Community-level plant palatability increases with elevation as insect herbivore abundance declines

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Summary

1. Plants protect themselves against herbivore attacks through a myriad of physical structures and toxic secondary metabolites. Together with abiotic factors, herbivores are expected to modulate plant defence strategies within plant assemblages. Because the abundance of insect herbivore decreases in colder environments, the palatability of plants in communities at higher elevation should shift in response to both abiotic and biotic factors.

2. We inventoried grasshopper communities to document changes in herbivore abundance along elevation gradients and quantified associated shifts in plant palatability. We measured plant palatability by measuring the growth of *Spodoptera littoralis* generalist caterpillars fed with the leaves of 172 plant species. We related plant palatability to leaf traits and elevation at the species and community levels.

3. In congruence with the decrease in grasshopper abundance with elevation, we found that the mean palatability level of plant communities increases with elevation. In addition, plant palatability was negatively associated with the community-weighted mean of leaf dry matter content. At the species level, plants with high carbon-to-nitrogen ratio were less palatable, while we found no effect of species mean elevation on plant palatability.

4. *Synthesis.* Our results suggest that plant communities at higher elevation are composed of species that are generally more palatable for insect herbivores. Shift in plant palatability with elevation may thus be the outcome of a relaxation of the *in situ* herbivore pressure and changes in abiotic conditions.

Key-words: alpine, bioassay, community-weighted mean, grasshoppers, herbivory, plant defence, plant resistance, plant–herbivore interactions, *Spodoptera littoralis*

Introduction

Changes in plant functional properties along environmental gradients are influenced by both abiotic conditions (e.g. temperature, edaphic factors; e.g. Asner *et al.* 2014) and biotic interactions (e.g. plant–animal interactions; Gentry 1988; Sundqvist, Sanders & Wardle 2013). Along elevation gradients, the degree of herbivory generally decreases (Reynolds & Crossley 1997; Garibaldi, Kitzberger & Chaneton 2011; Metcalfe *et al.* 2014; Pellissier *et al.* 2014), concomitantly

with changes in climatic and soil factors (Körner 2007), which should influence functional composition of plant assemblages. For instance, it can be postulated that plants at higher elevations should invest their limited resources more in resistance against abiotic stressors (e.g. cold, wind, UV radiation), other than the unnecessary production of defences against herbivores (Pellissier *et al.* 2014). While examples of intraspecific and interspecific defence relaxation at high elevations or latitude exist (Pennings, Siska & Bertness 2001; Scheidel & Bruelheide 2001; Salgado & Pennings 2005; Pellissier *et al.* 2012, 2014; Rasmann *et al.* 2014a; but see Moles *et al.* 2011a,b), it remains unclear whether those genotypic- or species-specific patterns can be generalized to entire communities.

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Plants have evolved a large diversity of defences to protect themselves against herbivores (Grime, MacPherson-Stewart & Dearman 1968; Rhoades 1979; Coley, Bryant & Chapin 1985; Agrawal & Fishbein 2006; Hanley *et al.* 2007). Chemical defences primarily rely on carbon- and nitrogen-based secondary compounds that act as toxins or digestibility reducers (Mithöfer & Boland 2012). In complement, physical defences act via traits that physically decrease the potential for food acquisition (e.g. leaf toughness, trichomes; Awmack & Leather 2002; Hanley *et al.* 2007). The different components of the plants' defence arsenal are expressed together in the form of syndromes to counter-attack a wide range of herbivore guilds (Agrawal & Fishbein 2006). How elevation gradients shape the deployment of plant defence syndromes has not been addressed across many species, partly because of the high endeavour required for identifying and quantifying defences of plant species belonging to a wide range of families, each one with a unique set of phytochemicals and forms (Wink 2003). An alternative approach for measuring the net outcome of plant defence traits is therefore to use bioassays that quantify the palatability of each plant species against a unique, but highly polyphagous herbivore (e.g. Grime, MacPherson-Stewart & Dearman 1968; Edwards, Wratten & Cox 1985; Pellissier *et al.* 2012).

Evidence suggests that herbivore communities can influence plant species composition (e.g. Carson & Root 2000; Fine, Mesones & Coley 2004) and related plant functional traits. For instance, Becerra (2007) or Kursar *et al.* (2009) detected a signal of chemical overdispersion within communities of closely related plant species and suggested that plant–insect co-evolution modulate plant communities' structure. Pellissier *et al.* (2013) found a correlation between herbivore and plant phylogenetic beta diversity, suggesting a link between plant and insect community assembly, while Richards *et al.* (2015) showed that the richness of herbivores correlated with phytochemical diversity in *Piper* species assemblages. In accordance, we therefore predict that in habitats where the abundance and richness of herbivores is large, the relative pressure of distinct herbivore taxa will impose a top-down control on plant composition and maintain a relatively strong and diverse defence syndrome (e.g. Kursar & Coley 2003; Becerra 2007). In contrast, in habitats with lower herbivory pressure, such as higher elevation, plant species should invest less in herbivore resistance and plant communities should be on average more palatable.

