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ORIGINAL PAPER

The spatial variation in ant species composition and functional groups across the Subantarctic-Patagonian transition zone

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Abstract The role of ecotones in the maintenance of species diversity is rather controversial; they may represent either biodiversity hotspots with unique and rare forms, or be transitional areas that hold marginal populations of species. We analyse the taxonomic and functional composition of ant species assemblages across the Subantarctic-Patagonian transition to evaluate the role that transitional shrublands may play in the maintenance of the taxonomic and functional differentiation. We collected ants using 450 pitfall traps within a $\sim 150 \times 150$ km area. Species were classified into functional groups in relation to stress and disturbance, and in foraging groups according to their foraging behavior. An indicator value for each species in each habitat was calculated. The steppes and the forests strongly differed in ant species and functional composition. Climatic effects combined with structural components of plant environment explained about 23–27 % of the variation in ant composition. The shrublands did not show a distinctive fauna, and show greater similarity in ant species composition and in the proportional occupancy of functional groups to the steppes than to the forests. They harbor neither rare nor indicator species, except for *Lasiophanes valdiviensis*, and thus this reinforces the idea that they are not a habitat source of species, but an area of encounter between two distinct forest- and steppe- ant faunas, where a high number of local distributional limits of ant species overlap.

Keywords Formicidae · Ecotone · Biogeographic transition · IndVal · RDA · Cluster analysis

Introduction

Ecotones are transitional areas detectable at multiple spatial scales, i.e. from limits between biogeographic regions to boundaries between local habitats (Risser 1995; Kark and van Rensburg 2006). These regions most often coincide with gradients in environmental conditions, associated with pronounced richness gradients, high turnover of species or a combination of both (Williams et al. 1999; Smith et al. 2001; Araújo 2002; Ruggiero and Ezcurra 2003). The species richness of birds and mammals may peak in ecotonal areas (Kark and van Rensburg 2006). This has led to the idea that ecotones are biodiversity hotspots, spatially congruent with range-restricted species, that contain unique evolutionary forms or morphologically divergent species (Araújo 2002; Kark et al. 2007; van Rensburg et al. 2009). Also, ecotones might provide essential habitats for rare species (Whitham et al. 1999).

Nonetheless, there is also some evidence suggesting that these transitional areas only hold marginal populations that depend on other parts of the range to subsist (Kark and van Rensburg 2006). Ecotones may also be not more diverse than adjacent areas, containing only a few ecotonal species (carabid beetles: Heliölä et al. 2001; arthropods, several taxa: Kotze and Samways 2001; Dangerfield et al. 2003; dung beetles: Spector and Ayzama 2003; spiders: Muff et al. 2009). For ants, patterns might be more complex. The ecotone between the shortgrass steppe and the

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Chiahuahuan desert has low levels of ant richness (Bestelmeyer and Wiens 2001). In contrast, the edge area between grasslands and forests in the southern Brazilian highlands (São Francisco de Paula) shows a peak in species richness, has a distinct ant composition, and is associated with attributes of ant nesting ecology (Pinheiro et al. 2010). Pfeiffer et al. (2003) shows slightly variation in the number of ant species but a distinct composition of genera and functional groups in the transitional semi-desert between the Gobi desert and steppe in Mongolia. Also, sharp edges in an agricultural landscape in Germany contain no more ant species richness than adjacent habitats, although high nest densities of aggressive species and more ant-homopteran associations are found there (Dauber and Wolters 2004). Thus, the role of ecotones in the maintenance of ant species diversity is still rather unclear. Here, we contribute with evidence to address this issue in a temperate region of the southern hemisphere.

The transition between the Subantarctic and Patagonian biogeographical subregions of the Andean region (Morrone 2002) is structured across one of the most pronounced environmental gradients in the world. The Andean Cordillera running along the west of southern South America stops the humid winds from the Pacific, causing intense rainfall on its western (Chilean) side, and an exponential decline of precipitation with distance from the Cordillera to the eastern (Argentinean) side (Barros et al. 1983; Jobbágy et al. 1995; Paruelo et al. 1998). In northwestern Patagonia (Argentina), major climatic, soil, and biotic differences along the Subantarctic-Patagonian transition generate three distinct dominant physiognomic units from west to east: forests, shrublands and steppes (Fig. 1) (Cabrera 1976; Ezcurra and Brion 2005).

About 70 % of the ant species found across the Subantarctic-Patagonian transition is endemic to temperate Patagonia. Substantial changes in ant species composition occur across the Subantarctic-Patagonian transition (Kusnezov 1953; Sackmann and Farji-Brener 2006; Fergnani et al. 2008, 2010). For instance, *Lasiophanes picinus* and *Monomorium denticulatum* are widespread in

