

## CLIMATE CHANGE AND SPECIES RANGE SHIFTS

## Climate-driven change in plant–insect interactions along elevation gradients

Sergio Rasmann<sup>1\*†</sup>, Loïc Pellissier<sup>2</sup>, Emmanuel Defossez<sup>3,4</sup>, Hervé Jactel<sup>5</sup> and Georges Kunstler<sup>3,6</sup>

<sup>1</sup>Department of Ecology and Evolution, University of Lausanne, UNIL Sorge, Le Biophore CH, Lausanne 1015, Switzerland; <sup>2</sup>Department of Bioscience, The Arctic Research Centre, Aarhus University, Aarhus 4000, Denmark; <sup>3</sup>Irstea, UR EMGR Ecosystèmes Montagnards, rue de la Papeterie-BP 76, St-Martin-d'Hères F-38402, France; <sup>4</sup>Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS UMR 5175, 1919 route de Mende, Montpellier cedex 5 34293, France; <sup>5</sup>INRA, UMR 1202 BIOGECO, Cestas F- 33610, France; and <sup>6</sup>Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia

## Summary

1. Global warming is predicted to dramatically alter communities' composition through differential colonization abilities, such as between sessile plants and their mobile herbivores. Novel interactions between previously non-overlapping species may, however, also be mediated by altered plants' responses to herbivore attack.

2. Syndromes of plant defences and tolerance are driven by inherited functional traits, biotic and abiotic conditions, and the geographical and historical contingencies affecting the community. Therefore, understanding climate change-driven herbivore responses and evolution towards a particular plant defence syndrome is key to forecasting species interactions in the near future.

3. In this paper, we first document variations in herbivory, and plant defences along altitudinal gradients that act as 'natural experiments'. We then use an empirical model to predict how specialist herbivore abundance may shift with respect to elevation in the near future.

4. Our field surveys and field experiment showed a decrease in herbivory with elevation. However, contrary to expectations, our meta-regression analyses showed that plant defences, particularly leaf toughness and flavonoid compounds, tend to be higher at high elevations, while secondary metabolites showed no clear trend with elevation.

5. Based on those results, we discuss how plant communities and species-specific plant defence syndromes will change in response to the climate-driven herbivore colonization of higher altitudes. Particularly, plant from high elevation, due to high protection against abiotic stress may be already ecologically fitted to resist the sudden increase in herbivory pressure that they will likely experience during global change.

**Key-words:** community ecology, ecological gradients, flavonoids, herbivory, leaf toughness, plant defences, predators

## Introduction

Assessing the consequences of climate change on ecosystems dynamics and species interactions is becoming increasingly urgent (Schröter *et al.* 2005; Tylianakis *et al.* 2008; Wu *et al.* 2011; de Sassi, Lewis & Tylianakis 2012). Among the well-documented responses to global warming

are organisms' range shifts to higher latitudes and altitudes (Grabherr, Gottfried & Pauli 1994; Parmesan 1996; Stange & Ayres 2001; Hoegh-Guldberg *et al.* 2008; Burrows *et al.* 2011; Pateman *et al.* 2012; Pauli *et al.* 2012). Such displacements of populations have raised several concerns, including loss of biodiversity (Parmesan 1996, 2006), population mismatches between predators and prey (Durant *et al.* 2007), parasitoids and their host insect herbivores (Harrington, Woiwod & Sparks 1999) or herbivorous insects and their host plants (Singer & Parmesan 1993),

\*Correspondence author. E-mail: Sergio.rasmann@unil.ch

†Present address. Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA.

and increased pestilence due to lessened population-regulating factors (Logan, Regniere & Powell 2003; Bentz *et al.* 2010). Indeed, more important than the effect on any single species are the effects of global warming on complex community-level interactions (van der Putten *et al.* 2004; Tylianakis *et al.* 2008; Jamieson *et al.* 2012).

Insects are among the groups of organisms that exhibit the strongest responses to climate change because they are ectothermic, so thermal changes have strong direct influences on their development, reproduction and survival (Bale *et al.* 2002). Additionally, shorter generation times and high reproductive rates, coupled with a better ability to disperse, lead insects to respond more quickly to climate change through range shift than longer-lived and less mobile organisms, such as plants (Menéndez 2007). Different migration rates between plant, insect herbivores and their predators may lead to reshuffled communities. Insect herbivores and plants together comprise more than half of the terrestrial macro-biodiversity (Strong, Lawton & Southwood 1984) and display trait-mediated complex networks of interactions that are expected to be affected by climate change (Harrington, Woiwod & Sparks 1999; Visser & Both 2005; Lurgi, López & Montoya 2012). For instance, plant resistance strategies against insect herbivores, including direct physical and chemical defences, the recruitment of natural enemies of the herbivore (i.e. indirect defences), and tolerance (the ability to compensate for tissue loss after herbivory) (Schoonhoven, van Loon & Dicke 2005), have been shown to vary along ecological gradients (Moles *et al.* 2011; Rasmann & Agrawal 2011; Pellissier *et al.* 2012) and to be affected by climate change (DeLucia *et al.* 2012). Therefore, predicting the community-level dynamics of plants and herbivores requires adopting an integrative approach that includes measuring community composition and herbivory dynamics as well as the bottom-up effects of plants on herbivores (i.e. plant defences) and top-down regulation of herbivores by predators and parasitoids.

Elevation gradients are optimal ecological surrogates for inferring global change-driven dynamics (Pickett 1989; Körner 2007; Garibaldi, Kitzberger & Chaneton 2011; Beier *et al.* 2012; Rasmann, Alvarez & Pellissier 2013) acting as ‘natural experiments’ by providing variation in abiotic factors under which biotic interactions can be evaluated (Preszler & Boecklen 1996; Darrow & Bowers 1997; Salmore & Hunter 2001; Yarnes & Boecklen 2005; Zehnder *et al.* 2009). Compared to much larger-scale latitudinal gradients, elevation gradients minimize the confounding effects of historical and biogeographical differences in, for instance, plants and herbivore species pools (Hodkinson 2005).

