Functional diversity decreases with temperature in high elevation ant fauna

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Abstract. 1. Severe environmental conditions filter community species compositions, forming clines of functional diversity along environmental gradients. Here, the changes in functional diversity in ant assemblages with severe environmental conditions in the Swiss Alps were investigated.

2. Eight sites were sampled along an elevation gradient (1800–2550 m). The variation in functional diversity was analysed along an elevation gradient considering four traits: social structure (monogynous vs. polygynous), worker size, pupal development, and nest structure.

3. Ant species richness and functional diversity decreased with decreasing temperature. Species found in colder habitats tended to live in subterranean nests rather than in mounds and exhibit a polymorphism in queen number, either within or across populations. The phylogenetic diversity did not decrease at colder temperature: Formicinae and Myrmicinae occupied the full range of elevations investigated.

4. An insulation experiment indicated that mounds are more thermally insulated against the cold compared with soil. The absence of a mound-building ant from high elevations probably results from a reduction in the amount of vegetal materials provided by coniferous trees.

5. More severe abiotic conditions at higher elevations act as a filter on ant assemblages, directly through physiological tolerances to the abiotic conditions and indirectly as the vegetation necessary for nest building shifts with elevation.

Key words. Community, environmental filtering, gradient, hymenoptera, phylogenetic diversity.

Introduction

Tolerances to environmental conditions vary across species as illustrated by the large differences in species distributions across the globe. Environmental niche discrepancies among species are mediated by species-specific physiological and behavioural adaptations (Pellissier *et al.*, 2011, 2012). While in milder and more productive environmental conditions, species display different strategies to reduce competition for the more diverse resources (Pianka, 1970); as environment severity increases, the number of successful strategies available can be greatly reduced (Weiher & Keddy, 1999). As a

consequence, in harsh environments, species often display convergent evolution towards a few successful strategies, a mechanism called environmental filtering (Violle *et al.*, 2007; Pellissier *et al.*, 2010). Hence, understanding species distributions and gradients of biodiversity requires prior information regarding the functional traits mediating species' survival under particular environmental conditions (Pellissier *et al.*, 2011; in press).

Many environments exhibit forms of severity that could potentially cause environmental filtering. In particular, elevation gradients from lowlands to mountain summits exhibit highly contrasting environmental condition over short geographical distances (Körner, 2007). In alpine habitats, species experience a stressful abiotic environment (Brinck, 1974; Hodkinson, 2005) as, for instance, air temperature declines with increasing elevation (Körner, 2007). In general, insect species

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living at a high elevation are hardy and can endure very extreme conditions (Brinck, 1974; Hodkinson, 2005). Increasingly cold temperatures may constrain many insect traits, such as wing size, body size, colour, thermal tolerance, diapause or phenology (Hodkinson, 2005). Relatively few species are likely to have evolved suitable traits to tolerate the increasing environmental severity; this hypothesis is supported by several previous studies documenting a decrease in insect diversity with elevation (Glaser, 2006; Palin *et al.*, 2011).

Ants provide an interesting case study in this regard, because they display a huge variety of adaptive traits in their respective environments. For instance, Andersen (1997) investigated ant community composition along an elevation gradient in North America and found that functional group composition (specialist vs. generalist) varied systematically along the elevation gradient. Molet *et al.* (2008) documented variation in body size in *Rhytidoponera* Mayr ants along a latitude gradient that is related to the efficiency of independent colony foundation. In the Alps, researchers have observed a great deal of variation, both within and between ant species, in a number of physical and behavioural traits that may influence their ability to colonise more extreme habitats (e.g. Dethier & Cherix, 1982; Chapuisat *et al.*, 2004; Cherix *et al.*, 2006). Recently, Wiescher *et al.* (2012) showed that ant physiology impacted ant assemblages in high temperature environments. In this regard, the study of traits is useful to understand species assemblages along environmental gradient (Bihn *et al.*, 2010).

In this study, we investigated ant richness as well as the functional and phylogenetic diversity of ant communities along an elevation gradient in the eastern Swiss Alps. We focused on four traits that may be important in thermal tolerance and/or colony fitness in montane environments: the social structure [colonies headed by a single queen (= monogynous) vs. colonies headed by multiple queens (= polygynous) vs. species wherein both strategies can be displayed (= polymorphic)], the worker size, the pupal development (with or without cocoon production) and the nest structure (subterranean nests vs. mounds). Our main hypotheses are as follows:

1. In accordance with an environmental filtering effect at high elevation as suggested by Machac *et al.* (2011), it was hypothesised that the functional diversity should decrease with increasing elevation; in cold and severe environments, only a limited number of strategies should confer the ability to survive. In addition, based on previous research, we expect the following trends for each life history trait.