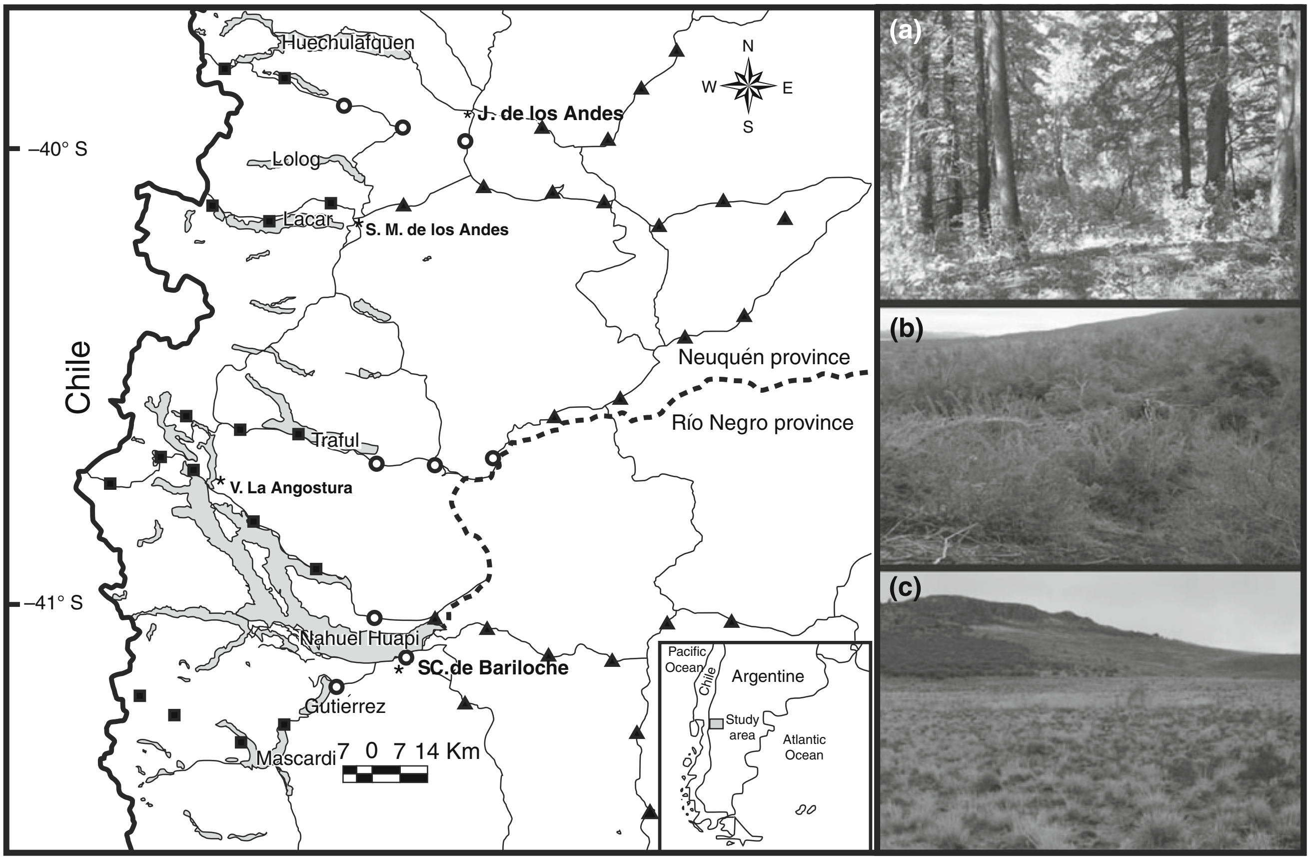

Fig. 1 Map showing locations of sampling plots within the **a** forests (*black squares*), **b** shrubland (*circles*) and **c** steppes (*black triangles*). The *dashed line* indicates the political limit between the Rio Negro and Neuquén provinces in Argentina. Other *lines* are roads. The change in the physiognomy of the vegetation from west to east reflects the replacement of **a** forests of *Nothofagus* species that grow at 1,500–3,500 mm of annual precipitation by **b** semi-arid shrublands, that grow along the foothill zone at 1,400–1,800 mm of annual precipitation, and **c** steppes, mainly composed of xerophytic shrubs and herbs that grow at 600–800 mm of annual precipitation toward the east

the western forested portions of this biogeographic transition (Kusnezov 1953; Fergnani et al. 2010). In contrast, many *Dorymyrmex* species, and the granivorous *Pheidole* are widespread in the steppes (Fergnani et al. 2010). Here, we adopt an ecological perspective to analyse in more detail taxonomic and ecological aspects of the structuring of local ant communities across this biogeographical transition.

Ant richness and composition are not necessarily determined by the same environmental factors (grassland and forest mosaic in Brazil: Pinheiro et al. 2010; Bornean rain forests: Mezger and Pfeiffer 2011). Across the Subantarctic-Patagonian transition, ant richness increases towards the steppes, in association with strong environmental variation, mainly in precipitation and canopy closure (Fergnani et al. 2010). Here, we show how climatic variables and vegetation structure are associated with the spatial variation in ant species composition. We also evaluate whether changes in ant species composition translate into differences in the proportional representation of ant functional groups, as previously found in other regions of the world (rain forest-savanna gradient in tropical Australia: van Ingen et al. 2008). We disentangle the role that transitional shrublands between the forests and steppes may play on the maintenance of ant species diversity across this biogeographic transition. If shrublands function as a distinct ecotonal habitat we would expect to find there a distinct ant species assemblage with ecotonal species, i.e. indicator taxa, with a higher proportional occupancy within the shrublands rather than in the adjacent forests and steppes. This would indicate that the transitional shrublands could be key areas to be conserved at local scale in temperate latitudes of the southern hemisphere.

