



Chapter 10

THE ALTITUDINAL NICHE-BREADTH HYPOTHESIS IN INSECT-PLANT INTERACTIONS

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Abstract: Studies aiming at explaining specialization along latitudinal gradients of plant-herbivore interactions have, to date, yielded inconclusive results. Here we propose the use of steep altitudinal gradients for dissecting factors driving evolution of polyphagy in insect herbivores. First, we test whether colonization of high elevation environment favours increased niche-breadth in two disparate insect groups – the wood-boring beetles and the pollinator group of bees – and show increased polyphagy at higher altitudes in both groups. We then assess classic assumptions transferred from the ‘latitude-niche-breadth hypothesis’, particularly the increase in environmental variability at high, compared to low, altitude. Finally, we discuss alternative mechanisms shaping the observed pattern of increased polyphagy in altitude, including variation in plant quality and predator pressure at different altitudes. We thus suggest evidence for the ‘altitude niche-breadth hypothesis’, in which both abiotic and biotic conditions, including increased variability and an increase of the potential feeding niche-breadth, promote evolution for increased insect polyphagy in altitude.

Keywords: Altitudinal gradient, Apiformes, Buprestidae, climatic variability, oligolectic species, oligophagy, plant-herbivore interaction, plant-pollinator interaction, polylectic species, polyphagy

10.1 Introduction – Variation of niche-breadth along ecological gradients

Explaining the heterogeneous distribution of species on earth and their gradients in ecological interactions are keystone questions in current ecology and are fundamental for understanding ecosystem dynamics (Stehli *et al.*, 1969; Currie & Paquin, 1987; Futuyma & Moreno, 1988; Gaston, 2000). Multiple hypotheses have been developed to explain ecological gradients, including explanations based on historical perturbation, environmental stability, habitat heterogeneity, productivity, speciation or interspecific interactions (Gaston, 2000). Darwin (1859) and Wallace (1878) were among the first to document the higher niche specialization of species accompanying higher species richness in the tropics and, ever since, a large body of literature has tried to unravel the causes of this fascinating pattern.

Behind the spurring of the concept of higher diversity in the tropics and, therefore, higher specialization, was Robert MacArthur's idea that niche-breadth decreases with decreasing latitude because of increased biotic interactions and less fluctuating environments at lower latitudes (MacArthur, 1972). MacArthur also postulated that latitude hides a stability gradient in which organisms should differ in their use of shared, limiting resources if they are to coexist. Specialization through character divergence reduces interspecific competition and facilitates species coexistence by partitioning niche space (MacArthur, 1972). Given that more resource partitioning induces more opportunity for species to coexist, MacArthur also pointed out that higher productivity in the tropics might create the conditions for a stronger partitioning of the ecological resources, which might result in a larger number of potential niches and higher rates of specialization and species diversity.

An alternate explanation for higher niche specialization of species accompanying higher species richness in the tropics was proposed by Huston and colleagues (Huston, 1994; Huston & Wolverton, 2009), who argued against the idea that ecologically relevant net primary productivity is lower in the tropics and, in contrast to MacArthur, showed evidence that lower (rather than higher) productivity helps explaining higher tropical species diversity and, thus, specialization.

Identifying the factors driving an increase in specialization rate along the latitudinal gradient thus remains an open task. However, specialization is only possible in stable conditions, so species in harsher and unstable environments (typical of high-latitude habitats) should display larger niches. Indeed, a generalist can use different resources as the availability varies, whereas a specialist is stuck with one resource and is at high risk of extinction when the resource is at low availability.

This concept, later referred as the 'latitude niche-breadth hypothesis', reposes on the fact that:

1. environmental variability decreases with decreasing latitude;

2. population size variability decreases with decreasing latitude;
3. niche-breadth and population size variability are negatively correlated.

Vazquez & Stevens (2004), through rigorous examination of each of these three assumptions, reached the conclusion that there was little evidence supporting the latitude niche-breadth hypothesis. They found that:

1. Temperature ranges increase and precipitation ranges decrease with increasing latitude.
2. Across 12 major taxa examined – which included orders of mammals, birds and insects – only two showed a significant increase in the spatio-temporal variation of population size with latitude, five showed a significant decrease and five showed no significant pattern.
3. Species with less variable population sizes tended to have narrower niches (although this was not supported by their meta-analytical statistics).

Hence, available evidence does not provide support for the hypothesis that niche-breadth increases with increasing latitude (Vazquez & Stevens, 2004).