    a. The social structure of nests may vary consistently with altitude, but the direction is unclear. Previous studies of social arthropods, including primitively eusocial bees and social spiders, have generally found that solitary species or populations tend to replace social ones at higher elevations (reviewed by Purcell, 2011). In line with this observation, ant species with colonies headed by a single queen might be more likely to colonise a marginal high elevation habitat, owing to their expected superior dispersal

ability (Keller, 1995). Given that high elevation environments exhibit a greater degree of temporal instability, the larger offspring of monogynous queens might also be better equipped to survive and to frequently recolonise these habitats (e.g. Ross & Keller, 1995). On the other hand, colonies headed by multiple queens tend to grow faster and reach larger sizes (e.g. Rosset & Chapuisat, 2007), which may be an asset in environments with a short growing season.

    b. In ants, smaller workers may be advantageous in cold habitats as they would be able to warm up quickly in the morning and start foraging (Bernstein, 1976). Moreover, according to Turner and Lennon (1989), ant body size should decrease with decreasing temperature because resource limitation and short growing seasons are expected to cause ants to reduce their development time at the expense of larger body sizes.

    c. Ants build different types of nest structures, including above-ground mounds built from organic materials or a set of subterranean chambers. These structures may differ in their ability to insulate the colony against temperature extremes. Species forming mound nests also need organic materials and therefore are expected to display distributions that closely match those of trees and shrubs (Maggini *et al.*, 2002). Given the latter expectation, we expected to find a higher incidence of subterranean nests at a high elevation.

    d. Many ant species exhibit variation in the presence of cocoons during pupation, but the function is still unknown (Hölldobler & Wilson, 1990; Cherix *et al.*, 2006). Cocoons may offer protection against many environmental dangers, including desiccation or freezing (reviewed by Danks, 2004) whereas pupating without a cocoon may allow a brood to complete their development more rapidly (Purcell & Chapuisat, 2012). Thus, we hypothesised that the presence of cocoons may be related to environmental conditions.

2. Machac *et al.* (2011) found a decrease in phylogenetic diversity at a high elevation as a result of environmental filtering. Hence, we expected a decrease in phylogenetic diversity, which would indicate that some lineages prevail over others in more severe conditions.

Methods

Study area and field sampling

The Swiss National Park is located in eastern Switzerland and ranges from 1400 to 3173 m a.s.l. The park is characterised by grasslands, forests, subalpine, and alpine meadows. During 4 years (from 1978 to 1981), eight sites were sampled along an elevation gradient within the Swiss National Park on Mount la Schera (Dethier, 1984; Dethier & Cherix, 1982). The sampling

sites were selected in open areas from 1800 to 2540 m (Table S1) within different types of grasslands and consisted of hectare surfaces. Using frequently sampled plots distributed along a continuous elevation gradient is a suitable approach and was used multiple times in the literature to study insect community variation along environmental gradient (Pellissier *et al.*, 2010). Using a continuous transect, it is possible to detect the shape of the variation of a community functional structure along an elevation (e.g. linear or non-linear decrease). This study spans an elevation range from 1800 to 2500 m. This part of the elevation gradient is especially interesting, because the increasingly stressful environment above the tree line could cause a change in functional community structure as has been documented in other insect groups (Pellissier *et al.*, in press, 2012). Low elevation sites near the tree line have vegetation consisting predominantly of shrub species (*Rhododendro-Vaccinietum* and *Erico-Mugetum*) interspersed with trees. The middle elevation sites are dominated by grasses (*Seslerietum* and *Nardetum*) and high elevation sites are dominated by low stature coriaceous grasses (*Curvuletum* and *Elynetum*). In each site, ant nests were found by visual search in the vegetation and under rocks either directly or using a net. The use of hand collecting in ant biodiversity assessments is thought to provide the most thorough estimate of ant community composition (Gotelli *et al.*, 2001). In complement, pitfall traps were also used to detect rarer species that are less active or more difficult to detect. During the 4 years of intensive trapping, in each station, 10 pitfall traps with baits (5 with deer dung and 5 with meat) and 5 pitfall traps without baits were set up and placed to cover the entire surface of the sampling site. Trap preservative was water with picric acid. Traps were distributed on a surface of 10 × 10 m with a minimal distance of 1 m between traps. The sampling period was from early June to end of September but only as soon as the sampling areas were free of snow. The traps were emptied each 7–10 days. Specimens were collected and identified to species in the laboratory (Table S2, S3). We added the species occurrences from visual search to the ones detected with pitfalls to obtain the final communities that were analysed below. By pooling catches from traps and active search, detailed knowledge of the composition of ant communities at each site was obtained.