Methods

Area of study

The study was conducted on the eastern slope of the Andes in Argentina, close to the border with Chile (39°S–42°S, 70°W–72°W; Fig. 1). The west-east gradient of precipitation is one of the main ecological controls of the replacement of forests in the west, by semi-arid shrub vegetation and steppes towards the east (Paruelo et al. 1998). At the western portion of the biogeographical transition, the temperate rainforests are dominated by *Nothofagus dombeyi*. At the intermediate portion of the gradient, forests are replaced by semi-arid shrublands, dominated by *N. antarctica*, and usually mixed with *Diostea juncea* and *Chusquea culleou*. Here, small groups or single isolated trees (e.g., *Austrocedrus chilensis* and *Maytenus boaria*) also grow. At the eastern portion of the gradient, the steppes are composed of short xerophytic shrubs and herbs, and lack tall vegetation. Dominant species include *Senecio bracteolatus*, *Mulinum spinosum* and *Stipa speciosa*.

Sampling methods

We collected epigaeic ants using 450 plastic pitfall traps arranged in 50, 100-m^2 grid plots of nine traps. The plots were ca. 15 km apart, within an area of 150 × 150 km (Fig. 1). A total of 17 sites were placed in the forests, 9 in the shrublands, and 24 in the steppes. Pitfall traps were operative for 1 week during each of the five sampling periods in the southern spring and summer (November 2004, January and March 2005, 2006). All plots were placed away from wet meadows and urban places, and at low elevations (i.e. between 893 and 1,154 m). Sampling sites lacked signs of recent fire, overgrazing or other anthropogenic disturbances (Ruggiero et al. 2009; Fergnani et al. 2010).

Specimens caught were identified using different taxonomic keys (Snelling and Hunt 1975; Kusnezov 1978), and specimens housed in the Kusnezov's collection (Instituto-Fundación Miguel Lillo, Tucumán, Argentina). Species were classified into foraging groups (Kusnezov 1949, 1952, 1959; Brown 2000; Kemp et al. 2000; Pirk and Casenave 2006; Pirk et al. 2009) with a second classification of functional groups in relation to stress and disturbance (Andersen 2000; Brown 2000).

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 from November 2004 to March 2005, which resulted in745 readings spread over 62 days. We estimated the average maximum daily temperature at each plot. We also estimated annual precipitation at each plot by an interpolation from an isoline regional map (Barros et al., 1983).

We distinguished among: (1) herbs (all vascular plants $<$0.30 m in height); (2) shrubs (all woody vascular plants between 0.30 and 2 m in height and trunks $<$10 cm in diameter at breast height); and (3) trees (all woody vascular plants $>$2 m in height and trunks $>$10 cm in diameter at breast height). We counted the number of tree, shrub and herb species found within each plot to estimate plant species richness. We estimated the herbaceous cover for each 10 × 10 m plot by randomly throwing four times a 0.50 × 0.50 m wood frame subdivided into a 25-celled nylon string-grid. In each placement, we estimated the proportion of cells covered by herbs. Then, for each plot we summed the four herb-cover values for a total of herb cover per m^2. We estimated shrub cover at each plot as the averaged diameter of individual shrubs, estimated visually, multiplied by the total number of shrubs of each species counted at each plot. We used a concave spherical densitometer to estimate the proportion of tree canopy cover.

We visually divided each 10 × 10 m plot into four quadrants to make four densitometer readings facing each of the four cardinal directions. These values were averaged to estimate canopy cover for each plot as in Speziale et al. (2010).

Nine 9-cm diameter samples (separated ca. 5 m from each other) per plot were harvested for litter biomass. They were stored in paper bags, oven-dried to constant mass at 60 °C and weighed to estimate dry litter biomass.

Analyses of data

Data on the presence-absence of species at each sampled site was used for all analyses throughout. The proportion of sites occupied by each species over the total number of sites sampled in the forests, shrublands, and steppes was a rough estimation of a local area of occupancy of each species within each macrohabitat, which we called "proportional occupancy" (Gaston 2003). Species with a significantly greater proportional occupancy in the shrublands were defined as *ecotonal* (Supplementary file 1). We tested whether ecotonal species fall in a single distinct cluster based on an R-mode cluster analysis with Bray Curtis similarity matrix and UPGM linkage (Primer 1 v5.0: Clarke and Gorley 2001).

The Indicator Value Method (Dufrêne and Legendre 1997) identified indicator ant species for each habitat type (forests, shrublands, and steppes) with an estimation of species specificity (=its uniqueness to a group of sites) and fidelity (=its frequency within any group). The indicator value for each species (IndVal) ranges from 0 % (no indication) to 100 % (perfect indication), and its significance was estimated using 999 randomizations (Dufrêne and Legendre 1997). An indicator species of a particular macrohabitat had a significant ($p < 0.05$) IndVal greater than 25 % (subjective benchmark used by Dufrêne and Legendre, 1997).

We performed a Q-mode Cluster Analysis, based on Bray Curtis similarity matrix and UPGM linkage, to establish groups of the sites with similar ant species composition (Primer 1 v5.0: Clarke and Gorley 2001). An Analysis of Similarity (ANOSIM in Primer 1 v5.0) detected significant differences in ant assemblages' composition between macrohabitats (Clarke and Green 1988). ANOSIM produces an R-statistic that is based on the difference of mean ranks between groups, and within groups. An R closer to one means high dissimilarity between groups; the significance of R is measured by 1,000 permutations of the grouping vector to obtain the empirical distribution of R under the null hypothesis of no difference between groups (Clarke and Green 1988).