One should keep in mind that the observed level of specialization of a given species might obviously rely on the available partners. For instance, due to dispersal limitations, insect species arising from radiation events are constrained to feed on the host plants available to them locally, forming the *realized trophic niche*, even if the *potential trophic niche* is much wider. For example, if a radiation event occurs in a region of low plant phylogenetic diversity, polyphagous species may be viewed as oligophagous. Similarly, the potential climate or the latitudinal extent that would be suitable for a species may be, in fact, much larger than its realized distribution because of dispersal limitation, which might bias any estimation of its latitudinal range. Therefore, any investigation along latitudinal gradients has to deal with the confounding effect of species evolutionary history and ecology.

In summary, the latitude niche-breadth hypothesis is much debated due to contradictory evidence, as well as potential confounding effects. Altitude and latitude are often discussed as comparable gradients. Altitudinal clines developing from the lowland to the summits of all mountain ranges of the world have always been assumed to display the same environmental gradient as latitude from the tropics to the poles (e.g. Chapin & Korner, 1995). As a consequence, we could formulate an 'altitudinal niche-breadth hypothesis'.

But are the hypotheses put forward by MacArthur for latitude valid for altitude? Here, we undertake first to assess evidence for increasing niche-breadth when moving into high altitude. We record feeding habits of two representative groups of herbivore and pollinator insects (both being functionally phytophagous), the wood-boring beetles in the family Buprestidae and the bee group Apiformes (see Michener (2007)). Both are distributed along the altitude gradient of the Alps (Figure 10.1). Second, because we



Figure 10.1 Examples of insect-plant interactions in the European Alps. Shown are two guilds of phytophagous insects discussed in the text. Top panels represent the wood-boring beetle of the family Buprestidae, including the most generalist species in our survey, *Chrysobothris affinis affinis*, found feeding on about 40 species of trees (a), and the *Quercus* spp. specialist *Anthaxia hungarica hungarica* (b). Photographs by Laurent Juillerat. Bottom panels represent bees in the group Apiformes including the highly generalist *Bombus terrestris* (c) and the specialist on *Lysimachia* plants, *Macropis europaea* (d). Photographs by Andreas Müller. (For colour details please see colour plate section.)

indeed observed higher niche-breadth with increasing altitude (Figure 10.2), we examine major assumptions of the latitude niche-breadth hypothesis which are now transferred to the altitudinal niche-breadth hypothesis, namely whether environmental variability increases with increasing altitude and whether population variability increases with increasing altitude. Finally, we discuss alternative but non-mutually exclusive mechanisms for the observed pattern.

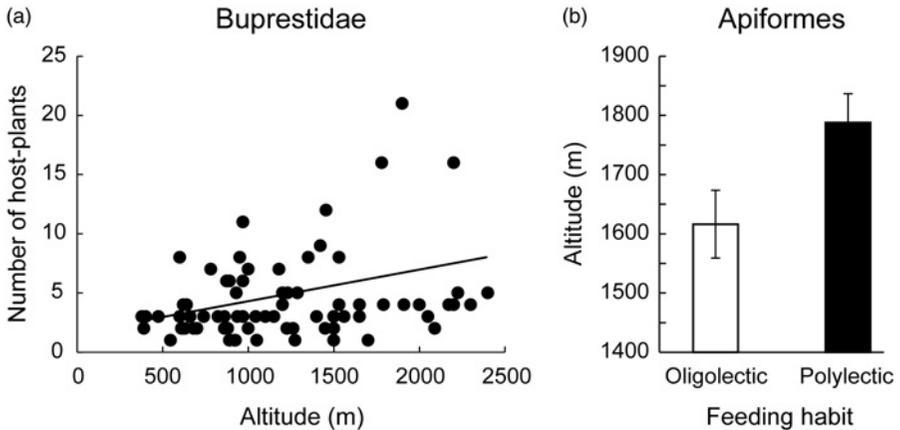


Figure 10.2 Increase of feeding niche-breadth along altitude in two groups of phytophagous insects, Apiformes and Buprestids. Shown are (a) the number of host plant genera for the wood-boring beetle (family Buprestidae) species along altitudinal gradients of the Alps, and (b) the average abundance of oligophagous (Oligo-) versus polyphagous (Polygo-) species of bees (group Apiformes). Figure A is the summary of $n = 79$ species of beetles and Figure B is the summary of $n = 274$ species of bees. In both feeding guilds, increase in altitude goes along with an increase in feeding niche-breadth (for beetles, Spearman's rank-order correlation; $n = 79$, $r = 0.281$, $p = 0.03$, and for bees, t-test; $t_{211} = 2.294$, $p = 0.023$). Data of feeding habit and host plants were taken from literature survey, with Brechtel & Kostenbader (2002) and Müller *et al.* (1997) for beetles and bees, respectively. Altitudinal maxima for each insect species were kindly provided by the Swiss Biological Records Center (www.cscf.ch).

