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ORIGINAL PAPER

Ants at the edge: a sharp forest-steppe boundary influences the taxonomic and functional organization of ant species assemblages along elevational gradients in northwestern Patagonia (Argentina)

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Abstract Biogeographic transitions may play a significant role in generating unique biodiversity patterns along different spatial dimensions of the geobiosphere. The extent, however, to which the presence of large-scale biogeographic transitions interacts with local environmental variation to account for elevational patterns in species diversity still remains elusive. To address this issue, we analysed the association of local variation in environmental variables (temperature, precipitation, vegetation cover, plant species richness and soil conditions) with the taxonomic and functional structuring of ant species assemblages on five elevation gradients across a well-established biogeographic transition between Subantarctic forests and high-Andean steppes in north-western Patagonia (Argentina). Data on the presence/absence of 15 ant species were obtained from 486 pitfall traps arranged in fifty-four 100 m^2 grid plots of nine traps, established at intervals of approximately 100 m elevation, measured from the base to the summit of each mountain. The elevational replacement of lowland shrublands and forests by stunted forests and high Andean steppes was associated with a decrease in species richness; minimum richness (or even absence of ants on some mountains) was recorded at intermediate elevations. Ant richness decreased as temperature decreased and as tree canopy cover increased; however, temperature was the strongest predictor of richness. About 13.8 % of elevational variation in richness was accounted for by temperature, independently of tree canopy cover and macrohabitats; another 18.9 % was accounted for by the shared effects of temperature and macrohabitats. The presence of some species was associated with lowland shrublands and forests but the high Andean steppes were inhabited mainly by ubiquitous species, i.e. widespread species whose presence was recorded in all macrohabitats. We concluded that the transition

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between the Subantarctic forests and high Andean steppes represents a sharp barrier to ant species' elevational distribution. This, in association with elevational variation in continuous environmental functions, mainly temperature, influences the richness and taxonomic and functional structuring of ant species assemblages at temperate latitudes of the southern hemisphere.

Keywords Biogeographical transition · Formicidae · Functional diversity · High Andean steppes · Indicator species · Subantarctic forests

Introduction

Transition zones have often been considered central areas for biodiversity conservation as they may support species from each adjacent area along with their own edge species, thus leading to high species diversity and rarity (Smith et al. 2001). In some circumstances, a transitional area may also constitute a sharp boundary between two adjacent regions supporting low species diversity, thus suggesting strong dependency of species diversity patterns on other parts of the range (van der Maarel 1990; Kark and van Rensburg 2006). Analysis of the taxonomic and functional response of species assemblages to environmental gradients (e.g. climate, vegetation, soils) occurring across biogeographical transition zones and/or ecotones between biomes may reveal the hierarchical interplay between regional and local environmental factors that contribute to maintaining the taxonomic and functional distinction between adjacent biogeographic regions (Ruggiero and Ezcurra 2003). Nonetheless, the interplay between different environmental factors influencing species diversity patterns on regional and local scales across biogeographic transitions have rarely been examined, and thus the structural and functional role of ecosystem boundaries in determining unique patterns of biodiversity still remains rather elusive.

Mountains are ideal systems for evaluation of the role of biogeographic transitions in accounting for species diversity patterns and species-environment relationships, since environmental changes occur over short distances on elevational gradients. The presence of mountains generates a vertical subdivision of environments that is similar to the replacement of vegetational zones on the plains (Walter 1979). The goal of the present study was to use a well-established biogeographic transition between the Subantarctic forests and high Andean steppes in northwestern Patagonia (Argentina) to evaluate how the elevational zonation of macrohabitats interacts with elevational variation in continuous environmental functions to account for patterns in ant species diversity and composition on different mountain peaks. Our general hypothesis was that elevational patterns in the richness and taxonomic and functional composition of ant species assemblages would reflect the signals of both regional and local factors. Regional factors were represented by the replacement of major macrohabitats and the presence of mountain peaks, and local factors were continuous functions of the environment. Accordingly, we predicted specific species richness/composition-environment associations, as follows:

Associations with elevational zonation of macrohabitats

Ants are good indicators of the west-to-east replacement of forest-steppe habitats that occur on a regional scale in the lowlands of NW Patagonia, along the longitudinal dimensions of the Subantarctic-Patagonian transition (Fergnani et al. 2010, 2013). Here, we evaluated whether ant species ranges respond to the vertical zonation of macrohabitats. If the elevational zonation of macrohabitats, i.e. in the form of distinct mountain belts (see description in methods) influenced the taxonomic and functional composition of ant species assemblages, we would expect to find distinct, abrupt changes in these, as well as indicator species in association with different vegetation types, especially for forests and steppes.

Association with the presence of mountain peaks

We evaluated the correspondence of distinct (taxonomic and functional) species assemblages with the presence of mountain peaks with different environmental conditions, i.e. dry mountains towards the east and moist mountains towards the west to evaluate whether distinct ant species assemblages were associated with the presence of different mountain peaks.

Climatic associations

An increase in elevation is often associated with an increase in climatic harshness that imposes physiological restrictions on insects (Mani 1968; Hodkinson 2005). A positive association between ant species diversity and temperature has frequently been observed on elevational gradients, and several mechanisms have been proposed to account for this (species-temperature hypotheses: Sanders et al. 2007; Machac et al. 2011). We evaluated whether the elevational decrease in temperature may represent a kind of environmental filter, reducing both the number and functional strategies of species at the top of the mountains (Hoiss et al. 2012; Bharti et al. 2013). We also tested whether ant species richness and composition respond to local spatial variation in precipitation. Availability of liquid water and optimal energy conditions that vary over space in a systematic fashion are fundamental to changes in the form and location of living organisms, including ants (e.g. Davidson 1977; Dunn et al. 2009).

Associations with vegetation

Although an increase in the biomass of vegetation may represent an increase in the overall amount of resources available to ants, the association of ant species diversity with primary productivity or biomass production has been rather controversial (e.g. Kaspari et al. 2000; Sanders et al. 2007). We evaluated whether an increase in vegetation cover and plant species richness represented an increase in the number of resources available to ants, and whether this may be associated with elevation patterns in ant species richness and composition.

Associations with soil conditions

The chemical and physical properties of soils may influence distributional patterns of ants. The proportion of sand, silt and clay content may be responsible for differences in microhabitat conditions. These can affect the capacity of ant species to become established in certain environments, influencing patterns in ant species abundance, richness and composition (Johnson 1992; Bestelmeyer and Wiens 2001; Boulton et al. 2005). Although soils with high humidity content and low insolation may limit ants' foraging activity (Brown 1973), the abundance of some species may be high in soils with high humidity (*Linepithema humile:* Holway et al. 2002; Menke and Holway 2006). We tested the associations of ant species richness and composition with several soil characteristics to evaluate whether local soil micro-habitat conditions influence species diversity and composition at different elevation gradients.