Phylogenetic inferences

Phylogenetic relationships were inferred using DNA sequences obtained from GenBank. The sequences included five loci (ArgK, CO1, cytb, EF-1a, and LwRH). We used MAFFT (Katoh *et al.*, 2009) to align the sequences in a final concatenated matrix of 4310 base pairs. We applied the Bayesian inference method with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) to reconstruct the phylogenetic tree. MrModeltest was used to infer models of sequence evolution, and for all partitions, the generalised time-reversible model accounting for a gamma distribution was selected. Six Metropolis-coupled Markov cold chains with six runs were computed in MrBayes for 10 million generations and were sampled every 1000th generation. We partitioned each locus. A burn-in of 2000 sampled generations was applied, and an all-compatible tree (i.e. according to the extended majority-rule criterion) was reconstructed with the remaining 8001 trees of each of the four runs (24 006 trees). The Bayesian posterior probabilities were then calculated (Fig. S1).

Functional trait collection and analyses

We conducted a literature search by species for traits potentially important to explain the elevation distribution of our species (Bernard, 1968; Della Santa, 1994; http://www.antweb.org/, Cherix & Higashi, 1979; Dethier & Cherix, 1982; Verhaege *et al.*, 1984; Hölldobler & Wilson, 1990; De Biseau & Couvreur, 1994; Seppa, 1994, 1996; Gertsch *et al.*, 1995; Dettorre *et al.*, 1997; Cherix *et al.*, 2006; Aron *et al.*, 2009; Rees *et al.*, 2010; Table S2). We found that potentially relevant traits had been measured in all of the species found in our transect; these traits were: (i) the social structure of the nest (monogyny vs. polygyny), (ii) the mean size of the workers of the species, (iii) the type of nest; built from vegetal debris or dug in the soil (Cherix *et al.*, 2006), and (iv) whether the nymph develops with or without a cocoon. We note that some of these traits, including social structure and body size, could exhibit intra-specific variation, and we take this possibility into account in our discussion of the results.

For each sampled community, we extracted the degree-days (DDEG) values from a climate raster at a resolution of 25 m. The DDEG values were calculated from interpolated monthly average temperatures from the Swiss network of meteorological stations collected from 1970 to 1990 using the method used by Zimmermann and Kienast (1999).

$$DDEG = \sum_{i=1}^{365} \max [0, Ti\text{-}T0] \qquad (1)$$

where Ti = daily mean temperature, $T0$ = threshold value, summed up over time for $Ti > T0$ (Zimmermann & Kienast, 1999). This value was averaged over the 20 years. Here we used a basis of 0 °C, which is commonly used in high altitude/latitude modelling (Lenihan, 1993). Degree-days provide a good approximation of a suite of environmental characteristics, including the length of the growing season and the length and severity of the winter, which may relate to the maximum duration of the colony cycle and the physiological tolerance to freezing in the resident species. Yet, temperature is not the only important factor correlated with elevation, and it should be assumed that the increase in environmental, spatial, and temporal instability with elevation can also affect species population structure and dynamics (Brinck, 1974). Moreover, the change in vegetation structure owing to the environmental factors may affect ant community composition.

For each site, using presence–absence data, we calculated the functional diversity considering all traits together and each of the four traits separately using the Rao index (Botta-Dukát, 2005) implemented in the FD package (Laliberté & Legendre, 2010) in the R environment (R Development Core Team,

2011). An explanation of the Rao's quadratic entropy index (1982) provides a unique standardised approach for comparing the different facets (e.g. phylogenetic or functional) of β diversity (de Bello *et al*., 2010). We related those diversities to degree-days using linear models and tested the significance of these relationships using *F*-tests. In addition, we computed the trait average in each community for continuous traits or the proportion of each trait category per community for discrete traits and related those to degree-day using linear models. We tested the significance of these relationships using *F*-tests. For each community, we additionally estimated phylogenetic diversity using the Rao diversity index using the Picante package in R (Kembel *et al*., 2010) and related it to the degree-days with a linear model associated with an *F*-test.

