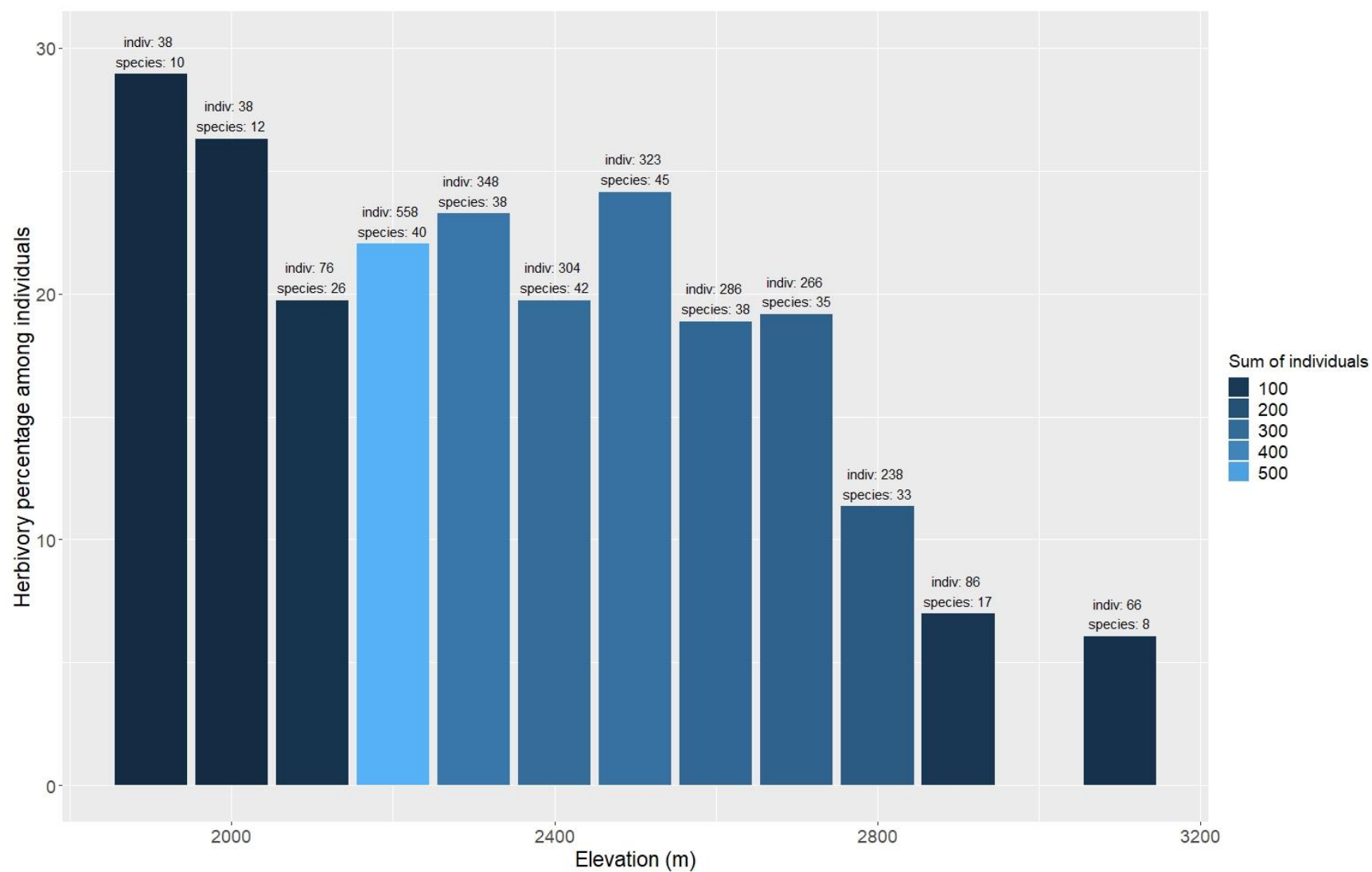


Figure 1 Herbivory percentage among individuals along elevation. Elevation was divided in groups of 100 m. The number of plant individuals and species is specified above each bar. Groups with less than 25 individuals were omitted.