Methods

Study area

The study was conducted in northwestern Patagonia (41°08′S, 71°02′W) within the Nahuel Huapi National Park (Argentina). Average temperature during the summer season is 18 °C and during winter, 4 °C. More than 70 % of the annual precipitation is concentrated during autumn and winter (Jobbágy et al. 1995). The Andean Cordillera blocks the humid westerlies from the Pacific, causing a greater amount and lower variability in precipitation towards the west, compared with the eastern extra-Andean zones. Currently, mean annual precipitation decreases from more than 3,000 to ca. 300 mm along a west-to-east gradient (Barros et al. 1983; Cabrera and Willink 1973; Jobbágy et al. 1995; Paruelo et al. 1998). The Andes also accounts for the presence of highly fertile volcanic soils (andesitic) towards the west, and soils of low fertility towards the east of the rainfall gradient (Kitzberger 2012).

The west to east gradient of decreasing precipitation across the Subantarctic–Patagonian transition is one of the main ecological factors that give rise to the replacement of *Nothofagus* forests that grow towards the west, where annual precipitation is 1,500–3,500 mm. Taking their place are semi-arid shrublands and forests of *Austrocedrus chilensis* and *Nothofagus antarctica* along the foothill zone, with 1,400–1,800 mm annual precipitation, and steppes towards the east, mainly composed of xerophytic shrubs and herbs, with 600–800 mm annual precipitation (Cabrera amd Willink 1973; Paruelo et al. 1998). Shrublands are locally distributed between the forests and steppes, and possibly originated after severe fires eliminated the forests (Mermoz M and Kitzberger T, pers. comm.).

A similar ecological and biogeographical transition occurs with altitude. As one ascends a northwestern Patagonian mountain, replacement of major vegetation types in the form of mountain belts is evident. Mountain peaks towards the eastern (dry) extreme of the gradient present shrublands of semi-arid scrub vegetation and forests of *Austrocedrus chilensis* and *Nothofagus antarctica* at the lowest elevations, which are replaced by mountain forests dominated by *Nothofagus dombeyi* and *N. pumilio* growing from 1,000 to 1,600 m.a.s.l. In general, forests of *N. dombeyi* grow downslope, and this species decreases in dominance with elevation. *N. pumilio* predominates with the increase in elevation, being the dominant species at the altitudinal treeline where it changes in growth form, from erect trees to krummholz trees (stunted forests). Temperature and precipitation interact to have a significant influence on treelines in northern Patagonia (Daniels and Veblen 2004). Above 1,600 m.a.s.l., there are changes in plant species composition and the physiognomy of plant communities leading to the high-altitude Andean steppes. The vegetation here lacks trees and is composed of xerophytic shrubs and herbs that often present adaptations to cold and windy conditions; for example, *Senecio, Nasauvia, Acaena, Perezia, Adesmia*, and *Valeriana* (Ferreyra et al. 1998).

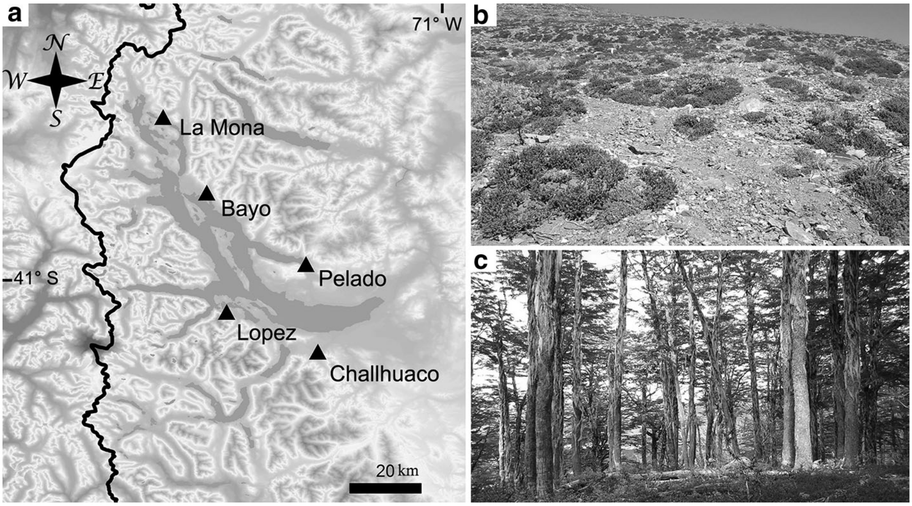


Fig. 1 **a** Map of the study area indicating the location of the five mountains: Bayo, Pelado, Challhuaco, López, and La Mona. **b** Example of a high Andean steppe habitat. **c** Example of a forest habitat

Five mountains were selected to represent the regional west-east precipitation gradient: (1) La Mona, located towards the western, humid end of the precipitation gradient (40°34′S, 71°42′W; mean annual precipitation at the base: 1,930 mm; sampled elevational range: 800–1,800 m), (2) Pelado (40°56′S, 71°20′W; 1,220 mm; 800–1,800 m) and (3) Challhuaco (41°13′S, 71°19′W; 1,100 mm; 900–2,000 m), towards the eastern, drier end, and (4) López (41°05′S, 71°33′W; 1,730 mm; 800–1,800 m) and (5) Bayo (40°45′S, 71°36′W; 1,650 mm; 900–1,782 m), located in an intermediate position (Fig. 1).

Ant sampling and diversity estimations

We collected ants using 486 plastic pitfall traps (diameter 9 cm, depth 12 cm), arranged in 54, 10 × 10 m grid plots of nine traps. On each mountain, 9–12 plots were established at intervals of about 100 m altitude, to represent the different vegetation types found within our study area. This resulted in a total of 6 sites established in the shrublands: 31 in the forests, 4 in the stunted forests, and 13 in the high Andean steppes. The geographic position of each plot was recorded using global positioning system (GPS) technology.

We nested two traps, one inside the other, to minimize ground disturbance while emptying traps, which can affect pitfall catches (Digweed et al. 1995). Traps were filled with diluted propylene glycol (40 %) and a drop of soap. Pitfall traps were operative as soon as established in the field and were opened for 7 days during four sampling periods in the summer season (January and March, 2005 and 2006). For each plot we pooled the contents of the nine pitfalls into one sample. All samples were preserved in 80 % ethyl alcohol. Specimens caught were identified using taxonomic keys by Kusnezov (1978) and comments by Snelling and Hunt (1975). Voucher specimens are held in Ecotono Laboratory, Universidad Nacional del Comahue, Bariloche, Argentina. Field data for the four sampling periods were obtained by V. W. and A. R. with the aid of field assistants (see acknowledgements).