In this contribution, we first aim to describe variation in herbivory levels and plant resistance strategies along elevation gradients. We purposely excluded an in-depth analysis of parasitism pressure along elevation gradients, subject of a quantitative review discussed below (Péré, Jactel & Kenis in review). Second, we forecast levels of plant–herbivore interactions along elevation gradients in warmer climates

and discuss the results in light of current elevation patterns in plant defence traits. Our working hypothesis is that if we can identify consistent trends in biotic changes along elevation gradients, we should be able to extrapolate our results to future global change dynamics such as increases in temperature.

## Herbivory along elevation gradients

Because insects are ectothermic, it is generally expected that insect herbivory rates decrease with increasing elevation. Most studies on the variation of herbivory rates with elevation (or even with latitude) have been framed by (i) focusing on the ambient herbivory rate resulting from all insects present at a given altitude on a single plant species, or (ii) analysing the ambient herbivory from all insects on all plants in a local community at a given altitude. These studies have generally shown that herbivory rates decrease with increasing elevation, but the pattern is quite variable, with some potentially increasing or nonlinear responses (Hodkinson 2005). Even within the same study site, opposing patterns (increasing or decreasing with latitude) have been reported, depending on the herbivory measurement method (Adams & Zhang 2009; Zhang, Adams & Zhao 2011). A recent study on herbivory of forest insects along 24 elevation gradients in Europe confirms this lack of consistent effect of elevation, reporting great variability among four sampled tree species (L. Marini *et al.* unpublished). However, overall, the responses of different insect feeding groups (e.g. leaf chewers, miners, sap feeders, gall makers) were found to be either neutral or positive (Marini *et al.* submitted). Some studies have reported that the pattern of decrease in herbivory rate with elevation is clearer for generalist herbivores than for specialists (Scheidel, Rohl & Bruelheide 2003; Hodkinson 2005). However, the relative importance of specialists and generalists may also vary with elevation, although the evidence is mixed [higher diversity and specialization with increasing altitude in the tropics (Rodríguez-Castañeda *et al.* 2010) but the opposite patterns for diversity and specialization in temperate zones (Pellissier *et al.* 2012)].

A third approach for measuring herbivore variation along elevation gradients is to analyse the average herbivory rate at the community level for all of the different species that are present in a community. This approach allows understanding how plant species succession, with contrasting ecological and antiherbivory strategies along an elevation gradient, may drive the observed herbivory rate, and reciprocally, how herbivory affects the plant community structure along the gradient. We here provide results for herbivory rates on natural and experimentally established community of plants along elevation gradients.

## METHODS

Briefly, leaf herbivory rates were analysed for six dominant tree species (i.e. *Quercus petraea*, *Fagus sylvatica*, *Abies*

*alba*, *Picea abies*, *Pinus uncinata* and *Pinus cembra*) commonly found along elevation in the French Alps from 500 to 2000 m (see Methods S1 in Supporting information for a detailed description of the methods). *Quercus petraea*, *F. sylvatica* and *A. alba* are associated with warmer habitats, whereas *P. abies*, *P. uncinata* and *P. cembra* are associated with colder climate. Six plots (4 × 4 m) per altitude were evenly distributed across seven altitudes. First, randomly selected natural seedlings (<50 cm height) were scored for leaf damage by visually assessing the percentage of leaf area eaten for every leaf on every individual seedling. For practicality, we decided to focus only on leaf chewer damage, omitting piercing-sucking damage as well as pathogen attack. Second, at the same elevations, we established common gardens of the same six species of trees. After germination, we monitored leaf herbivory on sown seedlings as above. Although we acknowledge that herbivory rates are likely to vary with ontogeny (Boege & Marquis 2005), monitoring herbivory on seedlings is valuable because this lifestage is key for community assembly and therefore herbivore impact is predicted to be stronger.

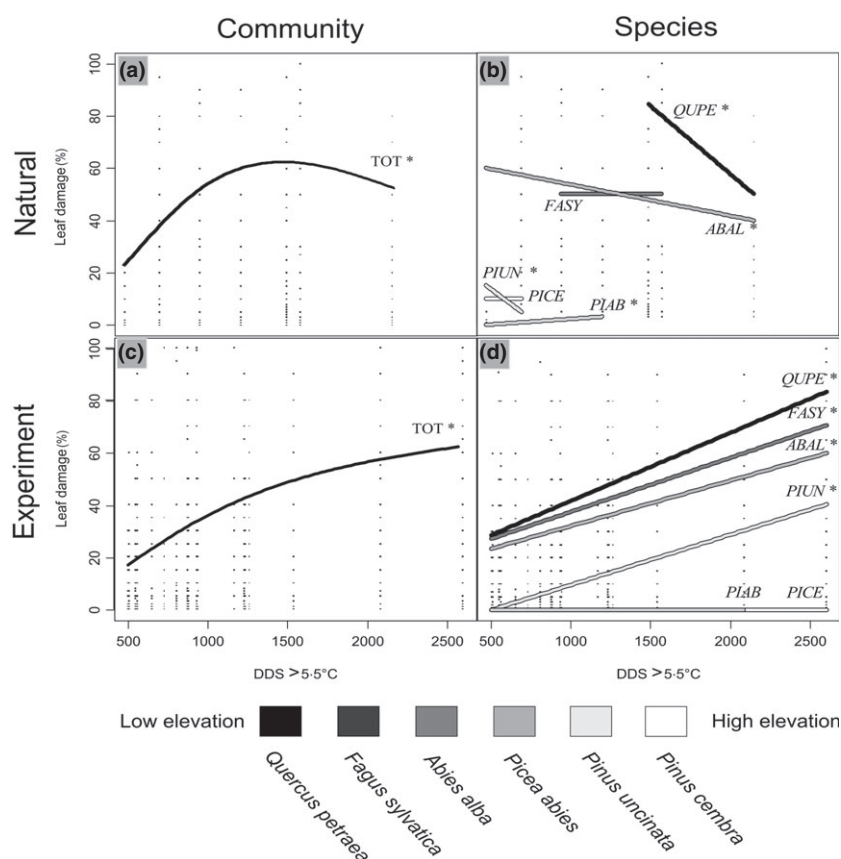
Herbivory levels were quantile-regressed against degree-days sum above 5.5 °C (DDS) for each elevation (Pearson correlation between DDS and elevation,  $r = -0.98$  for natural sites and  $r = -0.85$  for experimental sites). Because our data were strongly skewed towards zero, we used quantile regressions, which do not require any assumption concerning the shape of the error distribution, to capture