10.2 Herbivorous insects, from specialists to generalists

The guild of phytophagous insects is among the most speciose group of organisms on earth. It has been estimated that nearly half of all existing species of insects consume vegetable material (including leaves, stems, roots, flowers, nectars and pollen) and are thus referred to as phytophagous species (Schoonhoven *et al.*, 2005). Additionally, most of the estimated two to five million phytophagous insect species are highly host-specific, usually feeding on a small fraction of the plant species that they encounter over their lifetime (Strong *et al.*, 1984; Mitter *et al.*, 1988; Jaenike, 1990). Classically, along the continuous gradient of host plant specificity, insects using only one or few closely related plant species (e.g. within the same genus) are commonly referred to as *monophagous*. When the use is limited to a restricted number of plant species all belonging to the same plant family, herbivorous insects are termed *oligophagous*, whereas *polyphagous* insect species are thought to exploit many plant species belonging to different plant families (Schoonhoven *et al.*, 2005).

Besides the obviously arbitrary nature of classifying phytophagous insects into three categories (i.e. first there is a completely graded spectrum between species that will eat only a single plant species to those that consume a high number of distantly-related plant species and, second, there may be high variation in host use among populations of the same insect species), it has actually been estimated that less than 10% of herbivorous species feed on plants belonging to more than three different botanical families (Bernays & Graham, 1988). Monophagy, on the other hand, is a common feature and, in certain groups or habitats, it is even the predominant habit (Brues, 1920).

Specialization of insects on tropical host-plants has historically been regarded as a major explanation for the mega-diversity of insects observed in the tropics. For example, Erwin's (1982) debated estimate of 30 million arthropod species overall (Adis, 1990) is based on the core assumption that tropical herbivorous insects are highly specialized, much more so than temperate insect herbivores. Recent analyses are, however, questioning a latitudinal gradient in specialization. For instance, when accounting for a lower level of observed host-specificity than that predicted by Erwin (1982), the re-estimated overall number of herbivorous insect species decreased to about five million (Odegaard, 2000; Novotny *et al.*, 2002). Further on, Novotny *et al.* (2006) also found that temperate and tropical tree species of comparable phylogenetic distribution supported similar numbers of folivorous insect species, and host specificity did not differ significantly between communities in tropical and temperate forests.

This would suggest that studying ecological specialization along latitudinal gradients might not be the appropriate approach to investigate the evolution of specialization along ecological gradients. Given this controversy, we argue here that altitudinal gradients are better in predicting patterns and providing mechanisms for explaining the evolution of diet breadth in herbivorous insects. We next examine, in two phylogenetically and functionally separated phytophagous insect groups, whether species display larger host-plant niche-breadth at high, compared to low, altitude.

10.3 Evidence for an altitudinal gradient in niche-breadth and climatic variability

To investigate niche-breadth of herbivorous insects along altitude on two disparate taxonomic groups, we survey the wood-boring beetles of the family Buprestidae and the bee group Apiformes (Figure 10.1). For Buprestids, we assessed host range using trait data found in Brechtel & Kostenbader (2002). For bees, we collected trait data for pollen preferences of two classes – oligolectic and polylectic – according to Müller *et al.* (1997) (we next use the term ‘-lectic’ as to better referring to the bees’ behaviour of *collecting* pollen, compared to the *feeding* behaviour of ‘-phagous’ beetles). Host range data were then contrasted to altitudinal maxima for each insect species for

which occurrence data were available in Switzerland. Occurrence data for each insect species were obtained from the Swiss Network for Fauna Cartography database (www.cscf.ch).

For Buprestidae, a Spearman rank order showed a positive correlation between maximum altitude at which an insect species is found and the number of host plant genera on which it feeds (Figure 10.2a). We chose the number of plant genera instead of plant families, because the total number of plant families on which Buprestidae species feed (mainly trees) is relatively low. For each Apiformes species with available trophic data (91 oligolectic and 183 polylectic species), we identified the maximum altitude at which it was recorded. We then compared the maximum altitudes of oligolectic and polylectic species using a t-test. We found a significant effect of the lectic-level, with polylectic species found at higher maximum altitudes (average = 1788 m) than oligolectic species (average = 1616 m) (Figure 10.2b).

Because we found strong support for increasing diet breadth and, thus, niche-breadth at higher altitude, also in accordance with recent work on butterflies (Pellissier *et al.*, 2012b), below we analyze available data on the increased variability of the environment with altitude that may explain the pattern observed here, and answer two specific questions:

1. Does environmental variability increase with increasing altitude?
2. Does vegetation variability increase with increasing altitude?