We estimated the mean proportional occupancy of each foraging/functional group in the forests, shrublands and steppes by simply averaging the proportional of occupancy of all species in each foraging/functional group for each macrohabitat. We also counted the number of species in each foraging/functional group in each macrohabitat to evaluate the proportional taxonomic representation of each group in the forests, shrublands and steppes. A Chi-squared test ($p < 0.05$) was used to test the association between the mean proportional occupancy of foraging/functional groups and macrohabitats. A permutation based Fisher-Freeman Halton test for small-sample categorical data (FI) was conducted using Stat-Xact-6 (2003) to test the association between the number of species in each foraging/functional group and macrohabitats.

We analysed the association of the environmental variables with the variation in ant assemblage composition using a canonical redundancy analysis (RDA) implemented in CANOCO v4.5 (ter Braak and Šmilauer 2002). RDA is an extension of multiple regression to the modeling of multivariate data (Legendre and Legendre 1998). Because annual precipitation, canopy cover, litter and maximum daily temperature were highly correlated with each other ($r = \geq 0.8$) we run four alternative statistical models that combined only one of those highly correlated variables along with the other independent predictors (plant species richness, shrub and herb cover). Hereafter, we refer to these models as "tree canopy-model", "temperature-model", "precipitation-model", and "litter-model". We compared the proportion of variation in ant taxonomic composition accounted for each model (as estimated by canonical R^2).

Results

Occurrence patterns in individual ant species

We collected 108,937 individuals, which represented 3 subfamilies, 10 genera and 32 ant species. We captured 80 % of the species known to inhabit the Lanín, Nahuel Huapi and Los Alerces National Parks in north-western Patagonia (Kusnezov 1953), with the addition of a new species for the region (*Pheidole spininodis*); there was also a new species for science (*Dorymyrmex* sp. nova, unpubl. data). No species inhabited the shrublands exclusively (Supplementary file 1). The majority of the species were (1) Ubiquitous, that inhabit the forests, the shrublands and the steppes (9 species, Supplementary file 1); (2) Restricted to either the forests (2 species, Supplementary file 1) or the steppes (6 species, Supplementary file 1); (3) Present in the forests and shrublands (4 species, Supplementary file 1), or in the steppes and shrublands (8 species, Supplementary file 1).

In general, ubiquitous species that showed a high proportional occupancy in the forests tended to diminish their occupancy towards the shrublands and steppes; the opposite pattern was found in ubiquitous species with high proportional occupancy in the steppes (Supplementary file 1). Forest-shrubland and shrubland-steppes species also showed a decrease in the proportional occupancy in the shrublands (Supplementary file 1).

A total of seven species showed a tendency to have higher proportional occupancy in the shrublands than in the surrounding habitats (Supplementary file 1); however, most of the species (*Dorymyrmex tener*, *Dorymyrmex antarcticus*, *Solenopsis patagonica, Solenopsis sp1* and *Pogonomyrmex angustus,* Supplementary file 1) showed only minimal (not significant, $p > 0.05$) differences in their proportional occupancy within the shrublands compared to the other macrohabitats (Supplementary file 1) and thus they could hardly be considered as ecotonal. Only *Lasiophanes valdiviensis* was caught in 78 % of the shrubland plots, being the only indicator species of the shrublands, although with a low IndVal (29 %) (Supplementary file 1). Rare species, which were present in only one site, were restricted to the steppes (*Myrmelachista chilensis*, *Dorymyrmex bruchi ebeninus*, *D. breviscapis*, *Solenopsis* (*Diplorhopthrum*) sp. 2) (Supplementary file 1).

Faunal similarity and identification of ant species assemblages

The Q-mode cluster analysis showed the distinction between the forests and the steppes; shrubland sites did not fall together in a single cluster but were interspersed, mainly within the steppe cluster (Fig. 2a). The similarity analysis (ANOSIM) confirmed that ant assemblage composition differed between macrohabitats (R-global test $= 0.673$, $p = 0.001$). The forests and the steppes were the most dissimilar ones ($R = 0.906$, $p = 0.001$). The shrublands, and the forests also showed differences in ant species composition ($R = 0.782$, $p = 0.001$); in contrast, the shrublands were similar in ant species composition to the steppes ($R = 0.138$, $p = 0.08$). The R-mode cluster analysis also showed two species assemblages associated with forests and steppes. Those species with high proportional occupancy within the shrublands did not fall together in a single cluster but rather were interspersed among forest- and steppe- species (Fig. 2b).

Relative representation of functional groups

The mean proportional occupancy of foraging/functional groups differed significantly across the forests, shrublands and steppes (foraging groups, overall Chi-squared test $= 70.64$, $p < 0.0001$, $df = 8$, Fig. 3a; Andersen's functional groups: overall Chi-squared test $= 168.22$, $p < 0.0001$, $df = 12$, Fig. 3c). In contrast, the number of species in each foraging/functional group did not differed significantly across the transition (foraging groups: Fisher-Freeman Halton test, $FI = 4.074$, $p = 0.908$, Fig. 3b; Andersen's functional groups: $FI = 4.853$, $p = 0.998$, Fig. 3d).

The mean proportional occupancy of some foraging groups differed significantly between the forest and steppe ant assemblages. Generalized foragers and cryptic species showed a significantly higher occupancy than expected by chance in the forests, and a significantly lower occupancy in the steppes (Fig. 3a). Cultivators of fungi were absent in the forests, and have a significantly higher occupancy in the steppes (Fig. 3a). Although the mean proportional occupancy of foraging groups in the shrublands did not differed from the expected by chance it was somewhat more similar to the steppes rather than to the forests (Fig. 3a).