the maximum potential herbivory rate by the 95% quantile. For both the natural population observation and the experimental data, we pooled all tree species to analyse community-level responses, as well as we scored individual species responses.

## RESULTS

In naturally established seedlings, we found a nonlinear response of herbivory to DDS, with a clear trend of lower herbivory at higher elevations (Fig. 1a, and see AIC table in Methods S1, Supporting information). However, individual tree species showed idiosyncratic responses to DDS (Fig. 1b). In contrast, experimentally sown seedlings exhibited an overall decrease in insect herbivory with increasing elevation (i.e. with decreasing DDS), both at the community level (Fig. 1c), and for all species analysed individually (Fig. 1d). The data for experimentally sown seedlings also showed that for similar elevations, species from warmer climates (*Q. petraea*, *F. sylvatica* and *A. alba*) experienced greater herbivory than species from colder climates (*P. abies*, *P. uncinata* and *P. cembra*) (Fig. 1d).

Overall, these results suggest that herbivore pressure on plants decreases with increasing elevation, which is consistent with recent work (Pellissier *et al.* 2012). The lack of a clear pattern at the species-specific level for the naturally established seedlings, as opposed to the pattern observed for the experimental planted seedlings, may be explained by



**Fig. 1.** Variation in leaf damage on tree seedlings along an elevation gradient in the French Alps for both naturally established seedlings and experimentally sown seedlings outside of their natural distribution. Panels (a) and (b) show results from the survey of natural populations, whereas panels (c) and (d) show results of the common garden experiment. Additionally, panels (a) and (c) the community response (i.e. overall average across six species), and panels (b) and (d) show individual tree species responses. The elevation gradient is represented by the degree-day sum (>5.5°C). A higher DDS represents a warmer climate at a lower elevation. Lines representing the 95% quantile of the leaf herbivory rate at the community level (all species together) and the species level, estimated using quantile regression, are presented. Grey points are individual herbivory rate measurements. Species and their abbreviations from low to high altitude are *Quercus petraea* (QUPE), *Fagus sylvatica* (FASY), *Abies alba* (ABAL), *Picea abies* (PIAB), *Pinus uncinata* (PIUN) and *Pinus cembra* (PICE).

the very restricted climatic conditions under which natural seedlings are found. Hence, the pattern of variation in herbivory rate at the community level may be strongly affected by the succession of species along the elevation gradient.

### Plant defences along elevation gradients

According to theory, high-elevation living plants, because they experience lower levels of herbivory, are expected to have lower levels of defences against herbivores, compared to their relatives at lower altitudes (Coley & Barone 1996). When measuring resistance against a generalist herbivore across 16 pairs of high- vs. low-elevation species, we recently found that caterpillars grew larger on high-elevation species overall (Pellissier *et al.* 2012). The exact reasons for this pattern, such as a decline in defences or the higher nutritional quality of the leaves of alpine plants, have not yet been determined. A number of plant quality traits, such as foliar nitrogen (Erelli, Ayres & Eaton 1998; Hengxiao *et al.* 1999; Richardson 2004), defensive chemistry (Erelli, Ayres & Eaton 1998; Hengxiao *et al.* 1999; Salmore & Hunter 2001; Alonso *et al.* 2005; Zehnder *et al.* 2009), structural compounds (Richardson 2004) and leaf morphology traits (Hengxiao *et al.* 1999), change with elevation, but not in a predictable manner. Very likely, both abiotic and biotic stresses contribute shaping secondary chemistry phenotypes. Leaves that have high concentrations fibre are stronger, more resistant to damage and potentially longer-lived than leaves with low fibre concentrations (Abrahamson *et al.* 2003; Richardson 2004). Additionally, phenolic compounds can simultaneously protect leaves from photodamage by acting as antioxidants and reduce insect performance (Close & McArthur 2002; Forkner, Marquis & Lill 2004).

Despite a relatively long history, a comprehensive analysis of plant defence traits along elevation gradients is still lacking. We thus resolved to explore the literature for putative defence traits of plants that were measured along elevation gradients and summarize this with a formal meta-regression analysis as in Castagneyrol & Jactel (2012).