10.3.1 Does environmental variability increase with increasing altitude?

Altitude gradients exhibit strong abiotic variation over extremely short geographical distances, and species at low or high altitudes should experience drastically different abiotic environments. In mountains that reach high altitude, such as the Alpine belt, the decline in air temperature with increasing altitude can become an important stress factor. In addition, Alpine environments form a series of marginal habitats characterized by strong fluctuation in physical factors, such as more pronounced temporal (daily and seasonal) climatic variability (Brinck, 1974). Thus, we here assess the hypothesis that, at higher altitude, the variance of temperature, wind and precipitation may increase, which may, in turn, affect the temporal and spatial availability of host-plants to insect herbivores. We used a 30 years dataset (from 1970 to 2000) from 11 meteorological stations at different altitudes in the western Swiss Alps. The lowest station was situated at an altitude of 450 m above sea level, while the highest was at an altitude of 2800 m above sea level. We found that high-altitude meteorological stations measured higher variability in climatic conditions (Figure 10.3), thus confirming that climate is more variable at high altitude compared to low altitude.

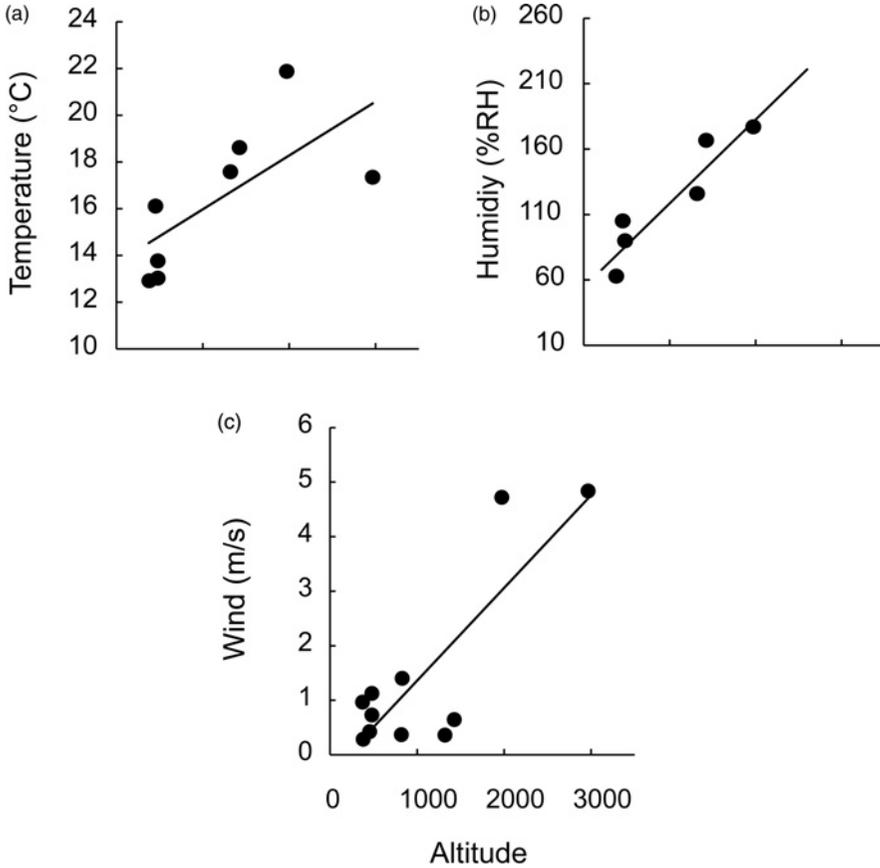


Figure 10.3 Variability of weather conditions along altitudinal gradients. Shown is variance of (a) temperature, (b) relative humidity, and (c) wind speed along altitudinal gradients. Data are records from 11 meteorological stations over the course of 30 years (1970–2000). Overall, variability of climatic variables increases with altitude (Spearman’s rank-order correlation for temperature, $n = 8$, $r = 0.689$, $p = 0.059$; for relative humidity $n = 6$, $r = 0.931$, $p = 0.007$; and for wind speed $n = 11$, $r = 0.829$, $p = 0.002$).

10.3.2 Does variability in host-plant population size increase with increasing altitude?

Higher climatic variability associated with higher altitude is expected to increase spatial and temporal fluctuation of species population sizes. Evidence indicates that populations fluctuate more at high, compared to low, altitude (Brinck, 1974). For instance, Gutiérrez & Menéndez (1998) found that butterfly community structure across years was more variable at higher altitude. For phytophagous insects, the most important component that may affect the evolution towards a generalized or specialized dietary regime is

host plant availability, and more generally vegetation density and composition. In Alpine habitats, the substrate is unstable due to extensive erosion and exposed rock surfaces and stone and gravel fields, which are characterized by strong solifluction over surfaces covered with vegetation (Körner, 2003). Therefore, with increased altitude, patches of productive vegetation should be increasingly interspersed among unproductive areas (Körner, 2003).

