



# Altitudinal variation in the taxonomic composition of ground-dwelling beetle assemblages in NW Patagonia, Argentina: environmental correlates at regional and local scales

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**Abstract.** 1. Altitudinal gradients offer a unique scenario to elucidate how the increase in harsh climatic conditions towards the top of the mountain interacts with other environmental factors at regional and local scale to influence the spatial variation in local species composition and biodiversity maintenance. We analysed the altitudinal variation in the taxonomic composition of epigaeic beetle assemblages across five mountains in north-western Patagonia (Argentina) to address whether substantial change in species composition was associated (i) at regional spatial scale, with changes in vegetation types, and the presence of dry and moist mountains, and (ii) at local spatial scale, with variation in temperature, plant cover and richness and several soil characteristics.

2. We collected beetles using 486 pitfall traps arranged in fifty-four 100-m<sup>2</sup> grid plots of nine traps settled at about 100 m of altitude apart from each other, from the base to the summit of each mountain. We used multivariate analyses to identify beetle assemblages and to evaluate their association with environment.

3. We identified different beetle assemblages, associated more with vegetation types rather than with mountains; indicator species showed higher degree of fidelity and specificity to vegetation types rather than to mountains. Local variation in temperature, plant cover and richness, and soil characteristics influence the variation in species composition.

4. Our study suggests the existence of a regional beetle fauna that is shared across these mountains. Major regional changes in vegetation types and local variation in environment drive the variation in the species composition of beetle assemblages at these latitudes.

**Key words.** Altitude, Coleoptera, high Andean steppes, indicator species, species composition, subantarctic forests.

## Introduction

Mountains offer a unique scenario to disentangle the influence of environment on the spatial variation in the taxonomic composition of insect species assemblages. They represent a kind of ‘natural experiment’ whereby to examine the extent to which substantial changes in environment may

be associated with evolutionary adaptation of organisms and biodiversity maintenance over relatively short spatial distances (Lomolino, 2001; Körner, 2007). From the base to the summit of the mountain, air temperature and oxygen partial pressure decrease, the air becomes less dense, contains less water vapour, and is more transparent (e.g. MacArthur, 1972; Körner, 2007). Therefore, organisms that live towards the summit experience more stressful conditions compared with those inhabiting the lowlands (see Hodkinson, 2005). Main altitudinal climatic trends usually co-vary with other factors at local and regional scale, such as variation in

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vegetation, regional climatic trends (e.g. seasonality and precipitation), land surface orientation and soil characteristics (Körner, 2007). Nonetheless, although it is well documented that insect species composition varies along altitudinal gradients (e.g. dung beetles in South Africa: Davis *et al.*, 1999; geometrid moths in Ecuador: Brehm & Fiedler, 2003; dung beetles in the Alps: Errouissi *et al.*, 2004; ground spiders in Greece: Chatzaki *et al.*, 2005; beetles in Spain: González-Megías *et al.*, 2008), the extent to which local and regional factors influence the spatial variation in species composition is still inconclusive.

Some evidence indicates that the variation in species composition of butterflies and carabids across different habitats in south-eastern Sweden are better explained by differences in local habitats rather than by habitat heterogeneity at landscape scale (Weibull & Östman, 2003). Similarly, differences in arthropod species composition in several functional groups in seminatural grasslands of the Netherlands are best predicted by local differences in plant species composition (Schaffers *et al.*, 2008). On the other hand, regional differences combined with local variation in physico-chemical factors within ponds account for differences in species composition of water beetle assemblages in two intensively farmed regions in Ireland (Gioria *et al.*, 2010). To our knowledge, similar analyses of the relative role of local and regional environmental factors on insect species composition are lacking for north-western Patagonia.

Altitudinal gradients in mountains of north-western Patagonia, in Argentina, reflect interactions between altitude-related climatic gradients, changes in vegetation and soil characteristics, and historical factors. At regional scale, the Andes act as a barrier to the humid westerlies at these temperate latitudes, causing greater amount and lower variability in precipitation in the Andean Cordillera compared with the eastern extra-Andean zones (Barros *et al.*, 1983; Jobbágy *et al.*, 1995; Paruelo *et al.*, 1998). This west-east gradient of precipitation is one of the main regional factors that control the replacement of forests of *Nothofagus* in the west, by semi-arid scrub vegetation and steppes towards the east (Paruelo *et al.*, 1998). Mountains located towards the west are more humid (hereafter referred to as 'moist mountains') compared with mountains located to the east (hereafter called 'dry mountains'). Within this regional scenario, general altitude-related phenomena are also perceptible. In general, climatic harshness increases with altitude concurrent with an altitudinal replacement of the subantarctic forests by the high Andean steppes (Cabrera & Willink, 1973); at the lowest elevations, in some, most often dry mountains, there are shrublands, which possibly originated after severe fires eliminated the forests (M. Mermoz & T. Kitzberger, pers. comm.).

We analysed the relative influence of local and regional environmental factors on the altitudinal variation in species composition of beetle assemblages across five mountains in NW Patagonia. Specifically, we analysed how much of the fauna is shared among different mountains and types of vegetation (i.e. shrublands – when present – forests and steppes), and which are the environmental variables (climate, vegetation, soil) associated with local altitudinal variation in the taxonomic composition of beetle assemblages.