Abiotic factors could also shape community-level trait variation, in turn also modifying plant responses to herbivory (Rasmann *et al.* 2014b). For instance, at high elevation, plant species may produce leaves with increased leaf dry matter content (LDMC) as an adaptation to severe climatic conditions (Körner 2003; Dubuis *et al.* 2013). Because LDMC is positively related to leaf toughness, where high LDMC plants are more resistant to physical hazards (i.e. wind, hail; Cornelissen *et al.* 2003), it might also indirectly confer increased resistance to insect herbivores (Schuldt *et al.* 2012; Ibanez *et al.* 2013). Therefore, the selective abiotic forces might promote functional changes in plant communities, which could

indirectly confer more or less resistance to herbivores. However, the link between herbivore abundance and richness, abiotic conditions and plant palatability at the level of communities has not been thoroughly investigated so far.

In this study, we assessed plant palatability for chewing insect herbivores, physical defence traits and nutritional composition of plant species growing between 400 and 3200 m of elevation, and comprising common plant community composition at each site. Plant palatability was quantified by measuring the growth of the larvae of the generalist moth *Spodoptera littoralis* (Brown & Dewhurst 1975) on leaves collected in their natural growing locations. The weight of the larvae should be considered as the integrated measure of the physical and chemical defence for each plant species, where high values of larval weight indicate lower defence against herbivores (Bossdorf *et al.* 2004; Schädler *et al.* 2007; Ruhnke *et al.* 2009; Pellissier *et al.* 2012). Additionally, we surveyed for natural grasshopper abundance and richness along the same elevation gradient to document the expected decrease in abundance and richness in colder environments. We chose grasshoppers as indicators of herbivore abundance since these insects are among the most important herbivores in calcareous grasslands, where they can remove up to 30% of the above-ground phanerogam biomass (Blumer & Diemer 1996). Using this data set, we investigated how plant palatability is simultaneously related to leaf functional traits and elevation, at the species and at the community level, and how it is likely associated to a shift in herbivore abundance.

Materials and methods

PLANT AND ORTHOPTERAN COMMUNITIES

The study area is located in the Western Swiss Alps (Switzerland, 46°10′–46°30′ N; 6°50′–07°10′ E) and covers about 700 km^2, with elevations ranging between 375 and 3210 m a.s.l (see Fig. S1 in Supporting Information). It is characterized by a temperate climate with annual average temperatures and precipitations varying, respectively, between 8 °C and 1200 mm at 600 m, and −5 °C and 2600 mm at 3000 m (Bouët 1985). The vegetation along the elevation gradient is typical of the calcareous Alps, but also strongly influenced by the human land use and pasture.

In order to sample vegetation data along elevation gradients, a total of 912 plots of 4 m^2 were selected between 400 and 3210 m using a random stratified sampling design with regard to elevation, slope and orientation (Hirzel & Guisan 2002), which were inventoried between May and September 2002–2010 (see Fig. S1). All plots were selected among open, non-woody areas by counting with a minimal distance of 200 m between plots in order to limit the potential spatial autocorrelation resulting from field inventories performed in the same meadow and presenting a very similar plant composition. All vascular plant species present in the plots were inventoried, and their relative abundance estimated using the simplified cover scheme based on Vittoz & Guisan (2007): <0.1, 0.1–1, 1–5, 5–15, 15–25, 25–50, 50–75 and >75%. The median values of these classes (0.05, 0.5, 3, 10, 20, 37.5, 62.5 and 82.5%) were used in all further analyses.

To assess the abundance of orthopteran along elevation gradients, we randomly selected 175 plots above 1000 m out of the initial 912 plots (see Fig. S1). Between 20th July and 20th September 2012, sites

were visited from low elevation to high elevation by following the species phenology. Most of the sites below 1800 m a.s.l. (corresponding approximately to the lower limit of the treeline ecotone in the study area; Gehrig-Fasel, Guisan & Zimmermann 2007) were visited a second time later in the season to collect data on late emerging species due to a longer growing season. The sampling took place between 10 a.m. and 5 p.m. with optimal temperature conditions for insects, and within a 50×50 m area. Most individuals were identified directly on the field to the species level by net catching and/or by their songs. Unknown species and larvae were collected for identification in the laboratory and by experts from the Swiss Center from Faunal Cartography (http://www.cscf.ch/). We inventoried a total of 36 orthopteran species, including members of the Caelifera and Ensifera suborder. The abundance of each species was then estimated for a 10×10 m area using four classes of abundance: 1–5, 5–20, 20–50, 50–100 individuals. This value of abundance was estimated by means of four 10×10 m subplots situated in each cardinal directions (North, South, East and West) at 10 m from the central point and sampled circularly by walking towards the centre. For sites visited a second time later in the season, only the abundance of the additional species was assessed (see Table S1 for the species list and abundance observed on each sampling site). A global measure of abundance for each plot was obtained for Caelifera and Ensifera separately, by summing the median values of the classes of abundance (3, 13, 35 and 75, respectively) of all species. We omitted members of the Tetrigidae family, since these species are principally feeding on algae, lichens, mosses and detritus (e.g. Paranjape & Bhalerao 1985; Kuřavová & Kočárek 2015). We assumed that the measure of global grasshopper abundance is correlated with overall herbivore pressure on the plant community at each site. We extracted elevation information for all sampled plots from a Digital Elevation Model at a resolution of 25 m.