Thermal insulation of nest material

We conducted an additional experiment in order to further investigate the causes of the altitudinal range limits of mound-building ant species. In particular, we wanted to distinguish between the following hypotheses: (i) mound building ant species are absent from high elevation habitats because of a paucity of vegetal material (Maggini *et al*., 2002) or (ii) they are absent from high elevation habitats because their nests do not provide sufficient thermal insulation (Hölldobler & Wilson, 1990). To assess whether the nest structure could influence the interior temperature, we tested the thermal insulation provided by vegetal material from mound nests and soil from subterranean nests. We collected a mound substrate from one active colony of *Formica lugubris* J.W. Zetterst, *F. paralugubris* Seifert, and *F. aquilonia* Yarrow, respectively, and soil substrate from one active colony of *F. selysi* Bondroit, *F. fusca* Linnaeus, and *F. lemani* Bondroit, respectively. We placed each type of substrate in a plastic container ($26.7 \times 20.7 \times 14.0$ cm) to a depth of 10 cm. We then placed iButton data loggers (two in each position as technical replicates) on the surface and at 5-cm depth in the centre of the box. For all boxes, we placed the pairs of each substrate together in a $-20\,^{\circ}$C freezer for 90 min and allowed them to return to room temperature. We then placed the boxes with *F. lugubris* and *F. selysi* substrate in an environmental chamber programmed to increase from 25 °C to 40 °C in 5 °C, 30-min increments, with a humidity of 90% to test their insulation in a heated environment. After these two tests, we recollected the iButtons and extracted the temperature data. We compared the cooling and heating rate of the iButtons from each position and in each substrate using paired Wilcoxon's signed-rank tests looking at the temperature each minute for 1 h after the boxes had spent 30 minutes at the respective ambient temperatures.

Results

Richness patterns

Considering the eight sites together, 25 ant species were found and these belonged to two sub-families (Myrmicinae

and Formicinae). For 18 species, we observed not only winged sexuals, but also workers, indicating the presence of a nest. The seven remaining species were only found in the form of winged sexuals, with the ability to move far from the nest of origin. As a consequence, for the following analyses, we only considered the 18 species for which both winged sexuals and workers were observed. We found a significant decrease of ant species richness with decreasing degree-days ($F_{6,1} = 5.9$, $P = 0.048$, Fig. 1).

Functional and phylogenetic diversity

We found no significant decrease in phylogenetic diversity with degree-days as measured using the Rao index using the reconstructed phylogeny ($F_{6,1} = 0.015$, $P = 0.94$). The lineages represented in communities at a high or low elevation span the whole phylogenetic tree and do not concern a particular clade. Communities across the elevation gradient were all composed of species belonging to the two sub-families Myrmicinae and Formicinae. The functional diversity of ant communities decreased significantly with degree-days ($F_{6,1} = 10.7$, $P = 0.017$, Fig. 1). Because both species richness and functional diversity are under the influence of environmental filtering, we found a significant correlation between those two community properties ($R^2 = 0.51$, $F_{6,1} = 8.44$, $P = 0.02$).

In looking at traits that may influence colony success, we found a significant relationship between the diversity of species with a different social structure to change with degree-days ($F_{6,1} = 15$, $P = 0.008$, Fig. 2a) with a strong increase in the proportion of polymorphic species in a low temperature ($F_{6,1} = 48.2$, $P = 0.0004$). In particular, only polymorphic species were found at low temperature, polygynous species were found at intermediate and warm temperature, and monogynous species were only found at warm temperature sites in both subfamilies (Fig. 3). The diversity in worker size did not decrease significantly with decreasing degree-days ($F_{6,1} = 3.9$, $P = 0.09$, Fig. 2d), nor the community mean worker size ($F_{6,1} = 5.4$, $P = 0.05$).

Across both subfamilies, we found that species inhabiting mound nests were not found in habitats with lower temperatures, as we predicted. Nest structure, then, decreased in diversity at higher elevations within these communities ($F_{6,1} = 15.4$, $P = 0.007$, Fig. 2c) as did the proportion in mound nests ($F_{6,1} = 20.5$, $P = 0.003$). Only Formicinae species exhibited variation in this trait. In contrast, we found no relationship between the distribution of species that produce cocoons at the pupal stage and degree-days ($F_{6,1} = 0.025$, $P = 0.87$) and the proportion of species that produce cocoons did not vary along the degree-day gradient ($F_{6,1} = 0.51$, $P = 0.5$), but this trait was found in all Formicinae species and in none of the Myrmicinae species that we investigated.