### METHODS

We scanned the literature in the ISI Web of Science data base, using combinations of relevant terms (plant\*, defen\*, elevation\*, altitude\*). The survey was completed using the Google Scholar search engine and a reference list of individual papers. We only considered studies in which plant traits were measured in relation to resistance against herbivore attack. Because of statistical constraints [the variance of the effect size =  $1/(n-3)$ ], we removed from consideration studies in which trait variation was measured with less than four elevation points. We also included our own data from the Baccara project (<http://www.baccara-project.eu/>), in which we measured leaf toughness in six woody plant species along elevation gradients of European mountain regions. We identified a total of 40 studies that met our conditions, providing

a total of 99 case studies (Table S1, Supporting information). The relationships between plant defensive traits and elevation were measured by extracting correlation coefficient ( $r$ ) values from the text and tables. If correlation coefficients were not directly available, the numerical values were extracted by digitising the figure and plotting simple linear regressions. A positive value implied that plant defensive trait values increased with increasing elevation (Table S2, Supporting information). We tested the effects of four covariates on the relationship between plant chemical defences and altitude. First, we divided plant species into herbaceous and woody plants (including shrubs). Second, we divided plant chemicals into flavonoid and nonflavonoid secondary metabolites (SM). This division was based on the assumption that flavonoid-based compounds can be involved in pigmentation, UV protection and freezing tolerance in plants (Close & McArthur 2002). Therefore, it is more likely to expect a positive correlation between flavonoids and elevation than between nonflavonoid SMs, which should only be involved in defence against herbivores and elevation. Third, we separated whether measures were taken on reproductive (flowers, seeds, fruits) or vegetative organs of the plants (leaves, branches, trunks). We carried out different meta-analyses, using a hierarchical approach to avoid the need to use individual data points more than once in any given analysis (Whittaker 2010). First, we tested the effect of the type of plant (herbaceous vs. woody plants) on a subset of data comprising flavonoids and nonflavonoids defences in reproductive and vegetative organs and found no significance differences. We therefore pooled data from both types of plants in further analyses. We then tested the effect of the type of chemical defence within each category of organs.

### RESULTS

Overall, we detected a significant increase in plant physical defence traits and flavonoids with elevation (Fig. 2). This was driven by leaf toughness and flavonoids in the reproductive organs (see positive regression coefficients in Fig. 2). We found no effect of elevation on other types of defences (nonflavonoids in general and flavonoids in vegetative organs).

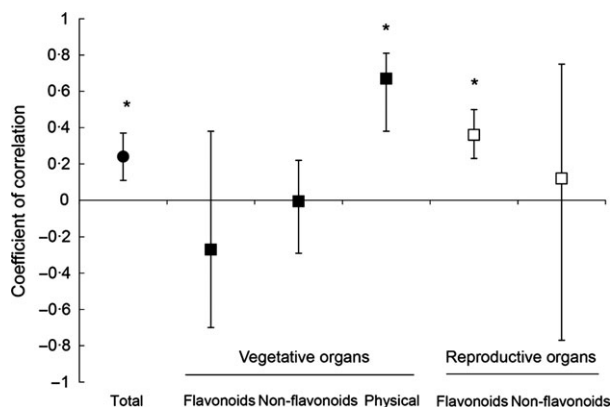
### Forecasting shift in herbivore abundance along elevation under warmer climate

As an illustration of how herbivore abundance may shift in response to climate change along the elevation gradient, we modelled the maximum abundance of butterflies with respect to elevation in response to temperature and projected the model under three different climate change scenarios.

### METHODS

Total butterfly abundance data were collected in 192 plots 50 × 50 m in size in a region of the Western Swiss Alps





**Fig. 2.** Coefficients of correlation (shown with confidence intervals) between elevation and direct chemical and physical plant defences for total defence (black circle), and the vegetative organs (black squares) and the reproductive organs (open squares). Chemical defences were separated into flavonoid-based compounds and nonflavonoid-based compounds. Physical defences were only analysed in woody species. Asterisks indicate significant deviations from a null relationship.

(700 km<sup>2</sup> Pellissier, Alvarez & Guisan 2012). All butterfly species belonging to the Papilionoidea superfamily (sensu Heikkilä *et al.* 2012) were monitored. We counted the number of individual butterflies as a measure of the abundance of herbivores at each site. For each site, we then determined the annual mean temperature, calculated as described by Zimmermann & Kienast (1999). We calculated the maximum abundance of butterflies in sampled communities in 20 equal classes of increasing temperature. Maximum abundance permits calculating an extreme scenario of herbivore pressure for a given set of

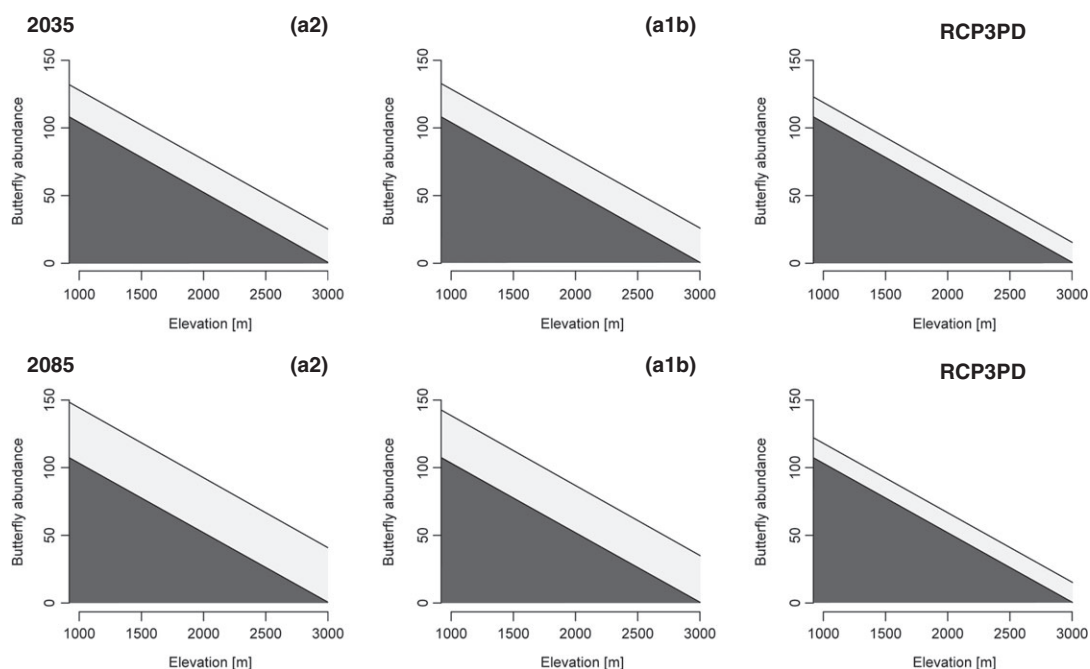
environmental conditions. We related the maximum abundance to the mean annual temperature of the corresponding class using a linear model. We projected this model considering temperature anomalies for three climate change scenarios, that is, A2, A1B1 and RCP3PD. Those scenarios were developed as part of the Swiss Climate Change Scenario CH2011 project conducted by the Center for Climate Systems Modelling (<http://www.c2sm.ethz.ch/>), with new generations of climate models with higher resolution combining global climate models (e.g. ECHAM) and regional climate models (COSMO).