#### *Regional and local associations between species composition and environment*

*Associations with climate.* Different species may present different levels of tolerance and adaptations to climatic changes (Terborgh, 1971, 1973). The increment in the harsh climatic conditions towards the top of the mountains imposes physiological restrictions for insects (Mani, 1968; Chown & Nicolson, 2004; Hodkinson, 2005), which may influence species composition. For instance, tolerance of cooler climatic conditions is the principal factor defining the dung beetle assemblage in the Upper Nama Karoo region, in South Africa (Davies *et al.*, 2008). Temperature contributed significantly to the separation of the ant species assemblages in the major vegetation types and biomes in the northern Cape Floristic Region (Botes *et al.*, 2006).

On the other hand, water availability affects insect diversity and distribution (Gullan & Cranston, 2005; Hodkinson, 2005). Different species may have different requirements and/or adaptations to survive in arid or humid climates (Gullan & Cranston, 2005). For instance, among beetles, about 50% of Tenebrionidae species are restricted to arid environments and show morphological, physiological, and ethological adaptations for regulating water balance (Watt, 1974; Flores, 1997). The strong west-east precipitation gradient across the subantarctic-Patagonian transition drives much of the spatial variation in functional and structural aspects of animal and plant species assemblages in NW Patagonia (e.g. abundance of beetles: Ruggiero *et al.*, 2009; plant richness: Speziale *et al.*, 2010). Here, we asked whether the altitudinal variation in the taxonomic composition of beetle assemblages can be accounted by local variation in mean daily minimum temperature and temperature range. We also examined whether the taxonomic composition of insect faunas differed between dry-eastern and moist-western mountains.

*Associations with vegetation cover and plant species richness.* Transition zones between biogeographical regions most often coincide with gradients in environmental conditions, which may be concurrent with changes in the structure and physiognomy of vegetation, and high turnover of species (e.g. Smith *et al.*, 2001; Araújo, 2002; Ruggiero & Ezcurra, 2003). These ecological changes are superimposed with historical effects to maintain the identity and differentiation of biogeographical units (Ruggiero & Ezcurra, 2003; Morrone, 2010). The transition between the subantarctic forests and the high Andean steppes implies strong changes in the structure and physiognomy of the vegetation. If insects responded to these major regional changes in the vegetation structure, we would expect to find different beetle assemblages and characteristic species in shrublands, forests, and high Andean steppes. At a local scale, we predicted that the spatial variation in the species composition of beetle assemblages was associated with local variation in plant cover and plant species richness.

*Associations with soil.* Different characteristics of soils are associated with differences in the composition of insect species assemblages. For instance, in high mountain regions of Israel, soil texture and surface compaction levels affect Tenebrionidae species composition (Krasnov & Shenbrot, 1996). Differences in

Carabidae composition among different habitats are related to preferences for certain soil types and soil acidity (Hosoda, 1999; Irmiler, 2003). In grasslands of northern California, soil structure affects the composition of ant species assemblages (Boulton *et al.*, 2005). Therefore, chemical and structural soil characteristics affect the ability of different insect species to establish and survive (Schowalter, 2006). Extremely acid soils may affect exoskeleton functions and other physiological processes, imposing special adaptations to inhabiting insects (Chown & Nicolson, 2004; Schowalter, 2006). The presence of volcanic ash in soils increases their permeability and thus causes high fluctuations in soil moisture, requiring a high degree of adaptability from inhabiting insects (Kusnezov, 1959). Nevertheless, volcanic ash also increases soil fertility (Warkentin & Maeda, 1980), which could favour insects indirectly through its beneficial effects on plants. On the other hand, soil texture, salinity, and moisture affect female oviposition preferences of many insect species; differences in soil texture may limit the capacity of many species to excavate them (Schowalter, 2006). We explored the relationship between soil characteristics and changes in the composition of beetle assemblages along the elevation gradient, and across the five mountains studied.

## Materials and methods

### Area of study

The study was conducted in five mountains in north-western Patagonia (41°08'S, 71°02' W, Fig. 1) within the Nahuel Huapi National Park, in Argentina. Average temperature during the summer season is <18 °C, and during winter, it is <4 °C (Rudloff, 1981). More than 70% of the annual precipitation is concentrated during fall and winter (Jobbágy *et al.*, 1995). Mean



**Fig. 1.** Map of the study area indicating the location of the five mountains: Pelado, Challhuaco, Bayo, López, and La Mona.

annual precipitation decreases from more than 3000 mm to ca. 300 mm along a west–east gradient (Cabrera & Willink, 1973; Barros *et al.*, 1983), which accounts for the presence of subantarctic forests towards the west, and the Patagonian steppes towards the east (Paruelo *et al.*, 1998). A similar ecological and biogeographical transition occurs with altitude. Subantarctic forests, dominated by several species of *Nothofagus*, and shrublands of semi-arid scrub vegetation and forests of *Austrocedrus chilensis* and *Nothofagus antarctica* grow downslope (Cabrera & Willink, 1973). Above 1600 m.a.s.l., changes in plant species composition and physiognomy of plant communities are associated with the transition between the subantarctic forests and the high-altitude Andean steppes. Here, the vegetation 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* (Ferreya *et al.*, 1998).

We selected five mountains to encompass the regional variation in precipitation from east to west: Pelado (40°56'S, 71°20'W, Neuquén Province, mean annual precipitation at the base, pp: ~1220 mm, sampled altitudinal range, sar: 800–1800 m), Challhuaco (41°13'S, 71°19'W, Río Negro Province, pp: 1100 mm, sar: 900–2000 m), Bayo (40°45'S, 71°36'W, Neuquén Province, pp: 1650 mm, sar: 900–1782 m), López (41°05'S, Río Negro Province, 71°33'W, pp: 1730 mm, sar: 800–1800 m), and La Mona (40°34'S, 71°42'W, Neuquén Province, pp: 1930 mm, sar: 800–1800 m) (Fig. 1).