To test this hypothesis, we analyzed the spatial variability of the vegetation along altitude, using the percentage of vegetation cover in 2 m² vegetation plots sampled along an altitudinal gradient in the western Swiss Alps. During the years 2002 to 2009, following a random stratified design, 912 vegetation plots were sampled over an area of more than 700 km², as described in Pellissier *et al.* (2010b) and Dubuis *et al.* (2011). The percentage of the vegetation cover of each species was estimated visually and was summed across all species occurring in the plots.

Analyses using Spearman's rank correlations found that, although vegetation cover decreases with increasing altitude, the coefficient of variation increases with altitude (Figure 10.4). Basically, at high altitude, plots may be almost either totally devoid of, or totally covered with, vegetation, suggesting that spatial variability of the vegetation is much higher at high altitude. The lower and more variable vegetation cover at high altitude may lead to

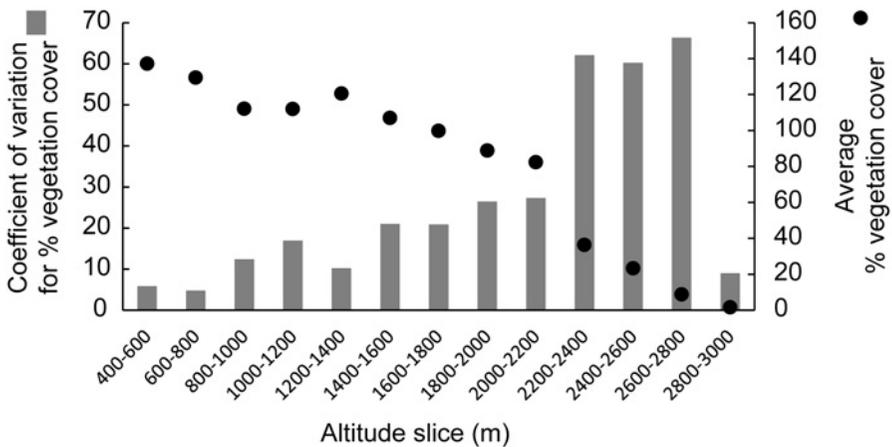


Figure 10.4 Relationship between variation in total vegetation cover and altitude. Shown is the coefficient of variation for 912 vegetation plots collected in the western Swiss Alps for slices of 200 m of altitude (left y-axis and bar graph), and average percent vegetation cover for the same altitude slices (right y-axis and black dots). Analyses using Spearman's rank correlations found that overall, vegetation cover decreases monotonically with increasing altitude (all plots; $n = 912$, $r = 0.585$, $p < 0.0001$), but the coefficient of variation increases with altitude (across altitude slices; $n = 13$, $r = 0.674$, $p = 0.012$). Because there is spatial overlap of plant species, total cover can be over 100%. Data were kindly provided by A. Guisan.

less dense and scarcer populations of suited host plants for herbivores. In such an environment, a strategy implying feeding on more host plant species should be more advantageous.

10.4 The altitudinal niche-breadth paradigm

Using available literature and our own empirical data, we measured insect species specialization and climatic, as well as vegetation, variability along altitudinal gradients. We found these parameters in agreement with predictions of a possible 'altitude niche-breadth hypothesis' (Hodkinson, 2005). Both wood and pollen phytophagous insects exhibit higher niche-breadth when in altitude, and both abiotic (temperature, precipitation, and wind) and biotic (vegetation cover) environments show increasing variability along altitude.

It is common knowledge that, when ascending an altitudinal transect, especially in Alpine regions of Europe, we experience a decrease in temperature and partial pressure of atmospheric gases, and an increase in precipitation as rain or snow (but see Körner, 2003), atmospheric turbulence, wind speed and radiation input (Barry, 1992; Körner, 2003). Such a pattern may vary, however, depending on the mountain range. This leads to different outcomes in insect-plant interactions, especially when comparing temperate and tropical mountain ranges. What we show here is that variability, measured as variance for temperature, precipitation, and wind speed, increases with altitude as well, thus potentially leading to more unpredictable conditions in the European Alps. Thus, at high altitude, being a specialized phytophagous species may not be advantageous. The time required to find the suitable host plant in the more spatially scattered vegetation structures may be increased. Since the length of the growing season is highly reduced, specialized insects may risk not being able to complete their life-cycle (Hodkinson, 2005).