## RESULTS

The model for maximum butterfly abundance vs. the mean annual temperature had a good fit to the data ( $R^2 = 0.61$ ). We found a decrease in maximum butterfly abundance in communities at higher elevations (Fig. 3). Subsequently, our model provides a way to forecast the relative increase in herbivore pressure with elevation. The ratio of 'future to current butterfly herbivore abundance' indicates that the impact of herbivores is likely to increase dramatically above a threshold of 2200 m, where the two worst climate change scenarios A2 and A1B indicate more than a doubling in abundance of lepidopteran herbivores (Fig. 4). Below this elevation, the increase in this ratio is less marked because of currently higher abundance of butterflies in those conditions.

## Discussion

Using our own empirical data and information available in the literature, we found evidence for a decrease in



**Fig. 3.** Relationship between butterfly maximum abundance for the current climate (dark) as well as for three climate change scenarios (A2, A1B, RCP3PD, light) for two time periods (2035 and 2085) and elevation.

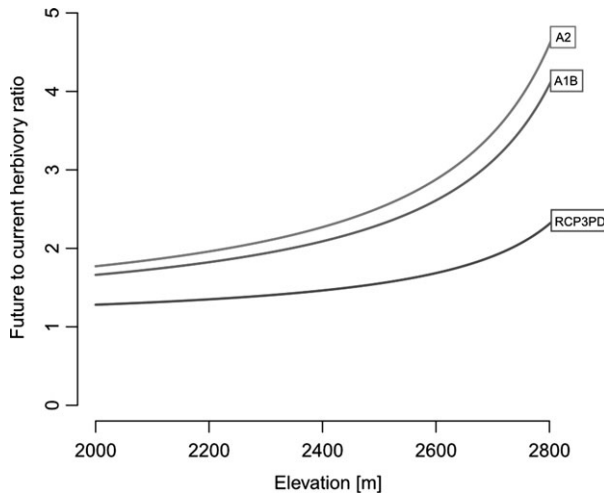


Fig. 4. Relationship between 'future to current butterfly abundance' ratio for three climate change scenarios (A2, A1B, RCP3PD) for the 2085 period. The ratio increases with elevation.

herbivory pressure along elevation gradients. This should lead to an overall reduction in plant defences in altitude; however, our meta-analysis showed that leaf toughness in trees and flavonoids in reproductive organs of herbs increase with elevation.

Several high-elevation plants might be thus selected by the abiotic environments to be ecologically fitted, and promptly respond to the sudden increase in herbivore abundance during global warming.

#### HERBIVORY AND PLANT DEFENCES ALONG ELEVATION GRADIENTS

Our results suggest that, contrary to classical predictions, a reduction in herbivory pressure in harsher environments does not necessarily lead to a decrease in plant defences (Schemske 2009). Accordingly, manipulative experiments to test plant palatability at different altitudes lead to contrasting results. Across three species of slugs, a decrease in herbivory with altitude was only detected in three out of six plant species (Scheidel & Bruelheide 2001). Across sixteen pairs of plant species from high and low altitudes, we found an overall reduction in resistance against a generalist insect herbivore, despite considerable variability of responses across pairs of species (Pellissier *et al.* 2012). These contrasting results demonstrate that how plant defences vary with elevation are complex and is not solely the result of herbivore pressure. Indeed, several abiotic factors may contribute to selection on plant traits that in turn also protect plants against herbivores. First, a severe climate might cause selection for increased leaf toughness and decreased specific leaf area (Wright *et al.* 2004). Second, drought has been shown to inhibit plant secondary metabolism (Gutbrodt, Mody & Dorn 2011), thus increase susceptibility to herbivores and pathogens (Jactel *et al.* 2012). And third, delayed snowmelt has been shown to increase leaf nitrogen and herbivory rates (Torp *et al.* 2010a,b).

Moles *et al.* (2011) proposed that climate affects the relative cost of losing leaf tissue, with the cost being higher in harsh, unproductive environments (Coley, Bryant & Chapin 1985), resulting in different selective regimes at different latitudes (Johnson & Rasmann 2011). Therefore, selection pressure due to herbivory may be greater in harsher climate even if the herbivory rate is lower than in a warm productive climate. Thus, along with climate influencing physical and chemical protective traits, herbivores should also be expected to select for higher defence at high elevations. At low elevations, low defence may also be selected because species have fast growth rates and a high capacity to recover after damage (Herms & Mattson 1992; Bee, Kunstler & Coomes 2007).

The results of the meta-analysis are consistent with the results of our herbivory survey on tree seedlings. At a given elevation, species from higher elevations (mainly conifers) experience lower herbivory rates (Fig. 1d) and are associated with a lesser diverse community of herbivores (Brandle & Roland 2001), than deciduous species from lower elevations.