### Beetle sampling

We collected beetles using 486 plastic pitfall traps (diameter, 9 cm; depth, 12 cm), arranged in fifty-four 100-m<sup>2</sup> grid plots of nine traps. In each mountain, 9–12 plots were settled at about 100 m of altitude apart from each other to represent the main habitats found at each elevation. The geographical position of each plot was recorded using Global Positioning System (GPS) technology.

We nested two traps one inside the other to minimise 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 over 7 days during four sampling periods in the summer season (January and March 2005 and 2006). At each plot, we pooled the contents from the nine pitfalls to one sample. All samples were preserved in 80% ethyl alcohol. Specimens were identified to species/morphospecies level. We were unable to identify Staphylinidae to species level or morphospecies without an expert opinion available; therefore, they were excluded from the analyses.

Voucher specimens of Curculionidae are held at the Museo de La Plata, Argentina. The remaining of the ground-dwelling beetle species are held at Ecotono Laboratory, Universidad Nacional del Comahue, Bariloche, Argentina.

The abundance of individuals for each species at each plot was the total number of individuals caught at each plot after the four sampling periods.

### Environmental variables

**Climatic variables.** We mounted one HOBO H8 logger (Onset Computer Corporation, Bourne, 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 summers of 2005, 2006, and 2007. In 2005, data loggers remained in the field for ca. 3 months during our sampling season (January–March). Owing to the harsh climatic conditions, some loggers broke down and their records were lost. To avoid the lack of records in any sampling plot, we obtained complementary records during the summer of the two subsequent years. The combination of all temperature records at each sampling plot allowed obtaining an overall number of temperature records that varied from 792 to 2148 across plots; however, in spite of these differences in the number of records, the altitudinal patterns of temperature variation obtained at each mountain over the 3 years resembled each other. Hence, we used all records obtained at each plot to estimate the average minimum daily temperature (TMIN), and the average daily temperature range (TVAR) at each plot.

We recorded slope aspect at each plot and created an ordinal variable to roughly represent qualitatively differences between slopes with high and low sunshine exposure at these latitudes (SUN = N > NW > NE > W > E > SW > SE > S).

**Vegetation variables.** We sampled the vegetation in each of the 54 (10 × 10 m) plots and classified all plants recorded according to their growth forms: (i) herbs, (ii) shrubs, and (iii) trees, as proposed by Ezcurra and Brion (2005).

**Vegetation cover** – We used a concave spherical densiometer to estimate the proportion of tree canopy cover in the forest and scrubland plots. We visually divided each 10 × 10 m plot into four quadrants to make four densiometer readings facing each of the four cardinal directions. We averaged the cover values to estimate an overall estimation of tree canopy cover (TREECOV) for each plot. We estimated shrub cover (SHRUBCOV) by adding the percentage cover of shrubs estimated visually in each of the four quadrants. We estimated the herbaceous cover (HERBCOV) 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. We averaged these four values to estimate herbaceous cover.

**Plant litter biomass** – 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 (LITTER).

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

**Soil variables.** We extracted samples from the top 10 cm of soil at three randomly selected points within each plot. We mixed the three top 10-cm samples to make one sample at each plot. For each plot-sample, we determined soil water pH (PH.H<sub>2</sub>O; potentiometric determination, Thomas, 1996), NaF pH as an indicator of volcanic influence in soil formation

(PH.VOLC; potentiometric determination, Blakemore *et al.*, 1987a,b), texture (TEXTURE; Klute, 1986), organic matter content (OM%; Pipette Method, Klute, 1986), and humidity (%HUM = [(wet weight – dry weight)/dry weight] × 100).

We randomly extracted three additional samples at each plot using a cylinder of known volume (96.21 cm<sup>3</sup>). These samples were dried at 105 °C for 24 h and sieved to 2 mm. From particles < 2 mm, we determined bulk density as BULDEN = dry weight/cylinder volume. Higher values of BULDEN are related to more compacted soils. From samples with larger particles, we estimated gravel percentage (GRAVEL% = gravel weight/total weight). We averaged BULDEN and GRAVEL% estimations over the three samples.

We also estimated the topographic slope (SLOPE) at each plot using a clinometer.

### Analyses of data

**Identification of plots with similar species assemblages.** We applied standard routines in Primer v5.0 (Clarke & Gorley, 2001) to conduct a cluster analysis, and an analysis of similarity (ANOSIM, Clarke & Gorley, 2001; Clarke & Warwick, 2001). This allowed the identification of plots with similar beetle's assemblages based on species' identities and their relative abundances, which we used to detect differences in the composition of beetles' assemblages across mountains, and habitats.

We 4th-root-transformed data before the analyses to down-weight the importance of the highly abundant species (Clarke & Warwick, 2001). We then created a Bray–Curtis similarity matrix (Bray & Curtis, 1957), which we used for subsequent analyses. Cluster analysis allowed the visual identification of groups of plots with similar species composition. ANOSIM produces an R statistic that is an absolute measure of distance between groups. A large positive R (up to 1) implies dissimilarity between groups. To display the relationships between different plots, we used non-metric multidimensional scaling (NMDS). NMDS provides a stress value that reflects how well the ordination summarises the observed relative distances among the samples. The weaker the stress, the better the quality of the representation. A common rule of thumb is that a stress below 0.2 represents a probably adequate fit (Clarke & Warwick, 2001).