Choice of environmental variables

Climatic variables

We mounted one HOBO H8 logger (Onset Computer Corporation, MA, USA) on a pole fixed at the centre of each 10 × 10 m sampling plot to record the temperature at ground level every 2 h during the summers of 2005, 2006 and 2007. We combined all temperature records for each sampling plot to obtain an overall estimation of temperature. For each plot we estimated the average daily temperature (TEMP) as in Werenkraut and Ruggiero (2013).

Precipitation values (PREC) for each plot were extracted from high resolution (30 arc s) digital WorldClim database v1.4 (Hijmans et al. 2005). In our study area, a considerable proportion of precipitation at high elevations falls in the form of snow (>1,200 m.a.s.l.), so we used summer precipitation as a proxy for rainfall, which more accurately represents liquid water availability during the main period of insect activity.

Vegetation variables

We sampled and classified all vascular plants recorded on each of the 54 plots according to their growth form: (1) herbs, (2) shrubs, and (3) trees, as proposed in Ezcurra and Brion (2005).

Vegetation cover We estimated the tree canopy cover (TREECOV), shrub cover (SHRUBCOV) and herb cover (HERBCOV) as explained in Werenkraut and Ruggiero (2013).

Plant species richness We counted the number of tree (TREESP), shrub (SHRUBSP), and herb (HERBSP) species, and total plant species (PLANTSP) found within each 10 × 10 m plot.

Soil variables

We extracted samples from the top 10 cm of soil at three haphazardly selected points within each plot. We mixed the three top 10 cm samples to make one sample for each plot. For each plot sample, we determined soil humidity (HUM = [(wet weight − dry weight)/wet weight] × 100) and percentage of SAND, SILT and CLAY (Klute 1986).

Analyses of data

The elevational variation in ant species richness and environment

The local ant species richness (RICH) was the total number of species caught at each plot over the four sampling periods. We did not interpolate the presence of ant species between the highest and lowest elevations at which they were collected, as this could raise the signal of a mid-elevation peak in species richness where it does not exist (Grytnes and Vetaas 2002).

We analyzed the relationship between ant species richness and continuous environmental functions based on 11 environmental variables we considered biological meaningful, and which were not highly correlated with each other (Pearson's product—moment correlations among environmental variables <0.60). These variables were TEMP, PREC, TREECOV, SHRUBCOV, HERBCOV, TREESP, SHRUBSP, PLANTSP, HUM, CLAY and SILT. We used automated multi-model selection based on Aikaike's information criterion (AIC) to perform an exhaustive search of minimum adequate models for species richness variation. We considered all different combinations of the eleven predictors, and mountain as a random factor with five levels (to deal with the nonindependence of data within each mountain). We used Generalized Linear Mixed Models (GLMM) assuming a Poisson error distribution with a log link function in R (R Development Core Team 2012). We tested for overdispersion by fitting the best-supported models with an overdispersion scale correction factor (quasipoisson model). All overdispersion scale correction factors were <1, thus the models were still estimated using the Poisson distribution.

We used the set of best supported models based on the ΔAICc < 2 criterion for model averaging as implemented in the MuMln package (Bartón 2013; Grueber et al. 2011). We estimated the relative importance of each predictor variable by using the Akaike weight (w*i*), which measures the relative likelihood of a model being the best supported by a dataset. The importance of a given *j* variable arose from the sum of w*i* of all models in which the variable participated (Burnham and Anderson 2002).

Partitioning of ant species richness variation

The replacement of vegetation types (macrohabitats) along the elevation gradient is not independent of the elevation variation in continuous environmental functions. Thus, we applied partial regression analysis (Legendre and Legendre 1998) using the routine implemented in SAM v.4 (Rangel et al. 2010) to statistically partition the proportion of ant richness variation explained by the shared contribution of the most important predictors of ant species richness identified by model averaging (i.e. temperature and tree canopy cover, see results) and major vegetation types, as well as by the contribution of temperature, tree canopy cover and macrohabitats, independently of each other. Macrohabitats (shrublands, forests, stunted forests, steppes) were added into the statistical models as dummy variables.

Variation in the taxonomic composition of ant species assemblages across mountains and macrohabitats

To summarise patterns in ant species composition and to test for differences between groups of sampling plots from different mountains or macrohabitats, we applied standard Analysis of Similarity (ANOSIM) routines in Primer v5.0 (Clarke and Gorley 2001; Clarke and Warwick 2001) on the basis of a Bray Curtis similarity matrix generated from data on the presence/absence of each ant species in each of the 54 sampling plots (Bray and Curtis 1957). ANOSIM provides a way to test statistically whether there is a significant difference between two or more groups of sampling units, assuming that all ranked dissimilarities within groups are approximately equal in median and range. If two groups of sampling units are different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups. ANOSIM measures the absolute distance between groups by the ANOSIM R statistic that is a simple (linear) function of the average of the rank dissimilarities between the groups. R values run from $+1$ (maximum dissimilarity between groups) to $R = -1$ (most similar samples lie outside the groups), where $R = 0$ is the null hypothesis of no difference in taxonomic composition. The statistical significance of R is assessed by randomly assigning samples to groups 1,000 times and then comparing the observed value of R against the random distribution of R (Clarke 1993).

Elevational variation in ant species composition and environment

We performed a canonical redundancy analysis (RDA) using CANOCO v4.5 (ter Braak and Šmilauer 2002) to analyse the association of environmental variables with variation in ant species composition. RDA is an extension of multiple regression to the modelling of multivariate data (Legendre and Legendre 1998). The analysis was conducted with assemblages from all mountains taken together. We analyzed the significance of the variation explained by each environmental variable using the stepwise selection method and Monte Carlo permutations (999 permutations). We displayed results as a triplot in which environmental variables and species are depicted as arrows, and samples as symbols (Lepš and Šmilauer 2003).

Identification of indicator species

We used the Indicator Value Method (Dufrêne and Legendre 1997; IndVal software available from http://old.biodiversite.wallonie.be/outils/indval/) to evaluate the degree of specificity (i.e., uniqueness of species to a group of sites) and fidelity (i.e., frequency of species within a group) of taxa to different macrohabitats or mountains. An Indicator Value (IndVal) is provided, as a percentage, for each species. Values approaching 100 % indicate higher specificity and fidelity of a particular species to a specific mountain or macrohabitat. We tested the significance of the IndVal for each species on each mountain or macrohabitat using 499 randomizations (Dufrêne and Legendre 1997). When a species had a significant ($p < 0.05$) IndVal greater than 25 % (subjective benchmark used by Dufrêne and Legendre 1997) it was considered an indicator of a particular mountain or macrohabitat.

Analysis of functional/foraging groups

Species were classified into foraging groups based on published information available for species or genera, as in Fergnani et al. (2013). We also classified species into functional groups in relation to stress and disturbance according to a New World genera classification proposed by Andersen (2000); complemented with Brown (2000). We calculated the proportional taxonomic representation of each group (number of species in the *i* foraging or functional group/total number of species present) in the shrublands, forests, stunted forests, and high Andean steppes. We applied resampling methods without replacement based on 1,000 repetitions (Manly 2006) using the sample() function in R (R Development Core Team 2012) to test the hypothesis that the number of species in each foraging/functional group was independent of macrohabitat.