Hence, plant species from higher elevations may have developed tougher leaves as an adaptation to severe climatic conditions, but this may indirectly confer increased resistance to herbivores. This suggests that the selective forces of abiotic conditions (e.g. cold hardiness) might be stronger than biotic ones (e.g. resistance to herbivores) along elevation gradients, although this might be organ-specific, depending on the trait analysed. Because it is generally harder to reproduce at high elevation, elevation itself would select for increased protection of the highest-value organs (i.e. more flavonoids in reproductive organs), according to the optimal defence theory (Zangerl & Rutledge 1996).

High-elevation plant species may thus be ecologically fitted (but not adapted) to herbivore pressure, so rapid shifts of herbivore range under climate change would result in limited damage to high-elevation plants, and ultimately, high plant defences in alpine environments could play an important role modulating the range expansion of mobile insects following increasing temperatures.

#### EFFECTS OF CLIMATE CHANGES ON INSECT HERBIVORY ALONG ELEVATION GRADIENTS

Under the scenario of increasing temperature, along with increasing winter precipitations and summer drought events forecasted by climate models (Rowell 2009; Raisanen & Eklund 2012), how would we expect insect herbivory to change? In this paper, we provide an example of a predictive model based on lepidopteran abundance along elevation gradients suggesting that climate change will lead to increased herbivore abundance at higher altitudes and that herbivory impact will be stronger, particularly above the tree line. Undoubtedly, incorporating other herbivore groups besides butterflies is needed to generalize this model. Nevertheless, our forecasted shift is also a function

of the potential evolution of plant species' defence abilities, and their natural insect enemies.

First, quantities of defensive secondary metabolites may be more easily modulated under changing herbivore pressure in some plant species groups (e.g. through phenotypic plasticity or epigenetic or genetic changes) while other may have reached an evolutionary dead end, having totally lost their ability to metabolise chemical defences as in Agrawal *et al.* (2009). Hence, plants may show adaptive responses to variation in the herbivory rate; however, the lability *vs.* the conservatism of plants defence traits is difficult to estimate for the purpose of climate change forecasts.

Second, global warming might also affect insect herbivore abundance through increased top-down regulation by herbivores' natural enemies (Hance *et al.* 2006; Thomson, Macfadyen & Hoffmann 2010; Björkman, Berggren & Bylund 2011; Klapwijk *et al.* 2011; de Sassi, Staniczenko & Tylianakis 2012). Previous reviews have reported that predation and parasitism generally appear to decline with altitude (Hodkinson 2005). A recent quantitative review of the scientific literature reported similar patterns of insect parasitoid richness and parasitism rate decrease along 140 elevation gradients in a wide range of natural habitats (Péré, Jactel & Kenis in review). On average, the relative decrease in the parasitism rate was approximately 15% per 100 m for individual parasitoid species. The decrease was greater for more exposed parasitoids, that is, ectoparasitoids and parasitoids of ectophagous insects (Péré, Jactel & Kenis in review). With increasing temperature, we should expect natural enemies to increase their frequencies at higher elevations, thus affecting community dynamics and herbivore pressure on plants. For instance, it has been shown that size-dependent predator shifts towards larger herbivores are mediated by the interactive effect of warming and nitrogen enrichment (de Sassi, Staniczenko & Tylianakis 2012). However, in some cases, climate change might favour host–parasitoid synchrony. For example, warmer temperatures early in the year were found to favour parasitoids being more in synchrony with their host, the butterfly *Melitaea cinxia* (Van Nouhuys & Lei 2004). Finally, predators might not be adapted to recognize volatiles emitted from the novel, high-elevation host plants, thus further limiting the efficacy of predators during climate-driven rapid range exaptation (Raffa, Powell & Townsend 2013).

## Conclusions

If we are to reliably predict the effects of future global change on ecosystems dynamics, then the greatest challenge resides in interpreting how biotic and abiotic ecological factors and evolutionary process act in concert. Our finding that plant defences increase with elevation, in contrast to the classical expectation, clearly show that the interplay of these factors may lead to nontrivial effects. Phylogenetic comparative studies and common garden experiments along elevation gradients for the survey of plant defence,

herbivory rate and predation pressure should help to advance our understanding of the potential effects of climate change on ecosystem functioning.

## Acknowledgements

Some of the research reported here was conducted as part of the BACCARA project, which received funding from the European Commission's Seventh Framework Program (FP7/ 2007–2013), under grant agreement no. 226299. GK was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Program (Demo- traits project, no. 299340), SR was supported by Swiss National Science Foundation Ambizione grant PZ00P3\_131956/1, and LP was supported by Danish Council for Independent Research grant no 12-126430. We are grateful to Lorenzo Marini for providing data on physical tree defence along elevation gradients.