PLANT PALATABILITY BIOASSAY AND PLANT TRAITS

In order to evaluate overall plant palatability for chewing insect herbivores, we performed a bioassay experiment on 172 plant species commonly growing within the study area, using larvae of the African cotton leafworm *S. littoralis* (Lepidoptera, Noctuidae; Brown & Dewhurst 1975) obtained from Syngenta (Switzerland). We used *S. littoralis* as a non-adapted species to remove the confounding effect of possible local adaptation to plants. In addition, *S. littoralis* is a highly generalist insect herbivore, reported to feed on more than 40 families of plants (Brown & Dewhurst 1975), therefore commonly used in similar bioassays (e.g. Edwards, Wratten & Cox 1985; Bossdorf *et al.* 2004; Schädler *et al.* 2007; Ruhnke *et al.* 2009; Pellissier *et al.* 2012). While herbivores are frequently specialized on a restricted range of host plants due to possible pre-adaptations to quantitative and qualitative leaf traits of a given plant species (e.g. Mopper 1996; Pellissier *et al.* 2013; Rasmann *et al.* 2014b), the assessment of differences in leaf quality by using a generalist herbivore such as *S. littoralis* should provide a more unbiased measure (Ruhnke *et al.* 2009). The 172 plant species were selected to represent the diversity of families (number of sampled species relative to total number in each family; Spearman correlation: 0.942) and to represent diversity variation along the elevation gradient (number of sampled versus total species in each elevation bands of 200 m; Spearman correlation: 0.991). Three individuals of each plant species were collected, by selecting plants in sites with contrasting environmental conditions along an elevation gradient transect in the study area (see Fig. S1) so as to cover as much of the total distribution range of each species as possible. Eggs were hatched on wet paper at 20 °C without food to ensure a standard size. Once hatched, three larvae were placed on

each individual plant, by placing leaves of each species in distinct Petri dishes for 5 days in a climatic chamber at 24 °C (L) and 18 °C (D), $55 \pm 5\%$ RH and a 14:10 L:D photoperiod. Completely eaten or dried leaves were replaced during this period with leaves that were stored at 4 °C. At the end of the experiment, all the larvae were dried for 72 h at 50 °C and weighed. We retained dead larvae into the analyses only if replicated experiments showed the same results (i.e. larvae died in the Petri dishes). Finally, we estimated the average palatability of the 172 plant species by averaging the dry weight of the larvae in and through replicates of the same plant species.

We next measured three traits related to physical leaf defence and leaf nutrient content: specific leaf area (SLA), leaf dry matter content (LDMC) and carbon-to-nitrogen ratio (C:N). SLA and LDMC were estimated for 245 plant species, while C:N was estimated for 251 plant species. We collected 4–20 individuals in sites with contrasting environmental conditions along an elevation gradient transect (see Fig S1) so as to cover as much of the total distribution range of each species as possible (see Dubuis *et al.* 2013). Species individuals were sampled at the same phenological stage whenever possible by following the growing season according to altitude, stored in moist bags in a cool box (10 °C) and rehydrated previous to measurements by using the partial rehydration method described in Vaieretti *et al.* (2007). One well-developed entire leaf was then collected per individual (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013) for trait measurement and dried at 60 °C for minimum 4 days. SLA (mm^2 mg^{-1}) was calculated as the area of the leaf divided by its dry mass. SLA is correlated with the potential relative growth rate or mass-based photosynthetic rate of a plant, where lower values are associated to higher investments in structural defence strategies, and long leaf lifespan (Cornelissen *et al.* 2003). LDMC (mg g^{-1}) was calculated as the ratio of the leaf dry mass to its saturated fresh mass. LDMC is positively related to leaf toughness, where high LDMC plants present higher resistance to physical hazards (i.e. herbivory, wind, hail; Cornelissen *et al.* 2003) and lower digestibility (Gardarin *et al.* 2014). Leaf nitrogen (mg g^{-1}) and carbon (mg g^{-1}) contents were analysed on one sample of mixed ground leaves per species by using an elemental analyser (NC-2500 from CE Instruments). C and N are linked to plant photosynthetic rates and nutrient cycling processes (Cornelissen *et al.* 2003). We used the average trait value among all sampled individuals for each species for further analyses.