The mean proportional occupancy of Andersen's functional groups confirmed the differences between the forests and steppes, and also suggested that shrublands are ecologically more similar to the steppes rather than to the forests (Fig. 3c). Generalized Myrmicinae showed a significantly higher proportional occupancy in the forests, and a significant lower proportional occupancy in the shrublands and steppes (Fig. 3c). The proportional occupancy of tropical climatic specialists was significantly lower in the forests, and higher in the steppes (Fig. 3c). Opportunists had a significantly lower proportional occupancy in the forests, and a significantly higher proportional occupancy in the shrublands (Fig. 3c).

Ant species composition-environment associations

Mean values and range of variation of environmental variables recorded in our 50 sampling plots showed climatic and vegetation differences among the forests, shrublands and steppes (Table 1). The four environmental models accounted for a similar proportion (between 23 and 27 %) of the variance in taxonomic composition across the Subantarctic-Patagonian transition; the tree-canopy model showed the highest canonical R^2 (0.27). In this model, tree canopy cover explained the highest proportion of variance ($R^2 = 0.21$, $p = 0.02$) in taxonomic composition; the remaining variables were not significant (herb cover: $R^2 = 0.06$, $p = 0.45$, shrub cover: $R^2 = 0.05$, $p = 0.24$), or weak predictors (plant species richness: $R^2 = 0.03$, $p = 0.02$) of the variation in taxonomic composition across the transition. Plant species richness was associated with variation within macrohabitats, and also influenced the species composition of a few shrubland sites that contained higher numbers of plant species (Fig. 4). The three remaining models (temperature-, precipitation-, and litter-models) confirmed a similar pattern in the ordination of sampling plots, and species (Supplementary file 2).

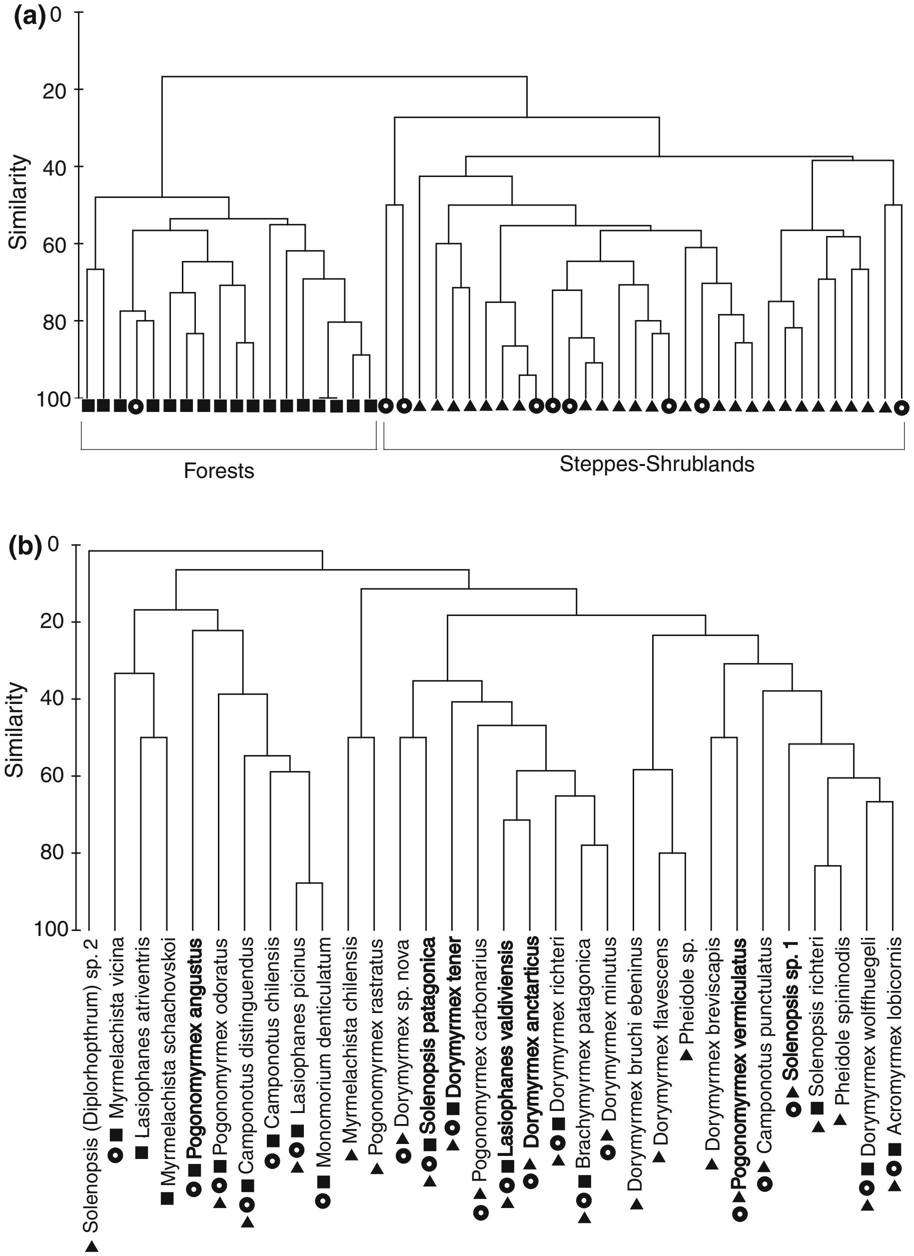

Fig. 2 Dendrograms obtained from (**a**) Q-mode cluster, and (**b**) R-mode cluster analysis, based on group average linking (UPGMA) of Bray-Curtis similarities. Sites are represented by *squares* (forests), *circles* (shrublands), *triangles* (steppes). Name of species that are given in *bold* correspond to those ant species with higher proportional occupancy in the shrublands