## References

- Abrahamson, W.G., Hunter, M.D., Melika, G. & Price, P.W. (2003) Cynipid gall-wasp communities correlate with oak chemistry. *Journal of Chemical Ecology*, **29**, 208–223.
- Adams, J.M. & Zhang, Y. (2009) Is there more insect folivory in warmer temperate climates? A latitudinal comparison of insect folivory in eastern North America. *Journal of Ecology*, **97**, 933–940.
- Agrawal, A.A., Fishbein, M., Halitschke, R., Hastings, A.P., Rabosky, D.L. & Rasmann, S. (2009) Evidence for adaptive radiation from a phylogenetic study of plant defenses. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 18067–18072.
- Alonso, C., Perez, R., Nieto, P.M. & Delgado, J. (2005) Gender dimorphism and altitudinal variation of secondary compounds in leaves of the gynodioecious shrub *Daphne laureola*. *Journal of Chemical Ecology*, **31**, 139–150.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- Bee, J.N., Kunstler, G. & Coomes, D.A. (2007) Resistance and resilience of New Zealand tree species to browsing. *Journal of Ecology*, **95**, 1014–1026.
- Beier, C., Beierkuhnlein, C., Wohlgenuth, T., Penuelas, J., Emmett, B., Korner, C. *et al.* (2012) Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters*, **15**, 899–911.
- Bentz, B.J., Regniere, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A. *et al.* (2010) Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *BioScience*, **60**, 602–613.
- Björkman, C., Berggren, Å. & Bylund, H. (2011) Causes behind insect folivory patterns in latitudinal gradients. *Journal of Ecology*, **99**, 367–369.
- Boege, K. & Marquis, R.J. (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology & Evolution*, **20**, 441–448.
- Brandle, M. & Roland, B. (2001) Species richness of insects and mites on trees: expanding southward. *Journal of Animal Ecology*, **70**, 491–504.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M. *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.
- Castagneyrol, B. & Jactel, H. (2012) Unraveling plant–animal diversity relationships: a meta-regression analysis. *Ecology*, **93**, 2115–2124.
- Close, D.C. & McArthur, C. (2002) Rethinking the role of many plant phenolics – protection from photodamage not herbivores? *Oikos*, **99**, 166–172.
- Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.
- Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.
- Darrow, K. & Bowers, M.D. (1997) Phenological and population variation in iridoid glycosides of *Plantago lanceolata* (Plantaginaceae). *Biochemical Systematics and Ecology*, **25**, 1–11.
- DeLucia, E.H., Nability, P.D., Zavala, J.A. & Berenbaum, M.R. (2012) Climate change: resetting plant–insect interactions. *Plant Physiology*, **160**, 1677–1685.