STATISTICAL ANALYSES

First, we evaluated phylogenetic signal of all plant functional traits described above and plant palatability, by pruning from the published phylogeny of the 231 most frequent and abundant plant species for the study area (Ndiribe *et al.* 2013), and by calculating Blomberg's K statistic with the 'phylosignal' function as implemented in the 'PICANTE' R package (Blomberg, Garland & Ives 2003; Kembel *et al.* 2010) in R (R Development Core Team 2014, R version 3.2.2). Blomberg's K statistic compares the observed distribution of the trait values to expectations under a Brownian motion model of trait evolution. K values close to one indicate trait evolution consistent with a Brownian motion model of evolution, while K values close to zero indicate a random distribution of trait values with respect to the phylogeny (Blomberg, Garland & Ives 2003). We tested the significance of this test by comparing the observed K value to a null distribution generated by comparing 999 randomizations of trait values across the tips of the phylogenetic tree (Kembel *et al.* 2010).

Next, we related species-level variation in plant palatability to plant trait (SLA, LDMC and C:N) and plant mean elevation, by fitting a phylogenetic least squares model (PGLS) with the package 'caper'

(Orme *et al.* 2013) in ʀ, with λ transformation for the phylogenetic tree optimized through maximum likelihood, and by square root transforming the response variable and rescaling all variables around their mean. We ensured that the model residuals did not deviate from a normal distribution. PGLS model allows correcting for phylogenetic non-independence among species while correlating two variables. Since collinearity can bias parameter estimation in regression-type models, we calculated a variance inflation factor (VIF; Quinn & Keough 2002) for our predictors by using the 'vifstep' function in the package 'ᴜꜱᴅᴍ' (Naimi 2015). This function calculates a VIF for all variables and excludes highly correlated variables from the set through a stepwise procedure based on a threshold. An ideal VIF has a value of one. While VIF values higher than 10 are clearly indicative of collinearity issues (Quinn & Keough 2002), it has also been suggested that values higher than three could also be indicative of potential collinearity issues (Zuur, Ieno & Elphick 2010; Mundry 2014). We kept all predictors since we found low collinearity (VIF values; SLA = 1.859, C:N = 1.343; LDMC = 1.269, species mean elevation = 1.341). Finally, to ensure that our conclusions were non-sensitive to the choice of the elevation metric at the species level, we run additional analysis using elevation range limits with quantile 5% and 95% in addition to the mean elevation.

To investigate the relationships between the plants traits and the environment at the community level, we computed the community-weighted mean (CWM), which represents the mean of a trait for a whole plant community, weighted by the abundance of each species that occur in the community (Garnier *et al.* 2004). We retained only plots (i.e. 307 plots) whose cover was composed with more than 70% of species for which species trait measurement was available. For each 307 plots, we computed CWM of plant palatability, SLA, LDMC and C:N by using the 'functcomp' function provided by the package 'FD' (Laliberté, Legendre & Shipley 2014). We related CWM of plant palatability to the plant traits and community elevation using an ordinary least squares regression model (OLS), by square root transforming the response variable and by rescaling all variables around their mean. We calculated a variance inflation factor (VIF; Quinn & Keough 2002) for our predictors following the same procedure as above. We excluded SLA from the regression model since this variable showed high VIF value (SLA = 4.440; C:N = 2.589; community elevation = 2.263; LDMC = 2.241). After removing SLA, VIF values reached 1.842 for C:N, 1.813 for LDMC and 1.025 for elevation. We also ensured that the model residuals did not deviate from a normal distribution and that the model residuals were not spatially autocorrelated. To ensure that our conclusions were non-sensitive to the choice of cover threshold used for selecting plot (Pakeman & Quested 2007), we run additional analyses when considering only plots whose cover was composed with more than 80% (*n* = 167) or 90% (*n* = 72) of species for which species trait measurement was available.

Finally, we related orthopteran (Caelifera and Ensifera suborder separately) richness (i.e. number of species) and abundance (i.e. counts of individuals) to elevation using a linear regression model (i.e. 175 plots). The proportion of variation in Caelifera and Ensifera richness or abundance explained by the model was quantified with the coefficient of determination (R^2).

Results

SPECIES-LEVEL ANALYSES

We found a weak phylogenetic signal for LDMC (Blomberg's *K*: *K* = 0.335, *n* = 218, Z-score = −4.981,

P-value = 0.001), SLA (*K* = 0.124, *n* = 218, Z-score = −2.702, *P*-value = 0.001), C:N (*K* = 0.138, *n* = 221, Z-score = −2.217, *P*-value = 0.001) and plant palatability (*K* = 0.122, *n* = 133, Z-score = −0.627, *P*-value = 0.265; Fig. 1), indicating that the variation of these plant traits is labile across the phylogeny. Despite general trait lability, we observed family-level differences in plant palatability (Fig. 1, see Fig. S2). Some plant families such as Apiaceae, Cyperaceae and Poaceae present lower palatability levels, while Polygonaceae and Salicaceae exhibited higher palatability. Other families such as Asteraceae and Saxifragaceae showed high variability (Fig. 1, see Fig. S2).