10.4.1 Pollinators

For pollinators, patterns of variation in plant-pollinator systems along environmental gradients have been addressed in a variety of ecological and spatial scales. It has been argued that a mutualistic relationship between plants and insects should be stronger at high altitude, since many Alpine plant species are highly dependent on insects for pollination (Bingham & Orthner, 1998). Various work has shown variation in plant-pollinator interactions along altitude (Moldenke, 1975; Kearns, 1992; Totland, 1994; Malo & Baonza, 2002; Medan *et al.*, 2002). Yet, despite the importance of biotic pollination for plants at higher altitude, plant species are much more generalist (Pellissier *et al.*, 2010b, 2012a), so that the plant-pollinator network is more randomly assembled (Ramos-Jiliberto *et al.*, 2010).

This, however, might not be true for all ecosystems. For example, despite an overall decline in the species richness of plants and their insect pollinator systems with increasing altitude, the level of connectivity did not change significantly across two altitudes in Argentinean systems (Medan *et al.*, 2002). Pellissier *et al.* (2010a) showed a change in flower structures along altitude. In altitude, more zygomorphic bilabiate flowers, which are mostly pollinated by bees, are replaced by more open disk-like flowers, which can be visited by any pollinator available.

The same pattern from the pollinator side is also likely to be valid. Since the timing of plant flowering can dramatically vary at high altitude from year to year, due to the more variable climatic conditions (Körner, 2003), being a generalist pollinator and visiting any flower available may be a much more successful strategy than being limited to a particular plant species. For instance, polylectic *Bombus* species, frequent at high altitude, can be seen foraging pollen on the normally wind-pollinated *Festuca* species when floral resources are particularly scarce (L. Pellissier, personal observations).

10.4.2 Herbivores, plant quality and plant defences

For herbivores, mechanisms explaining variation of niche-breadth along altitudinal gradients include environmental abiotic conditions, resource availability and plant defences.

High-altitude harsh environmental conditions, as described above, have been shown to affect phenology, size, morphology, physiology, chemistry and spatial configuration of the host plants (Kronfuss & Havranek, 1999; Hodkinson, 2005). Also, high altitude soils are shallower and less mature, often with lower water retention capacity, and lower nutrient levels (Körner, 2003), likely affecting resource allocation within the plant (Oleksyn *et al.*, 1998; Grime, 2001; Richardson, 2004) and also likely to affect herbivore preference and performance.

For a herbivorous insect, available nitrogen concentration of leaves or other target tissues has been argued to be of extreme importance (Mattson, 1980; Bernays & Chapman, 1994; Huberty & Denno, 2006). For instance, Dubuis *et al.* (2013) observed that high-altitude foliar vegetation exhibits lower nitrogen concentration. Such decrease along the altitudinal gradient might have limited high-altitude colonization by insects showing high nutrient requirements, such as Lycaenid butterflies (Pellissier *et al.*, 2012c). However, the trend towards a decrease (Hengxiao *et al.*, 1999; Hodkinson *et al.*, 2001) or an increase (Bernays & Chapman, 1994; Erelli *et al.*, 1998; Oleksyn *et al.*, 1998; Cordell *et al.*, 1999) in nitrogen availability as a function of altitude is still debated. Since nitrogen is one among many chemical substances of importance for herbivores (Behmer, 2009), it is quite unlikely that nitrogen *per se* is affecting patterns of host-plant choice along altitudinal gradients.

Plant defences also determine host-plant choice and insect feeding behaviour (Schoonhoven *et al.*, 2005). Plants have been categorized generally

as having two major modes of resistance against feeding insects. First, they can directly ward off the phytophagous insect by producing physical structures such as trichomes and spines, or by producing toxic secondary metabolites through a bottom-up process (Schoonhoven *et al.*, 2005). Secondly, plants can benefit from the top-down impact of predators on herbivores (Price *et al.*, 1980; and see Chapter 9).

High altitude has been shown to affect structural compounds such as lignin and cellulose (Richardson, 2004), and leaf morphology (Hengxiao *et al.*, 1999) which, in turn, may affect herbivore performance (Baldwin & Schmelz, 1994). Indeed, leaves that have high concentrations of cellulose and lignin (i.e. fibre) are stronger, more resistant to abiotic and biotic damage at high altitude, and are potentially longer-lived than leaves with low fibre concentrations (Abrahamson *et al.*, 2003; Richardson *et al.*, 2004). High concentrations of phenolic compounds, which can protect leaves from photodamage by acting as antioxidants (Close & McArthur, 2002), may deter insect feeding, reduce insect growth and survival, and also reduce herbivore densities and herbivore species richness (Forkner *et al.*, 2004). Finally, defensive chemistry has been shown to vary along altitudinal gradients (generally decreasing as elevation increases), such as for alkaloids, coumarins, phenolics and terpenes (Erelli *et al.*, 1998; Hengxiao *et al.*, 1999; Salmore & Hunter, 2001; Alonso *et al.*, 2005; Zehnder *et al.*, 2009).