Estimation of the proportional occupancy of species and functional/foraging groups

The proportion of sampling plots occupied by each species over the total number of plots sampled in the shrublands, forests, stunted forests, and high Andean steppes was a rough estimation of the local area of occupancy of each species (Gaston 2003) within each macrohabitat, which we called "proportional occupancy". We used resampling methods without replacement based on 1,000 repetitions (Manly 2006) to test the null hypothesis that the proportional occupancy of each species was independent of the macrohabitat.

We estimated the mean proportional occupancy of each foraging/functional group in the shrublands, forests, stunted forests, and high Andean steppes by simply averaging the proportional occupancy of all species in each foraging/functional group for each macrohabitat. We applied resampling methods without replacement based on 1,000 repetitions (Manly 2006) to test the hypothesis that the mean proportional occupancy of each foraging/functional group was independent of macrohabitat.

All resampling analyses were performed in R using function sample() (R Development Core Team 2012).

Results

A total of 35,056 individuals were collected, which represented 3 subfamilies, 8 genera, and 15 species (Table 1). We collected 11, 14, 7, 8 and 10 species in López, Pelado, Bayo, La Mona, and Challhuaco, respectively, and captured $\sim$43 % of the species known to inhabit the Lanín, Nahuel Huapi and Los Alerces National Parks in NW Patagonia (Kusnezov 1953; Fergnani et al. 2010). Details of the completeness and efficiency of our survey along with the species list for each site are shown in Online Resource 1.

The elevational variation in ant species richness and associations with environment

Local species richness was higher at the base of the mountains than on the summit, but at intermediate elevations we captured no ants or fewer than 10 individuals on four out of five mountains studied (López 1,500 m.a.s.l, and Pelado 1,300-1,500 m.a.s.l, 0 individuals; La Mona 1,400 and 1,500 m.a.s.l, 9 and 3 individuals, respectively; Challhuaco 1,300 and 1,500 m.a.s.l, 6 and 1 individuals, respectively) (Fig. 2).

We obtained a subset of 14 environmental best models that were equally supported by our data (ΔAIC < 2) to account for the elevational variation in ant species richness (Online Resource 2). After model averaging, temperature and tree canopy cover were the most important factors accounting for ant species richness (Fig. 3). Ant species richness increased in sites with higher TEMP ($b = 0.28$) and decreased with an increase in TREECOV ($b = -0.15$).

The partition of variation in ant species richness also indicated the predominance of TEMP over TREECOV (Fig. 4). The proportion of variation in richness explained by TEMP independently of the TREECOV and macrohabitats (MH) was higher (13.8 %) than the proportion of variation explained by the independent effects of TREECOV or MH; however, the proportion of elevational variation in richness explained by the shared effects of TEMP and MH was higher (18.9 %) suggesting that richness is accounted for by the interplay between altitudinal climatic gradients and major vegetation belts (Fig. 4).

Differences in the taxonomic composition of ant species assemblages between mountains and macrohabitats

Moist (La Mona, Bayo and López) and dry (Challhuaco and Pelado) mountains did not differ significantly in their ant species composition. López showed a distinct ant fauna

Table 1 List of species caught, and proportional occupancy of ant species across five elevational gradients in north-western Patagonia

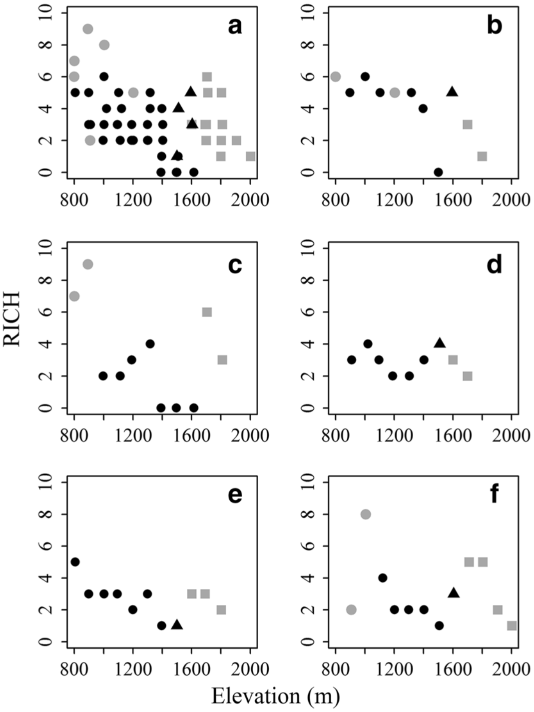
Habitat distribution	Species (subfamily)	Proportional occupancy (%) IC 95 %				IndVal (%)	Foraging behaviour	Functional groups (sensu Andersen 2000)
		Shrublands	Forests	Stunted forests	High Andean Steppes			
Ubiquitous	*Camponotus distinguendus* (Formicinae)	83.33 (33.33,100)	**48.39** (54.84, 77.42)	75 (25, 100)	**100** (46.15, 84.62)		Generalised forager (Brown 2000)	Subordinate Camponotini
Ubiquitous	*Camponotus punctulatus* (Dolichoderinae)	33.33 (0, 50)	**6.45** (12.9, 32.26)	25 (0, 75)	**61.54** (7.69, 46.15)			
Ubiquitous	*Pogonomyrmex odoratus* (Myrmicinae)	33.33 (0, 66.67)	22.58 (16.13, 35.48)	75 (0, 75)	15.38 (7.69,46.15)	38.45 (StF)	Seed harvester (Kusnezov 1959)	Hot climate specialist
Ubiquitous	*Solenopsis patagonica* (Myrmicinae)	**100** (0, 66.67)	**16.13** (22.5,41.94)	50 (0, 75)	30.77 (7.69, 53.85)	50.79 (Sh)	Generalised forager (Brown 2000)	Hot climate specialist
Shrubland	*Brachymyrmex patagonica* (Formicinae)	16.67 (0, 16.67)	0 (0, 3.23)	0 (0, 25)	0 (0, 7.69)		Generalised forager (Brown 2000)	Tropical climate specialist (Brown 2000)
Forest	*Monomorium denticulatum* (Myrmicinae)	0 (0, 66.67)	**51.61** (19.35, 41.94)	0 (0, 75)	**0** (7.69, 53.85)	51.61 (F)	Generalised forager (Brown 2000)	Generalised Myrmicinae
Shrubland–Forest	*Camponotus chilensis* (Formicinae)	**83.33** (0, 50)	19.35 (12.82, 29.03)	0 (0, 50)	**0** (7.69, 38.46)	67.63 (Sh) 28.81 (Lop)	Generalised forager (Brown 2000)	Subordinate Camponotini
Shrubland–Forest	*Lasiophanes picinus* (Formicinae)	16.67 (16.67, 83.33)	**77.42** (35.4,58.06)	0 (0, 100)	**0** (23.08, 69.23)	63.71 (F)	Generalised forager (Brown 2000)	Cold climate Specialist
Shrubland–Forest	*Lasiophanes valdiviensis* (Formicinae)	33.33 (0, 33.33)	3.23 (0, 9.68)	0 (0, 25)	0 (0, 15.38)	30.39 (Sh)		