At the species level and among all predictor variables, only C:N was significantly associated with plant palatability in the PGLS model, which showed a low explained deviance of the relationship (Table 1a; Fig. 2). We found no relationship between plant palatability and LDMC, SLA and mean elevation of sites where the species was found (Table 1a). The results were consistent, whether we used the mean elevation at the species level, the quantile 5% or the quantile 95% representing niche limits (see Table S2).

COMMUNITY-LEVEL ANALYSES

We found that the CWM of plant palatability was significantly associated to the CWM of LDMC and community elevation in OLS multiple regressions (Table 1b, Fig. 3). Plant communities are more palatable at higher elevation, where they are composed of plant species affording lower levels of LDMC (Table 1b, Fig. 3). In contrast to the results at the
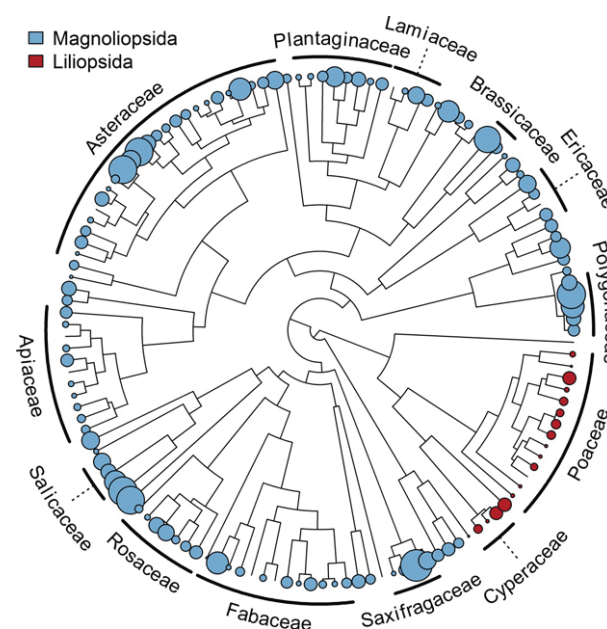

Fig. 1. Phylogeny of angiosperms palatability (*n* = 133). The trait mapped correspond to the mean larval weight (square root transformed) of *Spodoptera littoralis* after 5 days of feeding on leaf plant samples, as a measure of plant palatability. Bigger circles indicate a higher palatability of the plant to generalist chewing insect herbivores (see Fig. S2 for a complete phylogeny with plant species names). [Colour figure can be viewed at wileyonlinelibrary.com]

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Table 1. (a) Relationships between plant palatability and four predictor variables at the plant species level ($n = 129$) estimated from phylogenetic least squares model (PGLS) including all predictor variables and bivariate linear regressions. (b) Relationships between community-weighted mean (CWM) of plant palatability and four predictor variables at the plant community level estimated from ordinary least squares multiple regressions (OLS) and bivariate linear regressions. CWM was estimated for communities whose plant cover was composed with more than 70% of species for which species trait measurement was available ($n = 307$). SLA was not considered in the OLS model since it was highly correlated to the other predictors. The table (a and b) shows the coefficient of determination (R^2), the t-value and the standardized regression coefficients (Estimate)

(a) Species level

	PGLS		Bivariate model		
	Estimate	t-value	Estimate	t-value	R^2
SLA	0.009	0.081	0.097	1.093	0.002
LDMC	−0.090	−0.698	−0.178	−2.037	0.024*
C:N	−0.256	−2.536*	−0.201	−2.312	0.033*
ELEV	−0.062	−0.650	0.009	0.101	−0.008
R^2	0.054*				
Lambda	0.416				

(b) Community level

	OLS		Bivariate model		
	Estimate	t-value	Estimate	t-value	R^2
SLA			−0.028	−0.489	−0.002
LDMC	−0.397	−6.132***	−0.429	−8.298	0.182***
C:N	−0.058	−0.893	−0.279	−5.079	0.075***
ELEV	0.343	7.034***	0.327	6.042	0.104***
R^2	0.292***				

SLA, specific leaf area; LDMC, leaf dry matter content; C:N, carbon-to-nitrogen content; ELEV, mean elevation.
*$P < 0.05$, ***$P < 0.001$.

species level, the CWM of plant palatability was not associated to the CWM of C:N in OLS multiple regressions (Table 1b). We found no autocorrelation in the residuals of the CWM model (Moran's $I = 0.009$; P-value = 0.209). Overall, we found that the results were not sensitive to the threshold considered for selecting plot communities, whether it is 70, 80 or 90% of cover in plots for which species trait measurement was available (see Table S3).