**Identification of indicator species.** We used the indicator value method (Dufrene & Legendre, 1997; IndVal software available from <http://old.biodiversite.wallonie.be/outils/indval/>) to identify characteristic beetle species for each mountain and vegetation type. This method evaluates the degree of specificity (uniqueness to a group of sites) and fidelity (frequency within that group) of each beetle species. An IndicatorValue (IndVal) is then provided, as a percentage, for each species. A high IndVal indicates a higher specificity and fidelity of a particular species to the sites where it occurs; hence, such particular species can be considered representative of those sites. We tested the significance of the IndVal measures for each species, at each mountain or habitat, using 999 randomisations (Dufrene & Legendre, 1997). When a species had a significant ( $P < 0.05$ ) IndVal

>25% (subjective benchmark used by Dufrêne & Legendre, 1997), it was considered as indicator of a particular mountain or habitat.

*Associations between taxonomic composition and environment.* To study the influence of environmental variables on the taxonomic composition of species assemblages, we applied canonical correspondence analysis (CCA) using CANOCO v4.5 (ter Braak & Šmilauer, 2002). To minimise the effect of highly abundant species, we followed Lepš and Šmilauer (2003) and log-transformed the abundance values ( $y$ ) in the species matrix ( $y' = \log(y + 1)$ ) prior to the analyses. We also centred and standardised environmental variables before these analyses. We analysed the significance of the variation explained by each environmental variable using the stepwise selection method and Monte Carlo permutations (999 permutations).

## Results

We collected 12 365 beetles (excluding Staphylinidae) from 52 families and 321 species/morphospecies. The most abundant families in our study were Staphylinidae (12 418 individuals,  $\approx 50\%$ ), Carabidae (6213 individuals,  $\approx 25\%$ ), and Leiodidae (1947 individuals,  $\approx 8\%$ ). The richest families were Curculionidae (66 species/morphospecies,  $\approx 21\%$ ), followed by Pselaphidae (37 species/morphospecies,  $\approx 11\%$ ) and Carabidae (25 species/morphospecies,  $\approx 8\%$ ).

### *Spatial patterns of variation in assemblages' composition*

Cluster analysis resulted in three main clusters based on species composition: (i) the high Andean region of the three moist mountains: La Mona, Bayo, and López ( $A_m$ ,  $N = 8$ ); (ii) high Andean regions and lowland shrublands of dry mountains, that

is, Challhuaco and Pelado ( $A_d + S_d$ ,  $N = 10$ ); (3) forests of dry and moist mountains, and shrublands from moist mountains ( $F_{d,m} + S_m$ ,  $N = 36$ ; Fig. 2).

ANOSIM confirmed significant differences, although with low  $R$  values, in the taxonomic composition of beetle assemblages between some moist and dry mountains (Table 1a). Conversely, the taxonomic dissimilarity was high among habitats, and most strong between  $F_{d,m} + S_m$  and  $A_m$  (Table 1b).

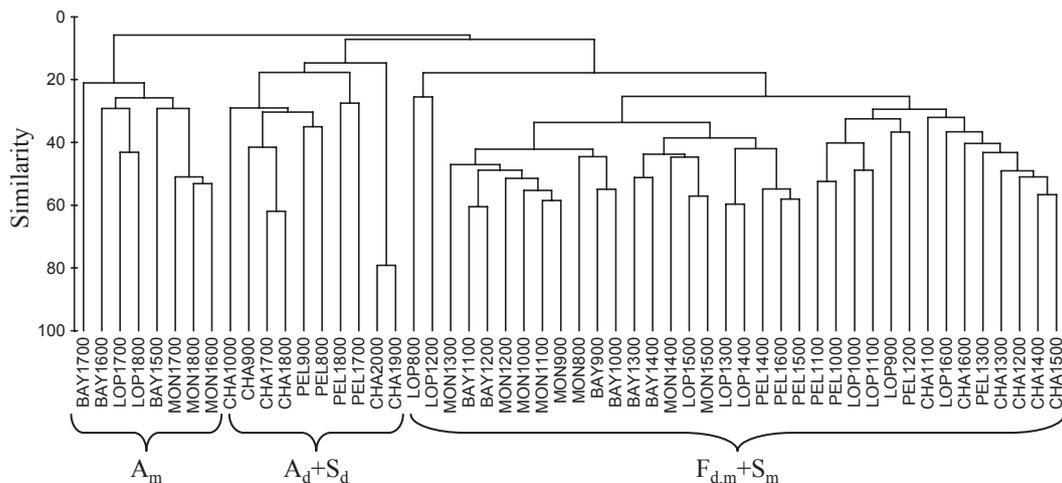
Non-metric multidimensional scaling also showed a clearer taxonomic distinction among habitats rather than among mountains (compare Fig. 3a,b).

*Indicator species.* In general, the IndVals were low ( $< 50\%$ ) for all mountains, showing a low specificity and fidelity of species to mountains. The López Mountain did not show indicator species, and there were few indicators of Pelado, Bayo, and Challhuaco. La Mona showed a more distinctive fauna represented by a greater amount of indicator species and higher values of IndVal (Table 2). Indicator species of Challhuaco were totally or partially absent in moister mountains (0/0 values of Table 2). Also, several indicator species of Bayo and La Mona were not found in the dryer mountains.