To our knowledge, evidence of plant direct defences in shaping herbivore feeding niche is still vague. We have recently discovered, that across 16 pairs of plant species from high or low altitude, spanning a large phylogenetic distance, growth rate of a generalist caterpillar is higher on high altitude plants (Pellissier *et al.*, 2012b). In the same study area, we have also observed an increase in butterflies' polyphagy. Such a result might be interpreted as a decrease in the investment towards defence along an altitudinal gradient, a pressure release on herbivores that would favour polyphagy at higher altitudes. This outcome is compatible with the results on Buprestidae and Apiformes presented here.

10.4.3 Predator effects on herbivores

Additionally, herbivore host plant choice might be affected by the top-down effect of predators along altitudinal gradients (Randall, 1982; Randall, 1986; Preszler & Boecklen, 1996; McMillin & Wagner, 1998). Overall, numbers on predation and parasitism generally appear to be declining with altitude (Hodkinson, 2005), suggesting a trend for predator-release in Alpine habitats. This would leave more open niches for herbivores not constrained in finding habitat where herbivores are less exposed to enemies, including leaf morphology or plant secondary metabolites to be sequestered.

However, most predators are opportunistic generalists, such as spiders, and it is difficult to draw general conclusions as to their overall impact on a particular prey species along altitudinal transects. For instance, larvae of

the Alpine chrysomelid beetle *Oreina elongata* has been shown to feed on two asteraceous species, the chemically defended *Alliaria petiolata*, from which the beetle can sequester toxic pyrrolizidine alkaloids, and the physically defended *Cirsium spinosissimum*, of which the dense spine system can provide refuge for the larvae (Gotthard *et al.*, 2005). It was thus argued that larval movement from one plant species to the other is an adaptive behaviour for optimizing protection against generalist but abundant opilions spiders in the system (Gotthard *et al.*, 2005).

10.5 Outlook – Other factors influencing altitudinal niche breadth evolution studies

In summary, we here found evidence for an ‘altitude-niche-breadth hypothesis’, in which more variable and unpredictable environment, in conjunction with higher population variability and possibly less overall defended plants, would lead to a reduction of insect herbivore specialization. However, confounding effects might blur our understanding of the observed patterns such as described below.

10.5.1 Phylogenetic constraints and correlated life-history traits

Testing the relationship between feeding niche-breadth and altitude should be performed within a phylogenetic framework to control for non-independence due to shared evolutionary history. For example, the social lineage of the bumblebees (*Bombus* spp.) is typically boreo-Alpine, and it displays a particular suit of traits that make it able to tolerate much colder conditions. All species are both highly polylectic and are generally found at high elevations. The species of this genus have a preponderant importance in our analysis so that, when removing the genus *Bombus*, no difference in maximum altitudes between oligo- and polylectic bees is found anymore ($F_{1,230} = 0.237$, $p = 0.627$). However, *Bombus* species only represent one single eusocial clade. Thus, in an approach considering how ecological modalities of a given character (here, oligo- or poly-lectic) distribute along the phylogeny, they would represent one single observation (and thus one single point instead of 41 in our regression).

Nonetheless, it is possible that polyphagy is linked indirectly to eusociality via constraining ecological factors. In particular, social bees require a large amount of floral resources during the entire season, which may constrain them to feed on a larger number of plant species, compared to solitary bees. This particular case illustrates the confounding nature of sociality and phylogeny in Apiformes and, thus, the importance of considering phylogenetic constraints when inferring ecological processes (i.e. eusociality may be a

conserved trait or, alternatively, both sociality and phylogenetic history may influence diet breadth).

Similarly, when expanding their trophic niche, phytophagous insects are constrained by their level of tolerance to new host defences. Because such tolerance is not independent of phylogeny (i.e. a given clade can show, or not, pre-adaptations to deal with a new defence compound), considering the phylogenetic relationships among the studied species, as well as the evolution of trophic niche-related ecological traits along the phylogeny allows a deeper insight in our understanding of herbivore evolution (Nyman, 2010). More generally, examining phylogenetic conservatism in a given trait is indispensable for disentangling the effects of trait evolution and those associated with phylogenetic constraints. Indeed, the latter potentially may cause a loss in the degree of evolutionary freedom of such a trait in a given clade, which might not respond to a given ecological pressure, unlike another clade less affected by constraints (Webb *et al.*, 2002).