Discussion

Whereas the forests and steppes show distinct ant compositions, transitional shrublands are not a habitat source of ant species but an area of overlap of distributional margins of most of the forest- and steppe- species. Ant species that crossed the transition showed a progressive decrease in their proportional occupancy from the forests to the steppes or from steppes to the forests. This suggests the Subantarctic-Patagonian transition in northwestern Patagonia is a strong ecological barrier for ant species (Kusnezov 1953; Sackmann and Farji-Brener 2006). Ants could be sensitive to variation in local climatic conditions that is concurrent with major vegetation changes across the Subantarctic-Patagonian transition. Changes in vegetation structure might represent a selective filter for species movements, thus influencing on ant species' distribution (Verdú et al. 2011).

The forest fauna has strong Gondwanan affinities (e.g. *Lasiophanes, Monomorium*) whereas the steppe fauna has strong Neotropical affinities (*Dorymyrmex*, *Acromyrmex Pogonomyrmex*) (Lattke 2003). Forest ant species are relicts of an ancient fauna which apparently evolved mainly in isolation (Kusnezov 1953). In contrast, there are ant species in the Patagonian steppes with relatives in northern locations of America (Kusnezov 1953; Lattke 2003). The shrublands are more similar to the

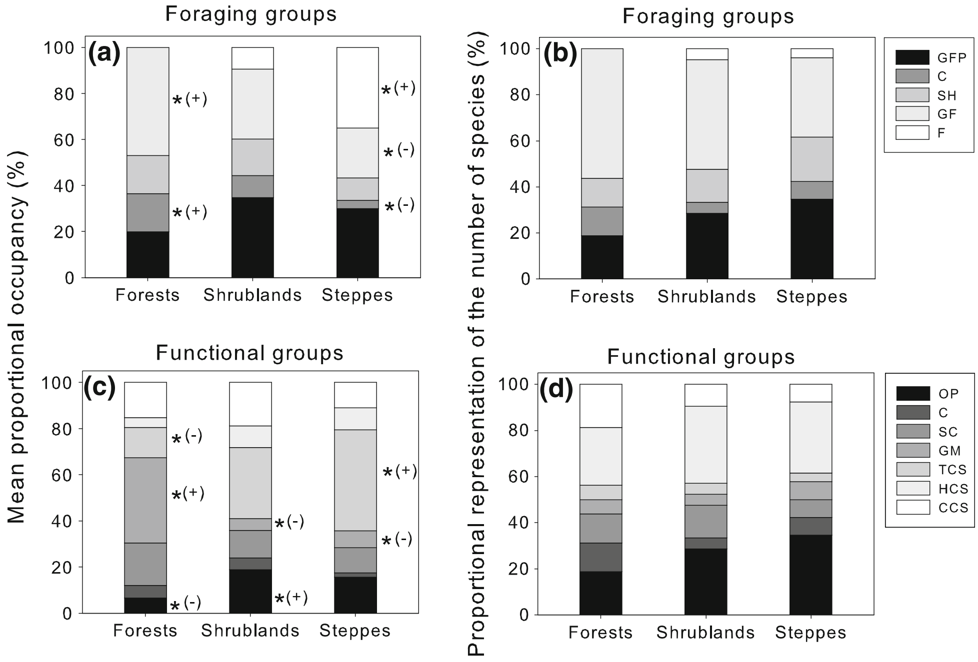

Fig. 3 Mean proportional occupancy, and proportional representation of the number of species of each foraging (**a**, **b**) and functional (**c**, **d**) group in the forests, shrublands and steppes. Foraging groups: *C* cryptic species, *GFP* generalized forager/predator, *GF* generalized forager, *SH* seed harvester, *F* Cultivator of fungi, Functional groups: *C* cryptic species, *OP* opportunist, *CCS* Cold-climate specialist, *TCS* tropical-climate specialist, *HCS* hot-climate specialist, *GM* generalised Myrmicinae, *SC* subordinate Camponotini. *Asterisks* indicate observed values that are significantly greater (+) or lower (−) than expected by chance (multiple Chi-squared test, $p < 0.05$)

Table 1 Mean values and range of variation of environmental variables used in the present study to analyse the association of taxonomic and functional composition of ants with climatic and vegetation variation across the Subantarctic-Patagonian transition

Environmental variables	Forests N = 17 plots		Shrublands N = 9 plots		Steppes N = 24 plots	
	Mean	Range	Mean	Range	Mean	Range
Maximum daily temperature (°C)	20.5	14.4–33.3	34.8	22.6–51.6	41.8	31.1–51.6
Annual precipitation (mm)	2,111.8	1,400–3,000	1,100.0	800–1,400	512.5	200–1,000
Herb cover (%)	18.4	0–62	56.7	30–87	40.1	18–94
Shrub cover (%)	35.1	6.5–84.8	33.3	8.2–59.1	17.2	1.2–36.6
Tree cover (%)	70.8	43.5–85.75	28.8	0–60.25	0.0	
Dry litter biomass (g)	113.0	24.9–187.4	42.8	3.3–111.2	4.3	0–26.7
Plant species richness	17.6	7–33	31.1	24–56	19.0	7–30

steppe- rather than to the forest- fauna, both in terms of ant composition, and foraging/functional groups. We identified only two rare species in the shrublands (*Pogonomyrmex angustus* and *P. vermiculatus*), which also inhabit other semiarid habitats of Argentina (Cuezzo and Claver 2009; Tizón and Quirán 2009). This is half the number of rare species found in the steppes (see results). *L. valdiviensis* is the only ecotonal indicator species (IndVal = 29 %) with a significant higher abundance in the shrublands ($p < 0.05$: Fergnani et al. 2008); it has also a tendency to have higher proportional occupancy in the shrublands, although it did not approach significance ($p = 0.119$, Supplementary file 1). A closely related species, *L. picinus*, is also present in the shrublands (Kuznezov 1951; Fergnani et al. 2008). Thus, the protection of this macrohabitat might be necessary to preserve this small genus endemic to Patagonia.