Table 1 continued

Habitat distribution	Species (subfamily)	Proportional occupancy (%) IC 95 %				IndVal (%)	Foraging behaviour	Functional groups (sensu Andersen 2000)
		Shrublands	Forests	Stunted forests	High Andean Steppes			
Shrubland–Forest	*Myrmelachista vicina* (Formicinae)	16.67 (0, 16.67)	6.45 (0, 9.68)	0 (0, 25)	0 (0, 15.38)		Cryptic species (Brown 2000)	Cryptic species (sensu Brown 2000)
Shrubland–Forest	*Myrmelachista schachovskoi* (Formicinae)	16.67 (0, 16.67)	3.23 (0, 6.45)	0 (0, 25)	0 (0, 15.38)			
Shrubland–high Andean steppe	*Pogonomyrmex vermiculatus* (Myrmicinae)	16.67 (0, 33.33)	0 (0, 9.68)	0 (0, 25)	15.38 (0, 15.38)		Seed harvester (Kusnesov 1959)	Hot climate specialist
Shrubland–Forest–Stunted Forest	*Dorymyrmex tener* (Dolichoderinae)	**83.33** (0, 50)	16.13 (9.68, 29.03)	25 (0, 75)	0 (0, 38.46)	55.8 (Sh) 41.44 (Lop)	Generalised forager/ Predator (Brown 2000; Kusnezov 1959)	Opportunist
Shrubland–Stunted Forest–high Andean steppe	*Dorymyrmex antarcticus* (Dolichoderinae)	50 (0, 50)	**0** (6.45, 22.58)	25 (0, 50)	30.77 (0, 30.77)		Generalised forager/ Predator (Brown 2000; Kusnezov 1959)	Opportunist
Shrubland–Stunted Forest–high Andean steppe	*Pogonomyrmex angustus* (Myrmicinae)	33.33 (0, 50)	**0** (9.68, 25.81)	50 (0, 50)	**46.15** (0, 38.46)		Seed harvester (Kusnezov 1959)	Hot climate specialist

Specieś habitat distributions were determined based on the presence of each species in one (shrubland; forest; stunted forest; high Andean steppe), two (shrubland–forest; shrubland–stunted forest; shrubland–high Andean steppe; forest–stunted forest; forest–high Andean steppe; stunted forest–high Andean steppe), three (shrubland–forest–stunted forest; shrubland–forest–high Andean steppe; shrubland–stunted forest–high Andean steppe; forest–stunted forest–high Andean steppe), or four (Ubiquitous: shrubland, forest, stunted forest and high Andean steppe) habitats, and without taking into account the relative frequency of occurrence of each species in each habitat. Species with significant IndVal (>25 %) are indicated for main vegetation types: shrublands (Sh), forests (F), stunted forest (StF), and high Andean steppes (HAS). Proportional occupancy (%) is the proportion of sites occupied by each species over the total number of sites sampled in the shrublands (N = 6), forests (N = 31), stunted forests (N = 4), and high Andean steppes (N = 13). Proportional occupancies that differed significantly by the expected by chance are highlighted in bold

Fig. 2 Altitudinal variation in ant species richness for **a** the full gradient, **b** López, **c** Pelado, **d** Bayo, **e** La Mona, and **f** Challhuaco mountains showing different macrohabitats: *grey circles* shrublands; *black circles* forests; *black triangles* stunted-forests; *grey squares* high Andean steppes



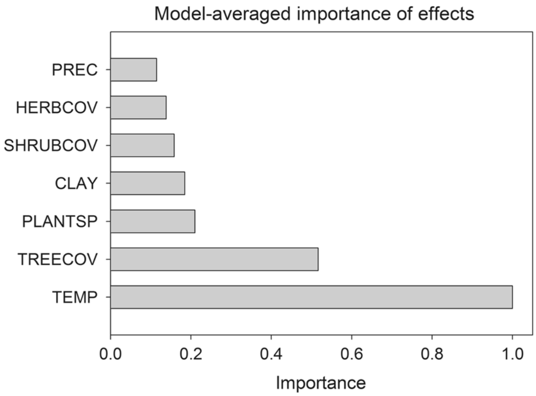


Fig. 3 Importance of variables included in the average model accounting for the elevational variation in species richness. Standardized b coefficients for the average model: temperature (TEMP) $b = 0.30$; tree canopy cover (TREECOV) $b = -0.15$; plant species richness (PLANTSP) $b = 0.12$; percentage of clay in soil (CLAY) $b = 0.14$; herb cover (HERBCOV) $b = 0.09$; percentage of silt (SILT) $b = -0.09$; shrub cover (SHRUBCOV) $b = 0.08$; precipitation (PREC) $b = 0.11$; shrub species richness (SHRUBSP) $b = 0.11$

(although with low ANOSIM R values) from Bayo, La Mona and Pelado but not from Challhuaco (Table 2). In contrast, most macrohabitats differed in their taxonomic composition, particularly the high Andean steppes from the forests (Table 2).

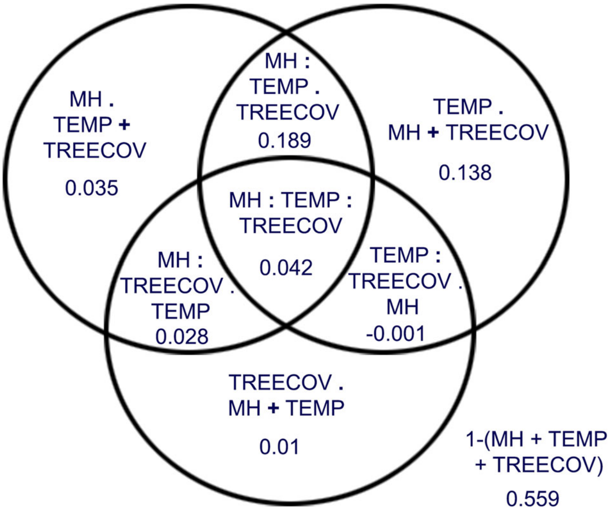


Fig. 4 Partition of the variation in ant species richness explained by independent and shared effects of macrohabitats (MH), temperature (TEMP) and tree canopy cover (TREECOV). Numbers within the diagram indicate the proportion of richness variation explained by MH independently of TEMP and TREECOV (MH.TEMP + TREECOV); TEMP independently of MH and TREECOV (TEMP.MH + TREECOV); TREECOV independently of MH and TEMP (TREECOV.MH + TEMP); shared effects of MH and TEMP independently of TREECOV (MH: TEMP.TREECOV); shared effects of TREECOV and MH independently of TEMP (MH:TREECOV.TEMP); shared effects of the three variables (MH: TREECOV: TEMP); unexplained variation (1-(MH + TEMP + TREECOV)). The decomposition of the variation has been carried out by partial regression analysis (Legendre and Legendre 1998) using SAM v.4