Species with high IndVal ( $> 50\%$ ) showed high degree of fidelity and specificity to habitats (Table 3). About 20%, 15% and 8% of total species present in  $A_m$ ,  $A_d + S_d$ , and  $F_{d,m} + S_m$ , respectively, were indicator of those habitats. Indicator species of  $A_d + S_d$  and  $F_{d,m} + S_m$  were absent in  $A_m$ . Conversely, several indicator species of  $A_m$  were not recorded in the other two habitats.

### *Associations between taxonomic composition and environment*

The eigenvalues of the first two CCA axes were 0.678 and 0.512, respectively. These two axes together explained about 30% of



**Fig. 2.** Dendrogram for hierarchical clustering of the 54 sampling sites, using group-average linking of Bray–Curtis similarities calculated on vv. Three main groups are evident: moist high andean ( $A_m$ ); dry high Andean + dry shrubland ( $A_d + S_d$ ); forest + moist shrubland  $F_{d,m} + S_m$ . 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 macro-habitat of each sampling site is detailed in Appendix S1.

**Table 1.** Similarity in the taxonomic composition of beetle assemblages between (a) mountains and (b) habitat types. *R* values obtained from ANOSIM are shown above the diagonal; the closer the value to 1, the greater the difference in the taxonomic composition between beetle assemblages. *P* values are shown below the table diagonal, with significant values shown in bold. *A<sub>m</sub>*: high Andean of moist mountains; *A<sub>d</sub> + S<sub>d</sub>*: high Andean and shrublands of dry mountains; *F<sub>d,m</sub> + S<sub>m</sub>*: forest of dry and moist mountains, and shrublands of moist mountains.

(a)					
	López	Pelado	Bayo	La Mona	Challhuaco
López		0.037	0.088	0.155	0.211
Pelado	0.217		0.205	0.294	0.061
Bayo	0.107	<b>0.011</b>		0.063	0.368
La Mona	<b>0.018</b>	<b>0.001</b>	0.143		0.425
Challhuaco	<b>0.005</b>	0.138	<b>0.003</b>	<b>0.001</b>	
Global <i>R</i> = 0.197, <i>P</i> = <b>0.001</b>					
(b)					
	<i>A<sub>m</sub></i>	<i>A<sub>d</sub> + S<sub>d</sub></i>	<i>F<sub>d,m</sub> + S<sub>m</sub></i>		
<i>A<sub>m</sub></i>		0.854	0.952		
<i>A<sub>d</sub> + S<sub>d</sub></i>	<b>0.001</b>		0.893		
<i>F<sub>d,m</sub> + S<sub>m</sub></i>	<b>0.001</b>	<b>0.001</b>			
Global <i>R</i> = 0.919, <i>P</i> = <b>0.001</b>					

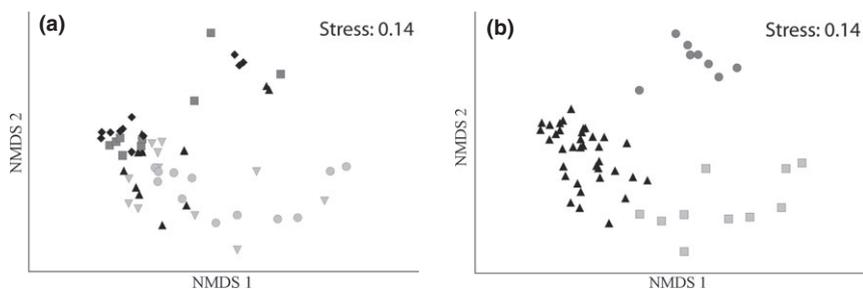
the variance in the species assemblages–environment relationship (axis 1: 17.1%, axis 2: 13%). The first axis showed that an environmental gradient of increasing BULDEN (correlation coefficient,  $r = 0.866$ ), GRAVEL% ( $r = 0.689$ ), and TVAR ( $r = 0.536$ ), and of decreasing TREECOV ( $r = -0.790$ ) accounts for the separation between beetle assemblages in the forests and moist shrublands and those in the high Andean steppes (i.e. *F<sub>d,m</sub> + S<sub>m</sub>* from *A<sub>m</sub>* and *A<sub>d</sub> + S<sub>d</sub>*) (Fig. 4). The second axis was mostly associated with decreasing values of TREESP ( $r = -0.516$ ) (Fig. 4), separating beetle assemblages in *A<sub>m</sub>* from those in *F<sub>d,m</sub> + S<sub>m</sub>* and *A<sub>d</sub> + S<sub>d</sub>*. The *A<sub>m</sub>* assemblage was associated with low TMIN; the *A<sub>d</sub> + S<sub>d</sub>* assemblage with high TVAR and PH.H<sub>2</sub>O. The *F<sub>d,m</sub> + S<sub>m</sub>* assemblage was associated with lower BULDEN and GRAVEL%, and higher TREECOV than *A<sub>m</sub>* and *A<sub>d</sub> + S<sub>d</sub>* (Fig. 4).

## Discussion

We confirmed that the spatial variation in the species composition of beetle assemblages in north-western Patagonian was associated with variation in environment at regional and local scales. At regional scale, we identified different taxonomic assemblages associated with different types of vegetation. At local scale, variation in soil characteristics, temperature conditions, vegetation cover, and plant species richness influenced on the taxonomic composition of beetle assemblages.