Thermal insulation of nest materials

Overall, both the vegetal material used by wood ants to build mound nests and the soil used by subterranean
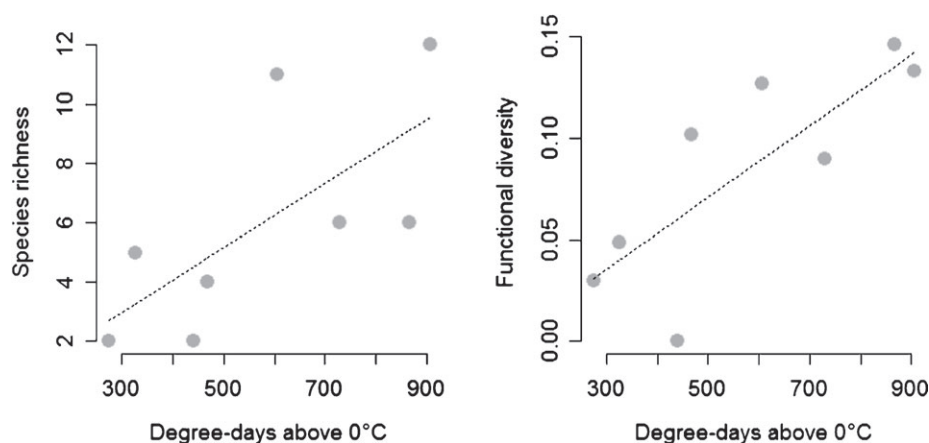
Fig. 1. Relationship between the ant species richness and the temperature measured in degree-days (left panel). Relationship between the functional diversity measured using the Rao entropy index and the temperature measured in degree-days (right panel).
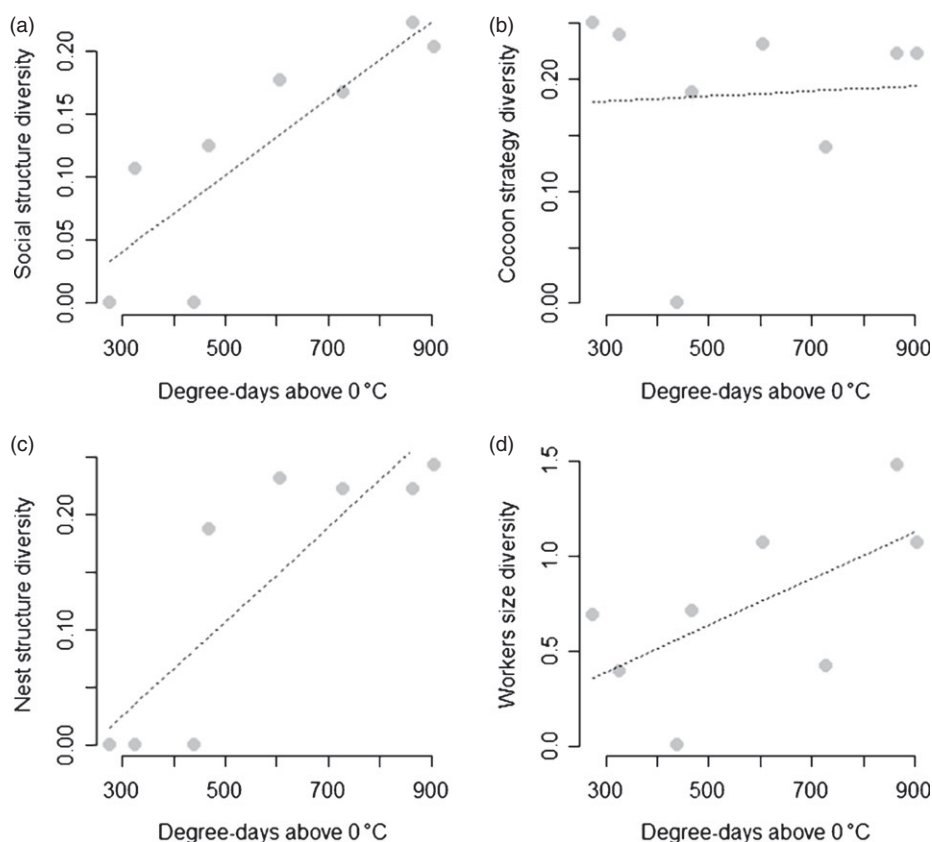

Fig. 2. Relationships between the diversity measured with the Rao quadratic entropy of the different traits investigated and the temperature measured in degree-days. (a) the social structure diversity $F_{6,1} = 15$, p=0.008, (b) the cocoon strategy diversity $F_{6,1} = 0.025$, $P = 0.87$, (c) the nest structure diversity $F_{6,1} = 15.4$, $P = 0.007$, and (d) the worker size diversity $F_{6,1} = 3.9$, $P = 0.09$.