The role of environmental variation in accounting for differences in the taxonomic composition of ant species assemblages

The two first RDA axes together explained 71 % of variance in the association between the taxonomic composition of species assemblages and environment (axis 1: 46 %, axis 2: 25 %). The first axis (eigenvalue = 0.21) showed an environmental gradient of decreasing TREECOV (correlation coefficient, r = −0.77) and SILT (r = −0.62), and increasing HERBCOV (r = 0.12) that accounts for the separation between ant species assemblages in the forests from those in the shrublands and high Andean steppes (Fig. 5). The second axis (eigenvalues = 0.11) showed that the increase in TEMP (r = 0.69) underlies the separation of ant assemblages in the shrublands from those in the high Andean steppes (Fig. 5). The forest assemblage was associated with high TREECOV and SILT and the shrubland assemblage with high TEMP and low TREECOV and SILT. There was no evidence of a distinct stunted forest assemblage. The high Andean steppe assemblage was associated with low TEMP, TREECOV and SILT (Fig. 5). The presence of seven species was partially associated (explained variance, $R^2 \geq 0.3$) with the presence of different habitats in the ordination subspace (Fig. 5).

Indicator species

Ant species showed low specificity and fidelity to mountains (i.e., IndVals < 20 % for all mountains); López alone showed indicator species (*Camponotus chilensis* and *Dorimirmex*

Table 2 ANOSIM statistic R that quantifies the absolute distance, in the taxonomic composition of ant species assemblages, between: mountains, and vegetation types; the closer the value to 1, the greater the difference in the taxonomic composition between ant assemblages; *p* values are shown between brackets and significant R are highlighted in bold

	Pelado	Bayo	La Mona	Challhuaco
López	**0.189** (0.042)	**0.204** (0.024)	**0.303** (0.007)	0.059 (0.184)
Pelado		0.001 (0.325)	0.135 (0.063)	−0.079 (0.854)
Bayo			0.09 (0.106)	0.052 (0.203)
La Mona				0.074 (0.106)
Global R = **0.094** (0.017)				

	Forests	Stunted forests	High Andean steppes
Shrublands	**0.58** (0.001)	**0.397** (0.005)	**0.633** (0.001)
Forests		**0.591** (0.001)	**0.661** (0.001)
Stunted forests			0.189 (0.101)
Global R = **0.58** (0.001)			

tener, Table 1). IndVals for macrohabitats were higher than for mountains. *Solenopsis patagonica*, *C. chilensis*, *Lasiophanes valdiviensis* and *D. tener* showed a high degree of fidelity and specificity to shrublands, and all species but *L. valdiviensis* showed a significantly higher proportional occupancy in the shrublands than in the surrounding habitats (Table 1). *Monomorium denticulatum* and *Lasiophanes picinus* were forest indicators, and they showed high proportional occupancy there. *Pogonomyrmex odoratus* was the only stunted forest indicator species; however, the proportional occupancy of all species within this macrohabitat did not differ from that expected by chance. Although some species showed higher occupancy in the high Andean steppes, no species had a significant IndVal > 25 % in this macrohabitat (Table 1).

Elevational replacement and occupancy of functional/foraging groups

We captured species representing four foraging groups and seven functional groups (Table 1), which represent all the functional groups and all but one of the foraging groups known to inhabit the Subantarctic-Patagonian transition at these latitudes (Fergnani et al. 2013). The mean proportional occupancy of some foraging groups differed significantly from that expected by chance (Fig. 6a). In the shrublands, generalised foragers and generalised forager/predators showed significantly high proportional occupancy; the latter also showed significantly low proportional occupancy in the forests. Seed harvesters occupied significantly more sites in the stunted forests and fewer sites in the forests (Fig. 6a).

The proportional occupancy of Andersen's functional groups showed further differences between macrohabitats (Fig. 6b). Cold-climate specialists and generalised Myrmicinae showed significantly higher proportional occupancy in the forests and lower proportional occupancy in the high Andean steppes. Hot-climate specialists, opportunists and subordinate Camponotini showed significantly lower proportional occupancy in the forests and significantly higher proportional occupancy in the shrublands. In addition, hot-climate specialists and subordinate Camponotini showed significantly higher proportional occupancy, respectively, in the stunted forests and in the high Andean steppes.

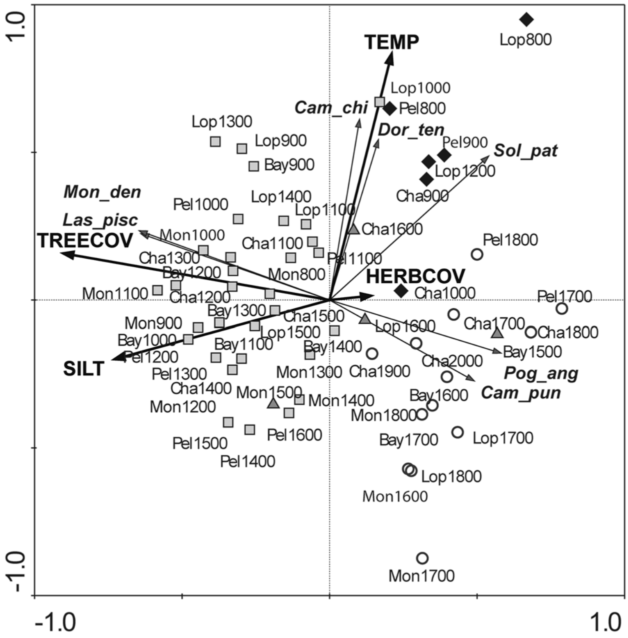


Fig. 5 Canonical redundancy analysis (RDA) ordination triplot of ant species assemblages in relation to environmental variation. Only significant environmental variables ($p < 0.05$) and species with more than 30 % of their variability explained by the ordination subspace were included in the triplot. Seven species were associated with the presence of habitats, namely forests (*Las_pis: Lasiophanes picinus, Mon_den: Monomorium denticulatum),* shrublands (*Cam_chi: Camponotus chilensis, Dor_ten: Dorymyrmex tener, Sol_pat: Solenopsis patagonica)* and high Andean steppes *(Pog_ang: Pogonomyrmex angustus, Cam_pun: Camponotus punctulatus).* Shrublands *black diamonds*; forests *light grey squares*; stunted forests: *dark grey triangles*; high Andean steppes: *white circles*. Sampling plots are named by the *first three letters* of the mountain name followed by elevation. Mountains: Lop: López; Pel: Pelado; Bay: Bayo; Mon: La Mona; Cha: Challhuaco

The proportional representation of the number of species in each foraging/functional group differed significantly from that expected by chance in only a few cases. Seed harvesters showed significantly more species in the high Andean Steppes (Fig. 6c). Generalised Myrmicinae and hot-climate specialists showed significantly lower numbers of species in the shrublands and higher numbers in the high Andean steppes respectively (Fig. 6d).