Our study showed that differences in species composition were less marked across mountains than across vegetation types. This suggests the existence of a regional mountain fauna with relatively low levels of isolation across the five mountains studied. The forest beetle fauna was similar across the five mountains examined, but there were significant differences in the high Andean assemblages between moist and dry mountains. Beetles might track differences in the structure and composition of high Andean plant species communities known to occur at these latitudes. For instance, it has been suggested that, in the Southern Andes, eastern drier mountains might have been free from ice during longer periods of times rather than western moist mountains since the last Pleistocene glaciations, which could have increased the time for colonisation by species, thus favouring high plant species richness in the eastern mountains (Moore, 1983; Ferreyra *et al.*, 1998). This pattern is consistent with evidence that suggests that patterns in genetic and taxonomic diversity in most temperate plant and animal species have been shaped by post-glacial colonisation of formerly glaciated areas (e.g. Southern Andes: Cosacov *et al.*, 2010; Western Palearctic: Habel *et al.*, 2010). Also, at present, the strong west–east gradient of precipitation is associated with lower accumulation and persistence of snow towards the east, which favours a longer growing season for plants (Ferreyra *et al.*, 1998; Premoli, 2004). It seems reasonable to envisage that these historical and current climatic factors may have also influenced directly or indirectly on the composition of beetle assemblages.

The forests and the high Andean steppes showed distinct beetle assemblages. But shrubland beetle assemblages were more similar either to species assemblages in the high Andean steppe or to the forest fauna, depending upon the location of



**Fig. 3.** Non-metric multidimensional scaling ordination of sampling plots based on the species composition of beetles. (a) mountain ordination: López (▲), Pelado (▼), Bayo (■), La Mona (◆), and Challhuaco (●); (b) habitat ordination: *A<sub>m</sub>* (●), *A<sub>d</sub> + S<sub>d</sub>* (■), and *F<sub>d,m</sub> + S<sub>m</sub>* (▲). See references in the text.

**Table 2.** Indicator species of each mountain.

	IndVal (%)	Species abundance/number of sampling plots where it was found				
		M1	M2	M3	M4	M5
López (M1) TOT = 0						
No indicator species						
Pelado (M2) TOT = 2						
<i>Cylydrorhinus</i> sp. M2 (Curculionidae)	29.35	2/1	25/4	1/1	0/0	3/2
<i>Frykius variolosus</i> (Geotrupidae)	26.27	0/0	14/5	1/1	9/2	0/0
Bayo (M3) TOT = 7						
<i>Salagosa</i> sp. 1 (Pselaphidae)	50.89	0/0	0/0	66/6	25/3	0/0
<i>Abropus carnifex</i> (Carabidae)	44.44	0/0	0/0	36/5	11/3	0/0
<i>Chiliopelates ventricosus</i> (Leiodidae)	37.56	35/1	5/3	172/6	122/8	1/1
<i>Salagosa</i> sp. 2 (Pselaphidae)	33.95	8/3	0/0	45/4	9/3	0/0
<i>Pyraconema</i> sp. A1 (Lampyridae)	30.73	1/1	0/0	11/4	5/3	0/0
<i>Copobaenus tristis</i> (Anthicidae)	28.31	1/1	0/0	14/4	6/4	3/2
<i>Eunemadus chilensis</i> (Leiodidae)	26.37	0/0	0/0	39/5	50/5	3/1
La Mona (M4) TOT = 18						
<i>Neohydnohius</i> sp. (Leiodidae)	56.76	28/2	6/3	23/5	237/8	5/2
<i>Creobius eudoxi</i> (Carabidae)	51.91	58/6	0/0	85/6	281/9	0/0
<i>Sericoides</i> sp. 6 (Scarabaeidae)	49.59	1/1	0/0	0/0	10/6	0/0
<i>Pselaphidae</i> sp. 2c	46.07	28/4	4/2	6/1	108/7	2/1
<i>Camiarinae</i> sp. (Leiodidae)	45.31	0/0	0/0	10/4	60/6	0/0
<i>Cryptorrhynchinae</i> sp. 9 (Curculionidae)	44.04	0/0	0/0	1/1	38/5	0/0
<i>Auxenocerus</i> sp. (Pselaphidae)	40.57	1/1	0/0	2/2	10/6	0/0
<i>Nemadotropis stenosoma</i> (Leiodidae)	40.29	0/0	0/0	11/3	38/6	0/0
<i>Dasytelates gracilis</i> (Leiodidae)	38.55	26/4	6/3	174/6	276/8	0/0
<i>Laderia oblonga</i> (Melandryidae)	37.22	0/0	0/0	18/7	31/7	0/0
<i>Bembidini</i> spp. (Carabidae)	33.61	19/2	0/0	0/0	254/4	2/2
<i>Ceroglossus chilensis</i> (Carabidae)	32.31	0/0	0/0	4/1	39/4	0/0
<i>Cryptorrhynchinae</i> sp. 10 (Curculionidae)	30.96	0/0	0/0	1/1	7/4	0/0
<i>Aderidae</i> sp.	27.27	0/0	0/0	0/0	3/3	0/0
<i>Aridius subfasciatus</i> (Lathridiidae)	27.27	0/0	0/0	0/0	5/3	0/0
<i>Sericoides</i> sp. 4 (Scarabaeidae)	27.27	0/0	0/0	0/0	18/3	0/0
<i>Sericoides viridis</i> (Scarabaeidae)	27.27	0/0	0/0	0/0	5/3	0/0
<i>Cryptorrhynchinae</i> sp. 13 (Curculionidae)	26.76	0/0	0/0	4/3	7/5	0/0
Challhuaco (M5) TOT = 4						
<i>Baripus gii</i> (Carabidae)	35.73	1/1	39/4	0/0	0/0	69/7
<i>Amecocerus</i> sp. (Melyridae)	33.33	0/0	0/0	0/0	0/0	6/4
<i>Arthrobrachus</i> sp. (Melyridae)	30.05	0/0	2/1	0/0	0/0	20/4
<i>Cylydrorhinus</i> sp. M5 (Curculionidae)	25	0/0	0/0	0/0	0/0	28/3

IndVal, IndicatorValue.