Finally, orthopteran richness (i.e. number of species) and abundance (i.e. counts of individuals) were both negatively correlated to elevation in Caelifera (linear regression; richness: $n = 175$, $R^2 = 0.407$, t-value = −10.970, slope = −0.004, P-value <0.001; abundance: $n = 175$, $R^2 = 0.212$, t-value = −6.925, slope = −0.093, P-value <0.001; Fig. 4) and Ensifera (linear regression; richness: $n = 175$, $R^2 = 0.528$, t-value = −13.99, slope = −0.002, P-value <0.001; abundance: $n = 175$, $R^2 = 0.257$, t-value = −7.828, slope = −0.017, P-value <0.001; Fig. 4). We also found a strong correlation between orthopteran richness and abundance in Caelifera (Spearman correlation:
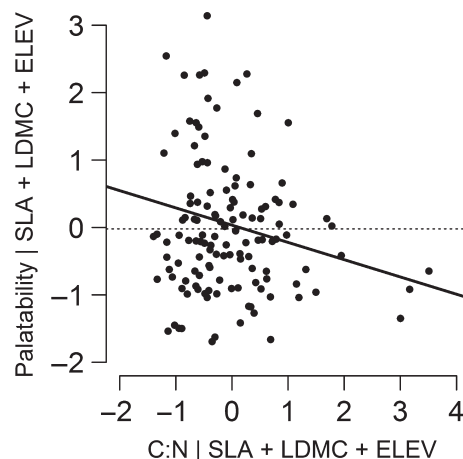

Fig. 2. Partial regression plot (i.e. added variable plot) calculated from PGLS model ($n = 129$) showing the independent contribution of C:N in explaining plant species palatability variation (i.e. solid black line; Table 1a) at the species level. The axis represents the residuals of the models (x-axis: C:N~ SLA + LDMC + ELEV; y-axis: Palatability~SLA + LDMC + ELEV). Before fitting the PGLS model, plant palatability was square root transformed and all variables were rescaled around their mean. The dashed line corresponds to the mean of the y-axis. SLA (specific leaf area); LDMC (leaf dry matter content); C:N (carbon-to-nitrogen content); ELEV (mean elevation). Plants are more palatable when their leaves are more nutrient rich (i.e. low C:N).

$\rho = 0.845$, $R^2 = 0.714$, P-value <0.001) and Ensifera (Spearman correlation: $\rho = 0.823$, $R^2 = 0.678$, P-value <0.001), as a result of the contrast between low elevation rich and abundant orthopteran communities versus high elevation poor communities (Fig. 4).

Discussion

SPECIES-LEVEL PLANT PALATABILITY ALONG ELEVATION GRADIENTS

Plant defence levels may vary along an elevation gradient by following two expectations. The first one relies on the fact that producing defensive chemicals is costly (Gulmon & Mooney 1986; Gershenzon 1994; Cipollini, Purrington & Bergelson 2003) and predicts a decrease of defence with elevation, in line with the concomitant decrease in herbivore abundance. The second one relies on the resource availability hypothesis (Coley, Bryant & Chapin 1985; Endara & Coley 2011), which states that plants with slow growth rates occurring in environments with low resources should be highly defended against herbivory because of the high cost of tissue loss in resource-poor environments. Accordingly, as environmental harshness and low resources availability limit plant growth rate at high elevation, we would expect high elevation plants to exhibit high levels of defence against herbivory. The fact that we found no effect of elevation on plant palatability at the species level (see similar results in Rasmann *et al.* 2014b) suggests that different species may show dissimilar sensitivities to herbivore abundance and abiotic conditions,
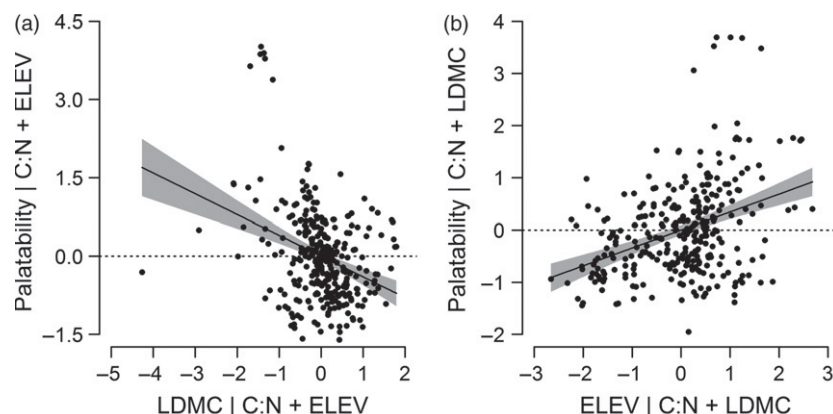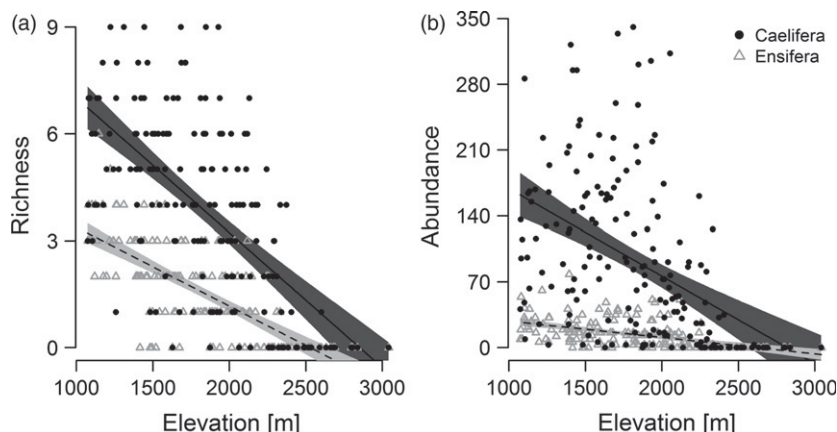
Fig. 3. Partial regression plots (i.e. added variable plots) calculated from OLS model showing the independent contribution of (a) LDMC and (b) community elevation in explaining plant community palatability variation (i.e. solid black line; Table 1b). The axis represents the residuals of the models. CWM of plant palatability was estimated for communities whose plant cover was composed with more than 70% of species for which species trait measurement was available ($n = 307$). Before fitting the OLS model, plant palatability was square root transformed and all variables were rescaled around their mean. The grey area corresponds to the 95% confidence interval around the mean. The dashed line corresponds to the mean of the y-axis. LDMC (leaf dry matter content); C:N (carbon-to-nitrogen content); ELEV (mean elevation). Communities are more palatable at high elevation sites and/or when they are composed of plant species presenting lower LDMC.