The shrublands are also floristically more similar to the steppes rather than to the forests (Speziale et al. 2010), which might affect arthropod species composition (Schaffers et al. 2008). In contrast to the forests, the shrublands and the steppes do not accumulate snow during winter, and thus they offer similar environmental conditions for overwintering ants' nests, which might affect ant species composition and the proportional occupancy of different foraging/functional groups. Shrublands might be also associated with a rapid dynamics (Rusch 1989; Veblen et al. 2003; Mermoz et al. 2005), which could favour the greater occupancy of opportunist species. Indeed, species found in the shrublands are unspecialized poorly competitive ant species that tend to predominate at sites where disturbance or stress limit ant productivity, and where behavioural dominance is low (Andersen 2000).

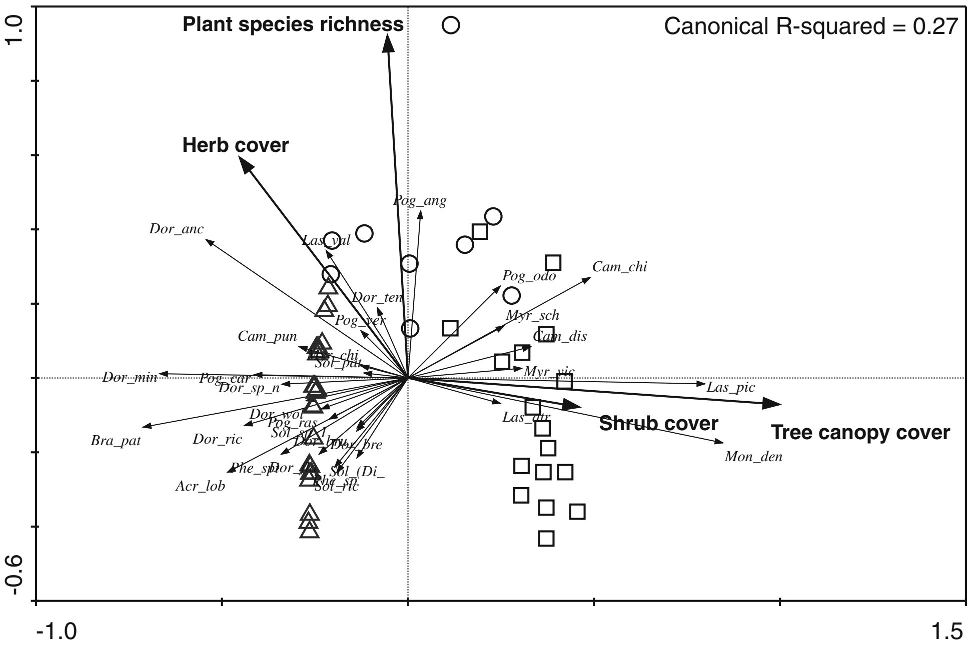

Fig. 4 Redundancy analysis (RDA) used to analyse the association of the environmental variables with the variation in ant assemblages' composition in the tree-canopy model (see methods). Sites are represented by *squares* (forests), *circles* (shrublands), and *triangles* (steppes). *Dor_ric* = *Dorymyrmex richteri*, *Dor_ten* = *Dorymyrmex tener*, *Dor_wol* = *Dorymyrmex wolffhuegeli*, *Bra_pat* = *Brachymyrmex patagonica*, *Cam_dis* = *Camponotus distinguendus*, *Las_pic* = *Lasiophanes picinus, Las_val* = *Lasiophanes valdiviensis*, *Pog_odo* = *Pogonomyrmex odoratus*, *Sol_pat* = *Solenopsis patagonica, Las_atr* = *Lasiophanes atriventris*, *Myr_sch* = *Myrmelachista schachovskoi*, *Cam_chi* = *Camponotus chilensis*, *Myr_vic* = *Myrmelachista vicina*, *Mon_den* = *Monomorium denticulatum*, *Pog_ang* = *Pogonomyrmex angustus*, *Acr_lob* = *Acromyrmex lobicornis*, *Cam_pun* = *Camponotus punctulatus, Dor_ant* = *Dorymyrmex antarcticus*, *Dor_min* = *Dorymyrmex minutus*, *Dor_sp_n.* = *Dorymyrmex* sp. nova, *Pog_car* = *Pogonomyrmex carbonarius*, *Pog_ver* = *Pogonomyrmex vermiculatus*, *Sol_sp.* = *Solenopsis* sp. 1, *Dor_bre* = *Dorymyrmex breviscapis*, *Dor_bru* = *Dorymyrmex bruchi ebeninus*, *Dor_fla* = *Dorymyrmex flavescens*, *Myr_chi* = *Myrmelachista chilensis*, *Phe_spi* = *Pheidole spininodis*, *Phe_sp.* = *Pheidole* sp., *Pog_ras* = *Pogonomyrmex rastratus*, *Sol_(Di)* = *Solenopsis* (*Diplorhopthrum*) sp. 2, *Sol_ric* = *Solenopsis richteri*