species provided substantial thermal insulation against cold temperatures (vegetal material surface vs. buried logger: Wilcoxon's $W = -1830$, d.f. $= 59$, $P < 0.0001$; soil surface vs. buried logger: $W = -1830$, d.f. $= 59$, $P < 0.0001$) and against warm temperatures ($W = 915$, d.f. $= 59$, $P < 0.0001$ for each comparison). During the 1 h spent in the $-20\,°C$ freezer (after

a 30-min acclimation period) and across the three biological replicates, the data loggers buried in the vegetal material remained warmer than those buried in the sand ($W = 1830$, d.f. $= 59$, $P < 0.0001$), but then remained colder for a longer period of time after the boxes were removed from the freezer (Fig. 4a). In contrast, the vegetal material provided less thermal
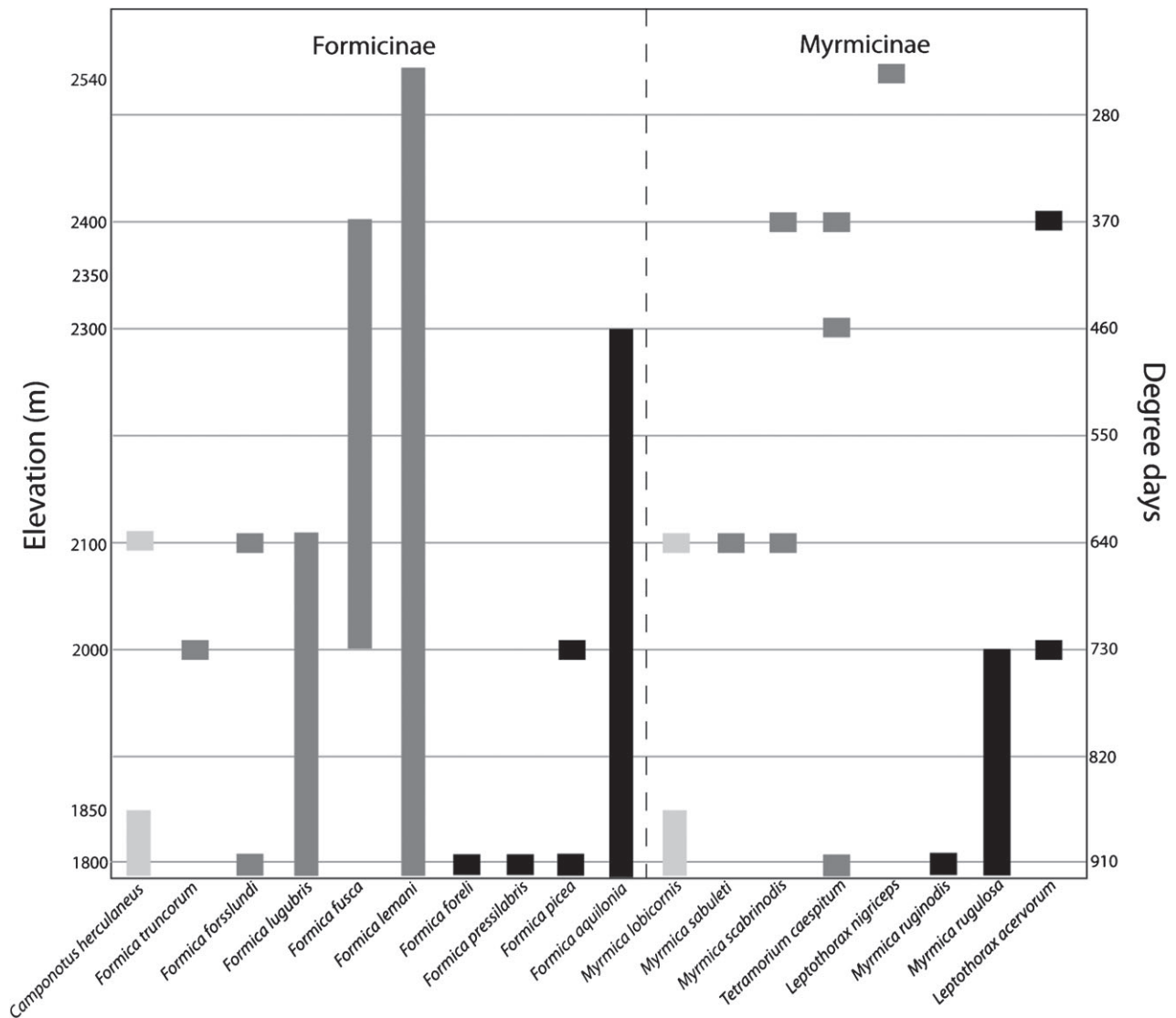
Fig. 3. Elevation distribution for each ant species, shown within their subfamilies and plotted against degree days. In white are the monogynous species, grey the polymorphic species, and black the polygynous species.

insulation when the boxes were heated to 40 °C and tended to warm quickly (W = −915, d.f. = 59, P < 0.0001; Fig. 4b). The iButton data loggers that were resting on top of soil were more insulated in both temperature conditions than those resting on top of the vegetal material (Fig. 4).