Fig. 4. Changes in (a) orthopteran richness measured as the number of species and (b) orthopteran abundance (i.e. counts of individuals) along the elevation gradient for Caelifera (black dots) and Ensifera (grey triangles) suborder. Each dot and each triangle represent a sampled community where orthopteran abundance and richness were estimated ($n = 175$; see Fig. S1). The grey and black areas correspond to the 95% confidence interval around the mean for Ensifera and Caelifera, respectively. Orthopteran Caelifera and Ensifera are more abundant and diverse on low elevation sites.

leading to a lack of a clear trend when considering all species individually (Rasmann *et al.* 2014b).

In accordance with the common rule of insects being mostly deficient in nitrogen, larvae performed slightly better on plants with a low carbon-to-nitrogen content (Table 1a, Fig. 2; White 1984; Elser *et al.* 2000). Other leaf variables such as leaf toughness (represented here by LDMC and SLA) were not associated to plant palatability, which is in contrast with previous results in which SLA was associated with investment in physical leaf defence (Coley 1983; Cornelissen *et al.* 2003; but see Louda & Rodman 1996). Since values of SLA and LDMC are highly plastic across sites, it is likely that more samples would be required to capture intraspecific variability and to accurately catch the multifaceted dimensions of plant defences based on physical traits only (Ackerly 2009; Cornwell & Ackerly 2009). In addition, this study did not take into account plant secondary metabolites specifically, which are known to play a preponderant role in driving insect performance (Fraenckel 1959; but see Carmona, Lajeunesse & Johnson 2011). Plants chemical defences are difficult to

study across such a large plant taxonomic scale because the secondary metabolites involved are extremely diverse (Mithöfer & Boland 2012; Kant *et al.* 2015), but may largely explain the observed difference in palatability among plant species.

We found a weak phylogenetic signal for plant leaf traits such as SLA, LDMC and C:N, even if the latter were significantly different from a random distribution of plant traits across the phylogeny. This suggests that variation of several plant functional traits across species shows a pattern of adaptation to the environment, with limited phylogenetic inertia (Wiens & Graham 2005; Losos 2008). Similarly, we found no phylogenetic signal for plant palatability suggesting that mechanisms of plant defence (physical and chemical combined) are probably species-specific, and independent of the phylogeny at the scale we performed our analysis. Indeed, palatability could show phylogenetic conservatism at deeper (e.g. family level) nodes of the phylogeny. For instance, most of the species in the Apiaceae, Poaceae and Cyperaceae show lower palatability to insect herbivores (Fig. 1), suggesting that

family-specific defence traits, such as secondary metabolites (e.g. furanocoumaris for Apiaceae; Berenbaum, Zangerl & Nitao 1986), or silica content in grasses and sedges (O'Reagain & Mentis 1989; Vicari & Bazely 1993; Massey, Ennos & Hartley 2006; Massey & Hartley 2009) might drive conservatism of plant–herbivore interaction (Futuyma & Agrawal 2009). However, testing for family differences would require a larger species sampling than considered here.

COMMUNITY-LEVEL PLANT PALATABILITY ALONG ELEVATION GRADIENTS

At the community level, we observed an increase of the overall plant palatability with elevation, suggesting that the most dominant species in plant communities growing at higher elevations are generally more palatable to herbivores than their low elevation counterparts. This result is in line with the observed decrease of orthopteran abundance and richness with elevation and suggests that dominant plants respond to reduced herbivore abundance by relaxing their defences overall (Pellissier *et al.* 2012), supporting the hypothesis of defence relaxation with elevation (Gulmon & Mooney 1986; Gershenzon 1994). Previous studies showed a similar relationship between plant chemical and biomechanical defence traits at the community level and herbivore abundance and richness (Becerra 2007; Peeters, Sanson & Read 2007; Richards *et al.* 2015). However, those study at the level of communities never extended at higher latitude or elevation.