All foraging/functional groups are represented by similar number of species although with different mean proportional occupancy across this transition. Cryptic species and generalized foragers have higher occupancy in the forests, tropical-climate specialists and cultivators of fungi (*Acromyrmex*) are more widespread in the steppes, and opportunist in the shrublands. Thus, changes in ecological structure of ant species assemblages at local scale across the Subantarctic-Patagonian transition appear as less severe than those previously reported for other regions of the world where substantial changes in the proportional representation of species in different functional groups have been reported (forest-savanna gradient in tropical Australia: van Ingen et al. 2008).

The four environmental models tested in our study accounted for a similar proportion (<30 %) of the variation in ant species composition, and hence, they can be considered equivalent. The tree-canopy model suggests that variation in plant cover is fundamental to explaining ant community composition across ecotones (Bestelmeyer and Schooley 1999; Steiner and Shlick-Steiner 2004; Pinheiro et al. 2010). Trees are considered keystone structures for animals, as they provide food resources, nesting sites and soil nutrients (Tews et al. 2004). Plant cover and litter represent components of habitat complexity, which ultimately may be the key driver of the variation in ant species composition, abundance and richness in the forests (Lassau and Hochuli 2004; Lassau et al. 2005). At regional scale, the variation in canopy closure can be considered a rough proxy to distinguish closed and open macrohabitats. However, there is also an effect at a local scale because some species nest only in open sunny places avoiding tree shadows (i.e. *Pogonomyrmex odoratus, Brachymyrmex patagonicus*, Kusnezov 1959; *Solenopsis patagonica*, Kusnezov 1949). Ants living in the Subantarctic forests also take advantage of tree holes, barks and fallen trees for nesting (see details of nesting ecology in Supplementary file 1). The increase in canopy closure might also account for the greater occupancy of cryptic species in the forests. The strong association of canopy closure with ant composition, ant richness (Fergnani et al. 2010), and beetle abundance (Ruggiero et al. 2009) across this biogeographic transition, suggests that this is a primary determinant of epigaeic insect diversity in northwestern Patagonia.

The local variation in maximum daily temperature is one of the strongest determinants of ant species richness across the Subantarctic-Patagonian transition (Fergnani et al. 2010). Here, the temperature-model shows that it also contributes to maintaining local differences in ant species composition. Temperature affects the physiological functions and behaviour of ants, and influences on ant species richness and abundance (Kaspari et al. 2000; Retana and Cerdá 2000; Sanders et al. 2007; Dunn et al. 2009a, b), community organization (Bestelmeyer, 1997), taxonomic composition (Retana and Cerdá 2000), and ecological structure (Andersen 2000). Tropical-climate specialists tend to prefer high temperatures (Andersen 2000); this might account for their significantly higher proportional occupancy in the steppes, where our data-loggers approached 70 °C during the hottest days (data not shown), along with their significantly lower occupancy in the forests.

Annual precipitation and accumulated litter were the other two environmental factors that likely contribute to account for the variation in ant species composition, although the litter- model explained the lowest proportion (23 %) of the variation in ant species composition across this transition. Precipitation may have a direct influence on ant species composition (Morton and Davidson 1988; Pfeiffer et al. 2003; Lassau and Hochuli 2004), as well as an indirect effect mediated by changes in vegetation and in the production of seeds (Davison et al. 1977; Pfeiffer et al. 2003). Accumulated litter affects ant species diversity (Vasconcelos 1990), identity (Andersen 1983; Hoffmann and Andersen 2003), and ant species composition (Lassau and Hochuli 2004; Uno et al. 2010). However, it is possible that accumulated litter might be a stronger predictor of assemblage composition in litter ants (Theunis et al. 2005) rather than in epigaeic ants captured with pitfall traps (Botes et al. 2006).

Although more plant species might represent different resources for ants, and this could influence on the identity of species present (Ribas et al. 2003), throughout the present study plant species richness, shrub cover and herb cover were of secondary importance to account for the variation in ant species composition (Boulton et al. 2005; Hill et al. 2008). Nonetheless, in our study, a substantial portion of the variance in ant species composition remained unexplained, which suggests that other environmental variables not considered in the present study might affect ant species composition. Future studies are needed to address the role of, for instance, soil attributes (Peck et al. 1998; Boulton et al. 2005; Hill et al. 2008), or competitive interactions (Pfeiffer et al. 2008; Mezger and Pfeiffer 2011).

Transitional shrublands in northwestern Patagonia may potentially represent zones of scientific interest. Although they do not contain a distinct ant fauna, as clearly shown in the forests or steppes, they are likely to contain peripheral populations of both forest and steppe ant species. Although the conservation value of marginal or peripheral populations is debatable, they are often more sensitive to environmental change (Guo et al. 2005), and they might be relevant to represent the adaptive variation in individual species (Smith et al. 2001; Gaston 2003 and references therein). Thus, transitional shrublands could provide a suitable scenario for monitoring changes in species' ranges, ant species declines and invasions in the face of future climatic change. The widespread occupancy of the Patagonian endemic *Lasiophanes validiviensis* within the shrublands also increases its conservation value. Further studies are needed to evaluate the conservation significance of shrublands for other taxa.

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