IndVal represents the percentage or degree of specificity and fidelity of species to each mountain. TOT: the total number of indicator species of each mountain. For each species, in each mountain, we reported its abundance/the number of sampling plots where the species was found (e.g. we found 25 individuals of *Cylydrorhinus* sp. M2 in four sampling plots in the Pelado). All IndVals were significant ( $P < 0.05$ ). Total number of species caught: López = 130; Pelado = 131; Bayo = 129; La Mona = 166; Challhuaco = 99.

each mountain along the precipitation gradient. At the base of the dry mountains, Pelado and Challhuaco, there were shrublands inhabited by beetle assemblages, taxonomically similar to those found in the high Andean steppes. Conversely, the shrubland beetle assemblage at the base of the moist López was similar to the forest assemblages. Shrublands in our study region are often post-fire communities that recolonised previously forested areas after severe fires (M. Mermoz & T. Kitzberger, pers. comm.). Environmental changes that occur after a fire modify resources and essential conditions for insects such as food characteristics, foraging and nesting sites, and refuges (Andersen, 1991; Swengel, 2001); hence, pre- and

post-fire insect assemblages' composition may differ (e.g. Farji-Brener *et al.*, 2002; Sackmann & Farji-Brener, 2006; Sasal *et al.*, 2010). Beetles have great colonising capacity (Borror *et al.*, 1992), which could have favoured the occupation of shrublands at the base of mountains by beetle species from nearby communities. The Patagonian steppes, which are relatively closed to Pelado and Challhuaco, could have acted as source of species for shrublands in these dry mountains. The high Andean beetle fauna from the southern half of Peru down to Tierra del Fuego is very similar to that of the Patagonian steppes, with many taxa shared at the genus and species level (e.g. Kuschel, 1969) This

**Table 3.** Indicator species of each habitat.

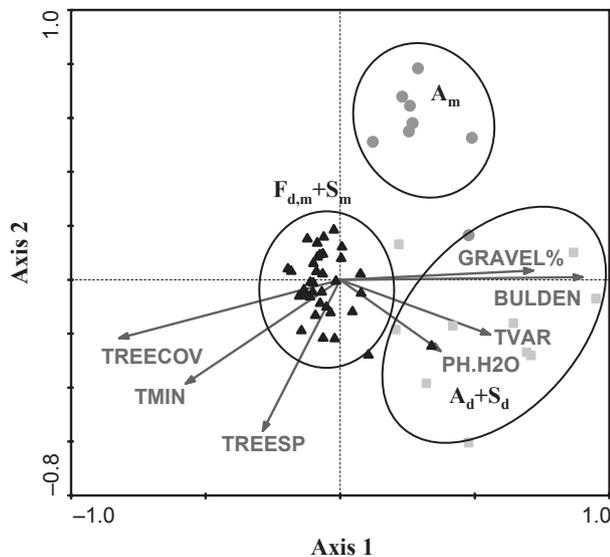
	IndVal (%)	Species abundance/ # of sampling plots where it was found		
		$A_m$	$A_d + S_d$	$F_{d,m} + S_m$
$A_m$ TOT = 10				
<i>Margaiostus magellanicus</i> (Elateridae)	84.69	79/7	3/2	1/1
<i>Berberidicola ater?</i> (Cuculionidae)	62.5	25/5	0/0	0/0
<i>Cylydrorhinus sp. 1</i> (Curculionidae)	62.5	32/5	0/0	0/0
<i>Sericoides faminaei</i> (Scarabaeidae)	59.69	39/6	0/0	45/9
<i>Pseudomeloe porteri</i> (Meloidea)	58.25	14/5	1/1	1/1
<i>Bembidini</i> spp. (Carabidae)	49.56	267/4	1/1	7/3
<i>Pselaphidae sp. 29</i>	45	6/4	0/0	3/2
<i>Coccinellidae sp. 4</i>	37.5	3/3	0/0	0/0
<i>Sericoides sp. 4</i> (Scarabaeidae)	37.5	18/3	0/0	0/0
<i>Pselaphidae sp. 20</i>	32.66	3/3	0/0	2/2
$A_d + S_d$ TOT = 12				
<i>Baripus giaii</i> (Carabidae)	78.05	0/0	100/8	9/4
<i>Nyctelia rotundipennis</i> (Tenebrionidae)	73.97	0/0	75/8	22/2
<i>Emmalodellara obesa costata</i> (Tenebrionidae)	59.81	0/0	87/6	1/1
<i>Arthrobrachus sp.</i> (Melyridae)	50	0/0	22/5	0/0
<i>Nyctopetus argentinus</i> (Tenebrionidae)	47.6	0/0	11/5	2/1
<i>Caneorhinus sp. 2</i> (Curculionidae)	40	0/0	4/4	0/0
<i>Ameocercus sp.</i> (Melyridae)	40	0/0	6/4	0/0
<i>Epuraeopsis maculipennis</i> (Nitidulidae)	38.08	0/0	11/4	2/2
<i>Baripus neuquensis</i> (Carabidae)	34.95	0/0	25/4	13/3
<i>Cnemalobus deplanatus</i> (Carabidae)	34.29	0/0	15/4	9/2
<i>Cylydrorhinus sp. M5</i> (Curculionidae)	30	0/0	28/3	0/0
<i>Peltidae sp. 1</i>	30	0/0	5/3	0/0
$F_{d,m} + S_m$ TOT = 21				
<i>Scaphidiidae gen. spp.</i> (Scaphidiidae)	86.05	0/0	11/2	305/35
<i>Newtoniopsis malleatus</i> (Leiodidae)	76.74	0/0	1/1	265/28
<i>Trechisibus nigripennis?</i> (Carabidae)	65.61	2/2	2/1	1004/24
<i>Ceroglossus valdiviae</i> (Carabidae)	61.11	0/0	0/0	2270/22
<i>Mimodromites nigrotestaceus</i> (Carabidae)	59.87	0/0	3/1	521/22
<i>Dasypelates gracilis</i> (Leiodidae)	58.33	0/0	0/0	482/21
<i>Sericoides similis</i> (Scarabaeidae)	58.33	0/0	0/0	66/21
<i>Apioninae sp. 1</i> (Curculionidae)	56.52	0/0	5/1	138/23
<i>Neohydnoebius sp.</i> (Leiodidae)	55.56	0/0	0/0	299/20
<i>Systolosoma brevis</i> (Carabidae)	54.8	1/1	0/0	328/20
<i>Pselaphidae sp. 4</i>	53.58	3/1	0/0	152/21
<i>Chiliopelates ventricosus</i> (Leiodidae)	52.78	0/0	0/0	335/19
<i>Creobius eudoxi</i> (Carabidae)	51.14	3/2	0/0	421/19
<i>Systolosoma lateritium</i> (Carabidae)	50	0/0	0/0	855/18
<i>Sericoides spp.</i> (Scarabaeidae)	47.89	2/2	9/2	92/25
<i>Pyraconema sp. B2</i> (Lampyridae)	44.44	0/0	0/0	72/16
<i>Hydnodiaetus brunneus</i> (Leiodidae)	41.67	0/0	0/0	65/15
<i>Perilopis flava</i> (Nitidulidae)	38.89	0/0	0/0	54/14
<i>Scydmaenidae sp. 1</i>	38.89	0/0	0/0	24/14
<i>Orchesia picta</i> (Melandryidae)	38.19	2/1	0/0	55/16
<i>Pocadionta dentipes</i> (Nitidulidae)	30.56	0/0	0/0	27/11