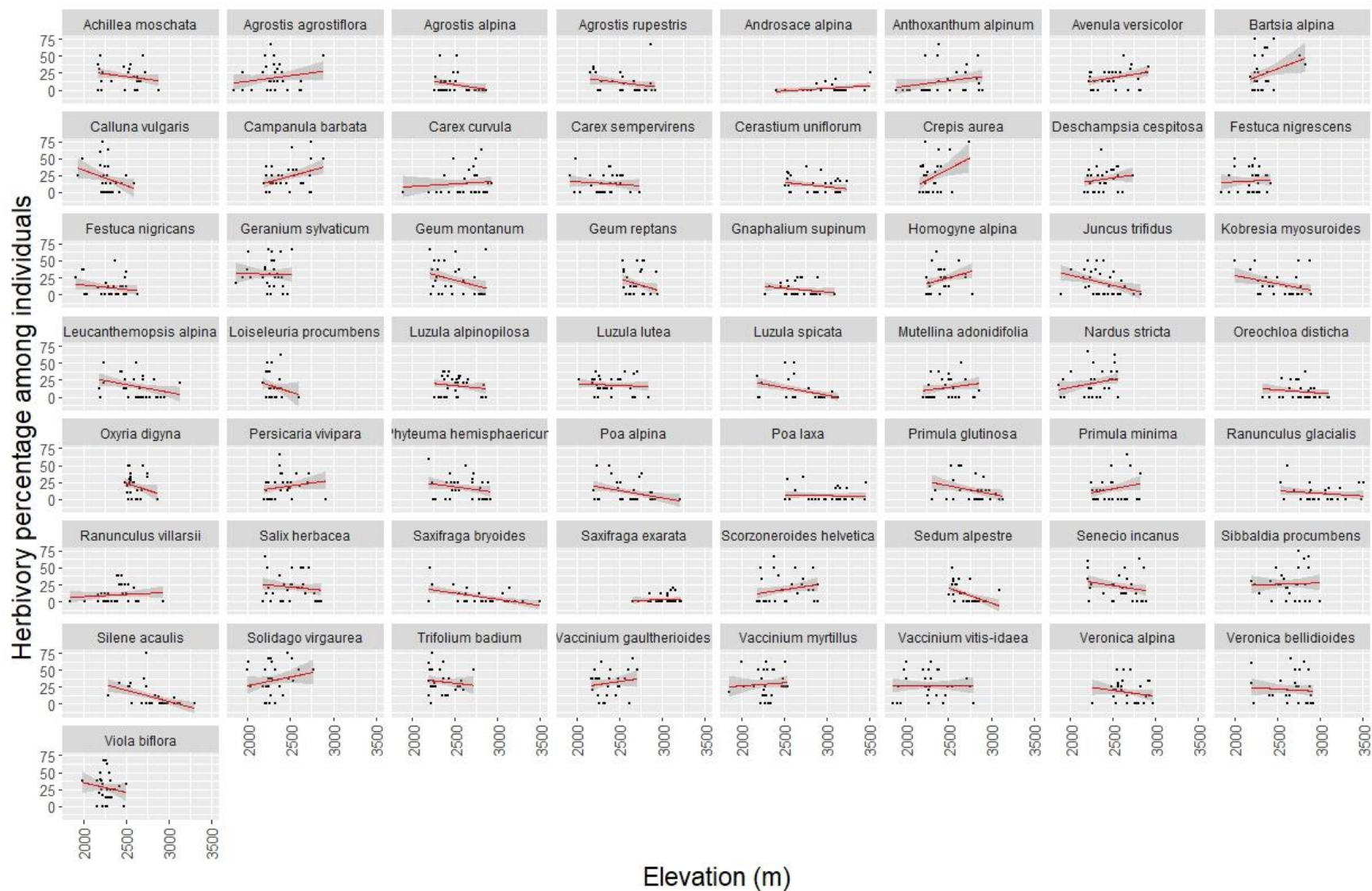


Figure 2 Herbivory percentages among individuals along elevation for each of 49 alpine plant species.