- Durant, J.M., Hjermmann, D.Ø., Ottersen, G. & Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Erelli, M.C., Ayres, M.P. & Eaton, G.K. (1998) Altitudinal patterns in host suitability for forest insects. *Oecologia*, **117**, 133–142.
- Forkner, R.E., Marquis, R.J. & Lill, J.T. (2004) Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*. *Ecological Entomology*, **29**, 174–187.
- Garibaldi, L., Kitzberger, T. & Chaneton, E. (2011) Environmental and genetic control of insect abundance and herbivory along a forest elevational gradient. *Oecologia*, **167**, 117–129.
- Grabherr, G., Gottfried, M. & Pauli, H. (1994) Climate effects on mountain plants. *Nature*, **369**, 448.
- Gutbrodt, B., Mody, K. & Dorn, S. (2011) Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos*, **120**, 1732–1740.
- Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2006) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology*, **52**, 107–126.
- Harrington, R., Woivod, I. & Sparks, T. (1999) Climate change and trophic interactions. *Trends in Ecology & Evolution*, **14**, 146–150.
- Heikkilä, M., Kaila, L., Mutanen, M., Peña, C. & Wahlberg, N. (2012) Cretaceous origin and repeated tertiary diversification of the redefined butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1093–1099.
- Hengxiao, G., McMillin, J.D., Wagner, M.R., Zhou, J., Zhou, Z. & Xu, X. (1999) Altitudinal variation in foliar chemistry and anatomy of yunnan pine, *Pinus yunnanensis*, and pine sawfly (Hym., Diprionidae) performance. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, **123**, 465–471.
- Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants – to grow or defend. *Quarterly Review of Biology*, **67**, 283–335.
- Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews*, **80**, 489–513.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. *et al.* (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A. *et al.* (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*, **18**, 267–276.
- Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, **160**, 1719–1727.
- Johnson, M.T.J. & Rasmann, S. (2011) The latitudinal herbivory-defence hypothesis takes a detour on the map. *New Phytologist*, **191**, 589–592.
- Klapwijk, M.J., Ayres, M.P., Battisti, A. & Larsson, S. (2011) Assessing the impact of climate change on outbreak potential. *Insect Outbreaks Revisited* (eds P. Barbosa, D.K. Letourneau & A.A. Agrawal), pp. 429–450. John Wiley & Sons, Chichester, UK.
- Körner, C. (2007) The use of ‘altitude’ in ecological research. *Trends in Ecology & Evolution*, **22**, 569–574.
- Logan, J.A., Regniere, J. & Powell, J.A. (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, **1**, 130–137.
- Lurgi, M., López, B.C. & Montoya, J.M. (2012) Climate change impacts on body size and food web structure on mountain ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3050–3057.
- Menéndez, R. (2007) How are insects responding to global warming? *Tijdschrift voor Entomologie*, **150**, 355–365.
- Moles, A.T., Wallis, I.R., Foley, W.J., Warton, D.I., Stegen, J.C., Bisigato, A.J. *et al.* (2011) Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist*, **191**, 777–788.
- Parmesan, C. (1996) Climate and species’ range. *Nature*, **382**, 765–766.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012) Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science*, **336**, 1028–1030.
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B. *et al.* (2012) Recent plant diversity changes on Europe’s mountain summits. *Science*, **336**, 353–355.
- Pellissier, L., Fiedler, K., Ndribe, C., Dubuis, A., Pradervand, J.-N., Guisan, A. *et al.* (2012) Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. *Ecology and Evolution*, **2**, 1818–1825.
- Péré, C., Jactel, H. & Kenis, M. (2013) Insect parasitism and parasitoid richness decrease with elevation. *Biology Letters*, doi 10.1098/rsbl.2013.0028.
- Pickett, S.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-Term Studies in Ecology* (ed. G. Likens), pp. 110–135. Springer, New York.
- Preszler, R.W. & Boecklen, W.J. (1996) The influence of elevation on trophic interactions: opposing gradients of top-down and bottom-up effects on a leaf-mining moth. *Ecoscience*, **3**, 75–80.
- van der Putten, W.H., de Ruiter, P.C., Bezemer, T.M., Harvey, J.A., Wassen, M. & Wolters, V. (2004) Trophic interactions in a changing world. *Basic and Applied Ecology*, **5**, 487–494.
- Raffa, K.F., Powell, E.N. & Townsend, P.A. (2013) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences*, **110**, 2193–2198.
- Raisanen, J. & Eklund, J. (2012) 21st Century changes in snow climate in Northern Europe: a high-resolution view from ENSEMBLES regional climate models. *Climate Dynamics*, **38**, 2575–2591.
- Rasmann, S. & Agrawal, A.A. (2011) Latitudinal patterns in plant defense: evolution of cardenolides, their toxicity and induction following herbivory. *Ecology Letters*, **14**, 476–483.
- Rasmann, S., Alvarez, N. & Pellissier, L. (2013) The altitudinal niche breadth hypothesis in plant-insect interaction. *Annual Plant Reviews* (eds C. Voelckel & G. Jander). Wiley, Hoboken, NJ, USA (in press).
- Richardson, A.D. (2004) Foliar chemistry of balsam fir and red spruce in relation to elevation and the canopy light gradient in the mountains of the northeastern United States. *Plant and Soil*, **260**, 291–299.
- Rodríguez-Castañeda, G., Dyer, L.A., Brehm, G., Connahs, H., Forkner, R.E. & Walla, T.R. (2010) Tropical forests are not flat: how mountains affect herbivore diversity. *Ecology Letters*, **13**, 1348–1357.
- Rowell, D.P. (2009) Projected midlatitude continental summer drying: North America versus Europe. *Journal of Climate*, **22**, 2813–2833.
- Salmore, A.K. & Hunter, M.D. (2001) Elevational trends in defense chemistry, vegetation, and reproduction in *Sanguinaria canadensis*. *Journal of Chemical Ecology*, **27**, 1713–1727.
- de Sassi, C., Lewis, O.T. & Tylianakis, J.M. (2012) Plant-mediated and nonadditive effects of two global change drivers on an insect herbivore community. *Ecology*, **93**, 1892–1901.
- de Sassi, C., Staniczenko, P.P.A. & Tylianakis, J.M. (2012) Warming and nitrogen affect size structuring and density dependence in a host-parasitoid food web. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **367**, 3033–3041.
- Scheidel, U. & Bruelheide, H. (2001) Altitudinal differences in herbivory on montane Compositae species. *Oecologia*, **129**, 75–86.
- Scheidel, U., Rohl, S. & Bruelheide, H. (2003) Altitudinal gradients of generalist and specialist herbivory on three montane Asteraceae. *Acta Oecologica-International Journal of Ecology*, **24**, 275–283.
- Schemske, D.W. (2009) Biotic interactions and speciation in the tropics. *Speciation and Patterns of Diversity* (eds R.K. Butlin, J.R. Bridle & D. Schluter), pp. 219–239. Cambridge University Press, Cambridge, UK.
- Schoonhoven, L.M., van Loon, J.J.A. & Dicke, M. (2005) *Insect-Plant biology*. Oxford University Press, Oxford, UK.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araujo, M.B., Arnell, N.W. *et al.* (2005) Ecosystem service supply and human vulnerability to global change in Europe. *Science*, **310**, 1333–1337.
- Singer, M.C. & Parmesan, C. (1993) Sources of variations in patterns of plant insect association. *Nature*, **361**, 251–253.
- Stange, E.E. & Ayres, M.P. (2001) *Climate Change Impacts: Insects*. eLS. John Wiley & Sons, Ltd, Chichester.
- Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific, London, UK.
- Thomson, L.J., Macfadyen, S. & Hoffmann, A.A. (2010) Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control*, **52**, 296–306.
- Torp, M., Olofsson, J., Witzell, J. & Baxter, R. (2010a) Snow-induced changes in dwarf birch chemistry increase moth larval growth rate and level of herbivory. *Polar Biology*, **33**, 693–702.
- Torp, M., Witzell, J., Baxter, R. & Olofsson, J. (2010b) The effect of snow on plant chemistry and invertebrate herbivory: experimental manipulations along a natural snow gradient. *Ecosystems*, **13**, 741–751.



- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Van Nouhuys, S. & Lei, G.C. (2004) Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. *Journal of Animal Ecology*, **73**, 526–535.
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561–2569.
- Whittaker, R.J. (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology*, **91**, 2522–2533.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wu, Z.T., Dijkstra, P., Koch, G.W., Penuelas, J. & Hungate, B.A. (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.
- Yarnes, C.T. & Boecklen, W.J. (2005) Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus gambelii*). *Entomologia Experimentalis Et Applicata*, **114**, 87–95.
- Zangerl, A.R. & Rutledge, C.E. (1996) The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. *American Naturalist*, **147**, 599–608.
- Zehnder, C.B., Stodola, K.W., Joyce, B.L., Egetter, D., Cooper, R.J. & Hunter, M.D. (2009) Elevational and seasonal variation in the foliar quality and arthropod community of *Acer pensylvanicum*. *Environmental Entomology*, **38**, 1161–1167.
- Zhang, Y.J., Adams, J. & Zhao, D.H. (2011) Does insect folivory vary with latitude among temperate deciduous forests? *Ecological Research*, **26**, 377–383.
- Zimmermann, N. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, **10**, 469–482.

Received 20 February 2013; accepted 14 May 2013

Handling Editor: Joseph K. Bailey

## Supporting Information

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

**Method S1.** Monitoring of herbivory rates on naturally-occurring seedlings.

**Table S1.** Summary table of dataset for meta-regression analysis.

**Table S2.** Effect of elevation on direct chemical and physical plant defenses on mean coefficients of correlation and on the slope of regression between woody and herbaceous plants.