Discussion

We confirmed that the sharp elevational boundary between the Subantarctic forests and the high Andean steppes influences the richness and the taxonomic and functional organization of ant species assemblages along elevational gradients in north-western Patagonia. The elevational replacement of lowland shrublands and forests by the stunted forests and high Andean steppes was associated with a complex pattern of variation in species richness and composition. The pattern in species richness showed minimum richness or absence of ants at intermediate elevations and a subsequent increase in richness at higher elevations. This

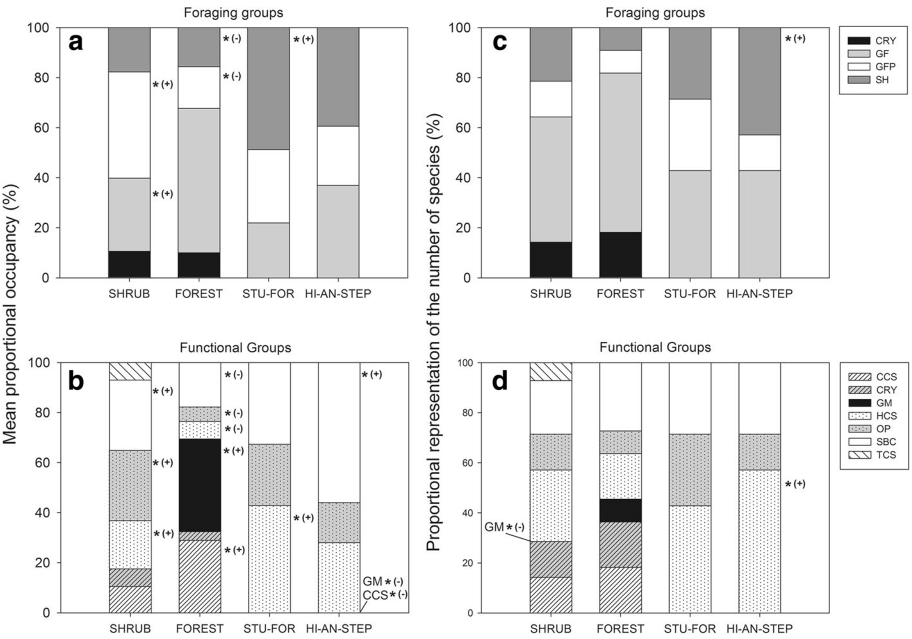


Fig. 6 Mean proportional occupancy, and proportional representation of the number of species of each foraging (**a**, **c**) and functional (**b**, **d**) group in the shrublands (SRHUB), forests (FOREST), stunted forests (ST-FOR), and high Andean steppes (HI-AN-STEP). Foraging groups: *CRY* cryptic species, *GF* generalised forager, *GFP* generalised forager/predator, *SH* seed harvester; Functional groups: *CCS* cold-climate specialist, *CRY* cryptic species, *GM* generalised myrmicinae, *HCS* hot-climate specialist, *OP* opportunist, *SBC* subordinate Camponotini, *TCS* tropical-climate specialist. *Asterisks* indicate observed values that are significantly greater (+) or lower (−) than expected by chance (resampling test, $p < 0.05$)

elevational pattern has been rarely found in arthropods (see Werenkraut and Ruggiero 2011), although it has been reported for ants in closed-canopy broadleaf forests of some tropical mountains (Brown 1973). Other studies have reported an elevational decrease in ant species richness (Malasya: Brühl et al. 1999; North America and Austria: Machac et al. 2011), an increase with increasing elevation (North America: Sanders et al. 2003) or a mid-elevation peak resulting from the contact between two different (lowland and mountain) ant faunas (Madagascar: Fisher 1998). The whole evidence suggests considerable variation in the shape of the elevational ant richness gradients.

Temperature is known to be a primary determinant of ant species richness (Kaspari et al. 2004; Botes et al. 2006; Sanders et al. 2007; Dunn et al. 2009; Longino and Colwell 2011; Machac et al. 2011; Munyai and Foord 2012), although ant species composition has been found to be associated also with vegetation structure (South Africa: Munyai and Foord 2012; Botes et al. 2006; North America: Sanders et al. 2003). Our study reinforces the idea that temperature is indeed a important determinant of ant species richness and composition but the highest proportion of richness variation was explained by the shared effects of temperature and the elevational zonation of vegetation types (macrohabitats). The latter was more important than the presence of individual mountain peaks (La Mona, Bayo, López, Pelado and Challhuaco) as a structuring factor of ant species assemblages, suggesting that ants are good habitat indicators that may disperse easily across mountain peaks following the distribution of major vegetation types at each elevation.

Elevational patterns in species richness

We confirmed that ant species richness increased with increase in temperature, suggesting the predominant role of direct climatic effects on ant species richness and distribution (Farji-Brener and Ruggiero 1994; Kaspari et al. 2004; Botes et al. 2006; Dunn et al. 2009; Longino and Colwell 2011; Machac et al. 2011; Munyai and Foord 2012). In the Subantarctic forests, ants prefer sunny places to nest, and construct simple nests that might not be as good a thermal refuge as those constructed by ants from the Patagonian steppes (Kusnezov 1959). Indirect (biologically mediated) climatic effects could also be important, since the increase in tree canopy cover had a negative influence on ant richness, as previously found along the west-east dimension of the Subantarctic-Patagonian transition (Fergnani et al. 2010).

Interestingly, the elevational pattern found in mountains of north-western Patagonia, showing minimum richness or absence of ants at intermediate elevations, parallels a pattern found in moist tropical mountain forests in the Andes and Himalayas, where the abundance of ant species decreases at about 2,100 m, before increasing at 3,500 m or even at higher altitudes. There, it was suggested that cold, shady mountain forests do not provide enough warmth to allow lowland tropical ants to forage efficiently, or their larvae to develop quickly enough, or both, while higher altitude habitats could provide sufficient radiant energy (Brown 1973). Although tropical organisms are more likely than temperate ones to encounter a climate at high altitudes to which they are not adapted (Janzen 1967; Ghalambor et al. 2006), it is possible that suboptimal environmental conditions towards the upper elevational limit of the Subantarctic forests might contribute to the lack or lower abundance of ants at intermediate elevations in mountains of north-western Patagonia.