Discussion

Recently, Machac *et al.* (2011) showed a decrease in ant species richness with temperature supporting an environmental filtering effect, but the trait that allowed ant species to persist in cold conditions remained uncertain. In this study, we focused on the most extreme part of the elevation gradient, corresponding to the subalpine to nival belts in the Alps, to investigate whether environmental filtering could cause a

decrease in ant functional diversity. Like Machac *et al.* (2011), we found a decrease in ant species richness but in addition, also a decrease in functional diversity associated with reduced temperature. Yet in contrast to their study, we showed that this decrease in functional diversity was independent of a decrease in phylogenetic diversity. Indeed, shifts in lineages represented in communities at an increasingly high elevation appear to span the whole phylogenetic tree and do not concern a particular clade. Species from two subfamilies, Myrmicinae and Formicinae, persisted along the entire elevation gradient. Within both subfamilies, species living at higher elevation displayed common adaptations, including a polymorphic social structure.

In accordance with the process of environmental filtering, ant species richness decreased at a higher elevation suggesting that only a restricted number of species with the suitable
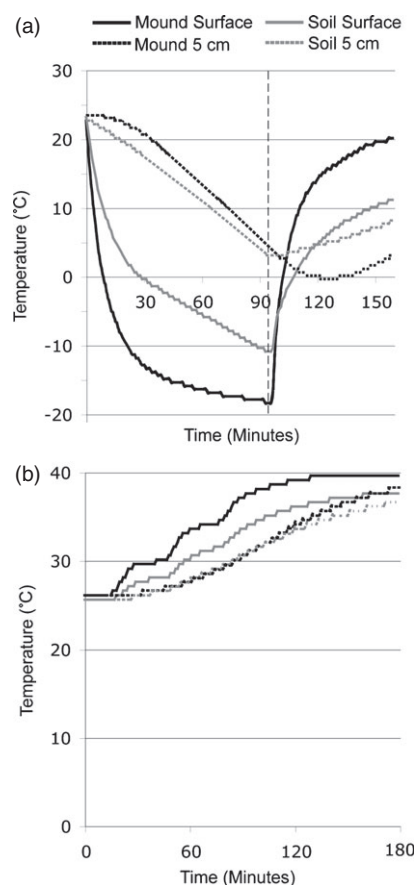
Fig. 4. Reaction for the four different experimental situations (Mound surface–Mound 5 cm–Soil Surface–Soil 5 cm) for the mound substrate of *Formica lugubris* J.W. Zetterst 1838 compared to the soil substrate of *F. selysi* Bondroit 1918 in decreasing then ambient temperatures (a) and in increasing temperature (b).

functional adaptations are able to tolerate the harsh environmental conditions (Cherix and Higashi, 1979; Dethier & Cherix, 1982; Gaston, 1996; Machac *et al.*, 2011). In light of the comment by Franks (1985) 'cold is the single most important enemy of life'; alpine environments exhibit a range of characteristics that are disadvantageous to insect establishment: short growing season, reduced primary productivity, and the occurrence of extreme climatic events. The most important factor is likely the low temperature experienced both during the winter and the summer with a low head budget and even possible freezing. Given the much higher ant diversity in a tropical region (Kaspari *et al.*, 2004) and that temperate lineages are nested in tropical lineages (Moreau *et al.*, 2006), early ants most probably evolved in a warm, stable environment and therefore should display an ancestral climatic niche optimum at a relatively high temperature. As a consequence, novel strategies are required to colonise and sustain populations in harsher alpine environments.

Differences in the number of queens may influence a wide range of colony characteristics, including the number of individuals in the colony, the size of the workers, growth rate, competitive ability, and efficiency (Keller, 1995; Ross & Keller, 1995; Rosset & Chapuisat, 2007). Variation in these factors, in turn, may affect the ability of a species to survive in habitats with severe climates and limited resources. Here, we found that the species from both subfamilies found in the highest elevation patches were known to be socially polymorphic in queen number, having the ability either to maintain a single queen or several within the colony. Some of these species are polymorphic within the populations where they have been studied, whereas other species exhibit only one strategy in a given population, but the strategy varies across different populations. Overall, socially polymorphic species may be able to adjust their social strategy to better match the requirements imposed by the environment. It remains unclear, however, whether colonies of polymorphic species at high elevation are monogynous or polygynous. Monogynous may be especially suited to a high elevation environment, as new gynes from monogynous colonies have superior dispersal and colony founding abilities owing to their large body size (Keller, 1995). These queens may therefore be more likely to colonise marginal and unstable high elevation habitat (Brinck, 1974). Further studies investigating the intra-specific variation of socially polymorphic species along environmental gradients are required to understand why and how polymorphic species are better able to sustain populations in more severe environmental conditions.