10.5.2 Phylogeography

Evolution of feeding habits must take into account constraints driving colonization of species into new geographic areas. History, and not only ecology, might restrict host plant availability for a given phytophagous species. For example, Alpine (and by extension Arctic-Alpine) plant species are known to have experienced massive distribution shifts through the ebb and flow of cold ages and warm periods during the Quaternary (Schönswetter *et al.*, 2005; Stewart *et al.*, 2009).

Such movements, despite having proven to follow the cline of available habitats (Alvarez *et al.*, 2009), are highly stochastic, depending on unpredictable micro-climates and capacities of long-distance dispersal, and they have led to numerous local extinctions (Hewitt, 1999). Thus, a given phytophagous insect might not be able to follow the track of its host-plant(s) and might become locally extinct if no other suitable feeding plant is present, thus favouring the emergence of generalist habits. Climatic oscillations that spanned the Quaternary may thereby have reduced the number of species-specific insect-plant interactions in Alpine habitats by limiting the timescale over which long-term co-evolutionary processes (key to the evolution of specificity) occur, due to recurrent local extinctions and continually moving species' ranges of available host plants.

10.5.3 Phytophagous insect abundance

Insect feeding choice might be driven by population size, with more abundant populations in altitude tending to increase their niche-breadth due to increased genetic variability and higher rates of random colonization events (Brinck, 1974). However, the most compelling review on the effect of altitude on insects (Hodkinson, 2005) has highlighted no trend in herbivore

population size. Variation in population size of different insect species unveiled increasing (Romero-Alcaraz & Avila, 2000), declining (Hebert, 1980; Lara *et al.*, 2002), peaking at mid altitude (Gagne, 1979; Wolda, 1987) or no altitudinal trends in abundance (Claridge & Singhrao, 1978; Casson & Hodkinson, 1991). This blurring pattern is very likely due to a geographical scaling effect across the different studies. Therefore, we suggest that optimizing an explanation for increased polyphagy in altitude should take into account population sizes of insect species.

10.5.4 Range size

For each insect species analysed here, we correlated the maximum altitude with the variance of altitude at which it was found. Results showed that, in both groups of insects, increase in altitude maxima correlated with increase in altitude variance (for Buprestidae, $n = 58$, $r = 0.31$, $p = 0.018$; and for Apiformes, $n = 438$, $r = 0.151$, $p = 0.002$). In other words, insect species found at higher altitudes are characterized by wider altitudinal ranges. Insect species with broader habitat occupation are thus more likely to encounter different host plants at different altitudes, thereby increasing feeding niche-breadth.

These results parallel the much-discussed Rapoport's rule, which suggests that latitudinal ranges of plants and animals are generally smaller at lower than at high latitudes (Rapoport, 1975; Stevens, 1989; Morin & Chuine, 2006). Similarly, Slove & Janz (2010) found a positive correlation between latitude and diet breadth in Nymphalid butterflies. However, when including range size in the model, the pattern was reversed, so that latitude of distribution showed a significant negative correlation with diet breadth. Hence, as for latitude, species altitudinal range should be accounted for when analyzing niche-breadth.

10.5.5 Non-linear relationship along the altitudinal clines

The change in niche-breadth along altitude may not be linear as suggested, with three species of Buprestidae that are highly generalist (feeding on more than 15 plant genera) and occupying the Alpine belt above 1800 m (see Figure 10.2b). In other studies investigating the variation of life-histories in insects or plants, the most drastic change occurred from the sub-Alpine to the Alpine belt, which approximately corresponds to the tree-line limit (Pellissier *et al.*, 2010a). Forests may temper the environmental change along the altitudinal gradient. In contrast, the open landscape in the Alpine belt may be more prone to environmental instability, affecting plant and insect populations (Brinck, 1974). This suggests that, in order to detect a pattern in niche-breadth along altitude, one should be careful that the investigated gradient encompasses the Alpine belt, which is the most stressful habitat and is most likely to select for different life-history strategies, compared to lowlands.

10.6 Conclusion

While niche-breadth variation along latitudinal gradients has received considerable attention, altitude patterns are much less investigated. Our results on the niche-breadth of phytophagous insects, as well as recent studies on other types of interactions, suggest that investigating the variation of life-history strategies may bring important insight into species' adaptation to severe and unstable conditions. Pellissier *et al.* (2012) observed that mutualistic butterflies interacting with ants are more generalist at higher altitudes, and Pradervand *et al.* (2013) showed that the parasitic bumblebee species within the sub-genus *Psithyrus*, occurring at higher altitude, are more generalist compared to species at lower altitudes. We thus advocate a more exhaustive exploration of altitudinal gradients in insect-plant interactions or other trophically-related systems to validate the altitude niche-breadth hypothesis.

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