Elevational structuring of ant species assemblages

The elevational variation in ant species composition was also associated with spatial variation in vegetation cover and temperature. Ant species showed greater fidelity and specificity to the lowland shrublands and forests than to the stunted forests and high Andean steppes. Several species inhabited the forests or the shrubland-forests exclusively, but none was restricted to the high Andean steppes. Species inhabiting the high Andean steppes and the stunted forests were ubiquitous, and these two macrohabitats showed a similar taxonomic composition. Towards the upper elevations, therefore, the stunted forests were inhabited by ubiquitous ant species, and only one species (*Pogonomyrmex odoratus)* showed high proportional occupancy, specificity and fidelity to this macrohabitat. *Pogonomyrmex odoratus* is both a seed harvester and hot climate specialist and may benefit in the stunted forest from the combination of relatively higher radiation (compared to the closed canopy forest) and higher availability of resources (compared to the high Andean steppes).This elevational increase in the ubiquity of species suggest that ants in north-western Patagonia may follow the elevational Rapoport “rule” of increasing geographic ranges with elevation (see Stevens 1992), as suggested by the distribution of ants in other regions of the world (Soutpansberg Mountain in South Africa: Munyai and Foord 2012; western North America: Sanders 2002).

As previously shown for ants across the west-east gradient (Fergnani et al. 2013), foraging/functional groups showed a similar proportional representation of species in different macrohabitats, although they differed in their mean proportional occupancy. The stunted forest and high Andean steppes were occupied by high numbers of hot climate specialists and subordinate Camponotini (functional groups) and seed harvesters (foraging groups). Hot climate specialists are common in open habitats (e.g., Andersen 2000; van Ingen et al. 2008); three out of four hot climate specialists found in the high Andean steppes are seed harvesters, which are common in the lowland steppes (Fergnani et al. 2013). The high proportional occupancy of subordinate Camponotini species at the top of the mountains might be related to the behavioural and physiological characteristics of the *Camponotus* species that allow them to survive at high elevations. For instance, *Camponotus distinguendus* has a widespread latitudinal distribution, from the north of Chile to the Strait of Magellan, extending from sea level in Valparaiso and Valdivia in Chile to almost 4,000 m.a.s.l. At high elevations the colonies are small but numerous, and are located in sunny places under stones, which compensates for the effect of low air temperatures (Kusnezov 1959). In addition, physiological adaptations are known for a North American relative, *Camponotus modoc*, which shows higher oxygen uptake rates in high elevation populations than in low elevation ones (Kennington1957); this pattern at high elevation might be associated with the maintenance of high growth rates over a short growing season in insects (Chown and Gaston 1999, and references therein).

The forests contained high proportional occupancy of generalized Myrmicine and cold climate specialists. Cold climate specialists are common ants at high elevation or in high latitude forests, where they often replace tropical climate specialists (Andersen 2000). Furthermore, the high proportional occupancy of generalized Myrmicine species is expected in undisturbed forests (Andersen 2000). The shrublands showed high proportional occupancy of opportunist species along the elevational gradient (the present study) as well as along the west-east gradient (Fergnani et al. 2013). The rapid dynamics of shrublands (Veblen et al. 2003; Mermoz et al. 2005), could favour the greater occupancy of opportunist species (Fergnani et al. 2013). Along the west-east gradient, species assemblages in the transitional shrublands tended to be taxonomically and functionally similar to those in the Patagonian steppes, and *Lasiophanes valdiviensis* was the only indicator species (IndVal = 29 %) (Fergnani et al. 2013). Along the elevational gradient, shrubland species assemblages shared some qualitative similarities with the forests (i.e. the presence of cold climate specialists and cryptic species) and also with the high Andean steppes (i.e. high occupancy of hot climate species and subordinate Camponotini species); although the present study indentified *Lasiophanes valdiviensis* (IndVal = 30 %) and *Dorymyrmex tener* (IndVal = 55.8 %) as two shrubland indicator species (Table 1), caution is necessary in the interpretation of this result, since *Dorymyrmex tener* is actually a generalised opportunistic species that also inhabits the eastern Patagonian steppes (not included on the elevational transects we studied).

We found a low representation of cryptic or arboreal ant species throughout the present study. In part, this is explained due to pitfall sampling not being an efficient method for the capture of arboreal species; however, there is also a low abundance of cryptic and arboreal species in NW Patagonia (Kusnezov 1959), which contrasts with the high diversity of arboreal ants in tropical rain forests (e.g., Wilkie et al. 2010). In spite of this, our results agreed with the idea that the abundance of cryptic forest species declines at increasing elevation or latitude (Andersen 2000).

Mountain summit showed a reduced set of foraging/functional groups. In general, at the highest elevation of all mountains we found only one or two species of *Camponotus* (generalised forager-subordinate Camponotini). We also recorded *Dorymyrmex antarcticus* (generalised forager-predator/opportunistic, on Pelado), *Solenopsis patagonica* (generalised forager/hot climate specialist, on Pelado), and *Pogonomyrmex angustus* (seed harvester/hot climate specialist, on Bayo). Thus, the number of ecological strategies at the top is reduced compared to the base of the mountain. This suggests that ant species at the top of the mountains may have been filtered out from the regional species pool by the harsh climatic conditions (environmental filtering hypothesis: e.g., Machac et al. 2011; Hoiss et al. 2012). High Andean steppes contained a small subset of the species and functional groups present in the lowland steppes (Fergnani et al. 2010). This reinforces the idea that high Andean steppes might represent extreme environmental conditions for ants, and the role of environmental filtering might be more relevant under these rigorous conditions (e.g., Chase 2007).

We conclude that marked changes in the physiognomy of vegetation types (forests-steppes) that occur across the Subantarctic forest-high Andean steppe transition play a predominant role in structuring ant species diversity on temperate mountains of north-western Patagonia. The elevational replacement of macrohabitats interacts with elevation temperature gradients to account for complex patterns in species richness, and there is also a taxonomic and functional difference in the composition of ant species assemblages between the Subantarctic-forests and high Andean steppes. Our study further suggests that as far as ants are concerned, shrublands at the base of the mountains and stunted forests at intermediate elevations may be transitional macrohabitats, sharing similar ant species composition with adjacent macrohabitats. The decrease in richness or the absence of ants at intermediate elevations, along with the reduction in the number of functional groups at high elevations are two elevational patterns that have no parallelism across the west-east biogeographic transition. It is likely that because environmental changes occur over short distances on the elevational gradient, the elevational zonation of vegetation types may represent a sharper barrier to ant species distribution than the west-east replacement of macrohabitats (shown in Fergnani et al. 2013). This suggests that understanding the kind of environmental changes that occur over multiple spatial dimensions of biogeographical transitions is fundamental to the understanding of the role of ecotones in the structuring of species diversity on a geographical scale.

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