Along our focal gradient, species that build mound nests were absent from higher elevations. Because no Myrmicinae species exhibited a mound-building behaviour, this difference was driven by variation among Formicinae species. Two non-mutually exclusive hypotheses may help to explain this pattern. First, soil substrate and the vegetal materials used by mound builders may differ in their ability to insulate the ants from extreme external temperatures. For example, Hölldobler and Wilson (1990) suggested that mound nests may be advantageous in cold environments because they heat faster than a dug nest, but that they may also provide less insulation in cold conditions. Second, mound builders may decline in abundance at higher elevations, because suitable vegetal materials become scarce. In line with this hypothesis, Punttila and Kilpeläinen (2009) found that the frequency of mound nesters decreased at a higher latitude and that the trait was not present north of the tree limit. Our experiment measuring thermal insulation suggested that vegetal material from a mound nest provided more insulation in a cold environment and heated faster compared with the soil substrate, in line with the prediction of Hölldobler and Wilson (1990). This suggests that mound builders may be limited by the presence of a suitable building substrate at a higher elevation, rather than by the ability of their nests to provide insulation. On the other hand, the temperature was slower to return to room temperature after cooling in the mound material versus the soil (Fig. 4a), so the thermal properties of the substrates may also contribute to the elevation range limit of mound builders. Among the species in our study area, we found no distribution patterns related to worker sizes or species producing pupal cocoons. Hence, environment does not appear to explain the variation of

those traits along the gradient. Further research should include a larger number of taxa with variation in those traits with more phylogenetically contrasted clades.

Contrary to previous results (Machac *et al.*, 2011), we found no decrease in phylogenetic diversity in colder conditions. In this study, we focused on the part of the elevation gradient at the tree limit and beyond, where the environmental conditions for insect life degrade rapidly. Thus, we miss species that are only found at lower elevations from subfamilies such as Ponerinae or Dolichoderinae. As a consequence, it is likely that investigating a longer gradient as done by Machac *et al.* (2011) in Austria, we would have found a decrease in phylogenetic diversity. Nevertheless, our results demonstrate that species from both the Formicinae and Myrmicinae display similar adaptations to tolerate cold and severe environments at a high elevation, despite Oberg *et al.*'s (2012) recent suggestion that the two dominants subfamilies Myrmicinae and Formicinae have a different tolerance to desiccation and temperature.

In this study, we considered only four functional traits that were available for the species in the literature. However, it is likely that traits not measured in this study are as or more important for the distribution of ant species along the elevation gradient. In addition, here we discussed only elevation and temperature. Other variables correlated with elevation (and therefore to degree-days) are likely to also be important for ant distribution. Moreover, the use of air temperatures may not be representative enough of clime severity at a higher elevation on ants, and therefore on their effects on the physiological tolerance to freezing, because they are likely to be insulated from temperature extremes inside their nests. Experiments provide complementary insight to the community analyses. The design used in this study could be expanded by increasing the number of replicates and collecting soil substrate from the mound building ant species as well as considering a wider range of depth. Also, the Rao diversity index is not totally insensitive of species richness when species richness is generally low (Laliberté & Legendre, 2010) and further studies spanning a larger gradient should confirm our findings. Finally, we acknowledge that our conclusions may only reflect the local conditions that we investigated in the Swiss National Park. It would be interesting to investigate a larger number of altitudinal transects in other areas in order to draw more broadly applicable conclusions.

In conclusion, our study suggests that the colder and more extreme abiotic conditions at higher elevations act as a filter on ant assemblages, as shown for other taxa (Graham *et al.*, 2009; Pellissier *et al.*, in press). Among species found at high elevations, members of both subfamilies investigated exhibit some common functional traits, which may serve as adaptations to the severe environmental conditions. However, in this study, we only considered a few traits that have been well described in the literature. Further research is still needed to investigate other physiological or behavioural traits (e.g. colony size, Kaspari & Vargo, 1995; Purcell, 2011) or mating strategy (Corley & Fjerdingstad, 2011). Moreover, it would be useful to look more in depth at intra-specific variation in traits such as queen number and the production of cocoons. We encourage the collection of more precise data on functional traits at the population level, which could then be used to improve our understanding of the spatial distribution of insects in general and ants in particular along environmental gradients.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12027

Figure S1. Phylogenetic inference obtained using a Bayesian approach. Values on nodes indicate Bayesian posterior probabilities (BPP).

Table S1. Sites studies along the elevation gradient. Coordinates are in the CH1903 projected system.

Table S2. Life traits selected for every species.

Table S3. Matrix of presence-absence. The sites are ordered from low to high elevation.

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