IndVal, IndicatorValue.

IndVal represents the percentage or degree of specificity and fidelity of the species to each habitat. TOT = total number of indicator species in each habitat. For each species, in each habitat, we reported its abundance/the number of sampling plots where the species was found (e.g. we found 79 individuals of *Margaiostus magellanicus* in seven sampling plots in  $A_m$ ). All IndVals were significant ( $P < 0.05$ ). Total number of species recorded:  $A_m = 51$ ;  $A_d + S_d = 79$ ;  $F_{d,m} + S_m = 267$ .

could explain the similarity in species composition we observed between beetle assemblages in the shrublands of dry mountains and high Andean environments. In contrast, the López is relatively far from the steppes, with

more humid climatic conditions. This might have favoured the presence of relatively more mesic shrublands at the base of this mountain that allowed colonisation by nearby forest beetle assemblages. Nonetheless, this



**Fig. 4.** Canonical correspondence analysis ordination (biplot) of beetle assemblages in relation to environmental variables. Arrows indicate the magnitude and direction of change of environmental variables that significantly explain changes in beetle assemblages' composition ( $P < 0.05$ ). For each axis, the eigenvalues associated are shown in brackets; (●)  $A_m$ , (■)  $A_d + S_d$ , (▲)  $F_{d,m} + S_m$ . Variables are defined in methods section.

interpretation is rather speculative and should be tested in future studies.

Different beetle assemblages were associated with variation in vegetation cover, temperature, and particular soil characteristics. Mean temperature and temperature variability may account for differences in the taxonomic composition of beetle assemblages between dry and moist high Andean environments. Species of high Andean habitats in moist mountains were associated with more extreme daily minimum temperatures than species of similar high Andean habitats and shrublands in dry mountains. Here, variations in daily temperature were greater.

Coleoptera assemblages in forest and moist shrubland environments were associated with lower surface compaction levels, gravel percentage, and soil acidity than those of high Andean and dry shrubland environments. Differences in soil compaction and soil pH have been previously associated with differences in insect species composition and survival (e.g. tenebrionids: Ayal & Merkl, 1994; Krasnov & Shenbrot, 1996; arthropods: Van Straalen & Verhoef, 1997; fruit flies: Eskafi & Fernandez, 1990; carabids: Hosoda, 1999; Irmler, 2003). Soil characteristics could also affect insects indirectly, through their effect on plant communities (Hodkinson, 2005); however, the influence of this indirect effect on the taxonomic composition of beetle assemblages was not estimated in the present study.

Our study reinforces the idea that insects perceive environments at a higher detailed level of resolution than the human eye (Kaspari & Weiser, 1999; Farji-Brener *et al.*, 2004). Nonetheless, beetle assemblages in north-western Patagonia emphasise the need of taking into account regional environ-

mental variation, mainly associated with the presence of different vegetation types or macro-habitats, along with variations in local environments for a comprehensive understanding of beetle diversity maintenance, and the design of local conservation strategies.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2012.00190.x.

Appendix S1. Geographic location of the sampling plots and main vegetation type.

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