Together with elevation, we found that the mean community-level value of LDMC was also related to plant community palatability (Table 1b, Fig. 3). In other words, plant communities situated at higher elevation and/or presenting higher mean community-level value of LDMC are generally less palatable to herbivores. This result parallels finding at the species level in which leaf toughness was associated with investment in physical leaf defence (Coley 1983; Choong 1996; Hochuli 2001; Cornelissen *et al.* 2003; Clissold *et al.* 2009; Ibanez *et al.* 2013; but see Louda & Rodman 1996). Abiotic factors could also shape community-level trait variation, in turn also modifying plant responses to herbivory (Rasmann *et al.* 2014b). For instance, plant species at high elevation may first produce leaves with increased leaf dry matter content (LDMC) as an adaptation to severe climatic conditions (Körner 2003; Dubuis *et al.* 2013), thus increasing resistance to physical hazards (i.e. wind, hail; Cornelissen *et al.* 2003). In turn, this might indirectly confer increased resistance to arthropod herbivores (Schuldt *et al.* 2012; Ibanez *et al.* 2013).

In sum, we found contrasted results in the species- and community-level analyses. Plant palatability was related to LDMC and elevation at the community level, while only C:N showed a trend in species-based analyses driven by a few species (Fig. 2). While in species-level analyses each species is given the same weight, at the community level, trait values are weighed by the dominance of species (i.e. higher weight to dominant plant species; Garnier *et al.* 2004; Pellissier *et al.* 2012). This suggests that the relationships between plant palatability, LDMC and elevation are driven predominantly by species with a higher cover. Dominant plant species are expected to be more frequently targeted by herbivores and to invest more energy in physical defence to generalist herbivore (Pellissier *et al.* 2015). For plant species predominantly relying on physical defences, a decrease in LDMC would directly result in higher palatability. In contrast, for species also relying on chemical defences, the relationship would be less clear. Moreover, the increase in plant palatability at higher elevation communities might suggest that dominant plants better modulate defences to shifting ecological conditions, such as biotic interaction with herbivores. Together, our results indicate that plant dominance should be included when addressing the ecology and evolution of plant defence strategies.

Our findings indicate that the measure of community-level plant palatability could be one of the processes explaining how climate change will affect plant community composition in the future. Many insects are currently limited in their distribution by temperature and length of the growing season (Maclean 1983; Strathdee *et al.* 1993; Whittaker & Tribe 1996; Miles, Bale & Hodkinson 1997; Bird & Hodkinson 1999; Hodkinson *et al.* 1999; Ritchie 2000). However, the higher temperatures associated with climate change will allow invertebrate herbivores to track climatic changes (Wilson *et al.* 2007) to an extent that plants cannot (Grabherr, Gottfried & Pauli 1994 but see Cannone, Sgorbati & Guglielmin 2007). For instance, Bässler *et al.* (2013) found an upslope shift of the upper range margin for insects that exceeded expectations based on climatic changes. The predicted future increase in herbivore abundance at high elevations under climate changes (Rasmann *et al.* 2014b) will increase the pressure on palatable plant communities. Herbivory could have in turn a disproportionate negative impact on the cover of these species (Brown & Gange 1989) and may cause severe shifts in the pattern of plant and soil carbon cycling (Metcalfe *et al.* 2014). Ultimately, palatable species could disappear from high elevation communities because insects may selectively feed on them, facilitating their replacement by lower elevation plant species (Rasmann *et al.* 2014b). Moreover, increasing stress conditions through climate change (e.g. drought) could also alter the defence of plants against insect herbivory by reducing investments in secondary metabolites (Gutbrodt, Mody & Dorn 2011).

In conclusion, our study showed that the decrease in plant palatability at higher elevation can be scaled up to entire communities. In contrast, we found only weak trends when looking at species individually. Future work using community-wide metabolomics approaches for obtaining more information on leaf chemistry, and identifying the dominant chemical defence strategies along the elevation gradient might help overcoming these obstacles (Van Dam & Poppy 2008; Jansen *et al.* 2009). High elevation areas represent refuges from herbivory for some alpine plants: they are excluded from low elevations because of the high herbivory pressure in lowland (Galen 1990; Bruelheide & Scheidel 1999; Bruelheide 2003). However, climate change is expected to lift current climate

barriers and herbivore colonization at higher elevation may promote fast plant communities turnover, in which less palatable high elevation plants will be selected.

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Data accessibility

Data from this paper can be accessed through figshare: http://dx.doi.org/10.6084/m9.figshare.3803955 (Descombes *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of the study area in the western Alps of Switzerland.

Figure S2. Phylogeny of angiosperms palatability.

Table S1. Species list observed on the sampling sites.

Table S2. Results of PGLS models at the species level.

Table S3. Results of OLS models at the community level.