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ORIGINAL ARTICLE

The richness and abundance of epigaeic mountain beetles in north-western Patagonia, Argentina: assessment of patterns and environmental correlates

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ABSTRACT

Aim Our aims were: (1) to study the shape of the species richness–elevation and abundance–elevation relationships (SRER and AER, respectively) in epigaeic mountain beetles; and (2) to analyse how richness and abundance of the beetles vary across the full gradient and within the forests and steppes in association with environmental variables representing productivity, thermal limitation, water–energy dynamics, environmental heterogeneity and soil characteristics.

Location Five mountains at temperate latitudes in north-western Patagonia, Argentina.

Methods We collected beetles using 486 pitfall traps arranged in fifty-four 100 m² grid plots of nine traps, established at intervals of about 100 m of elevation from the base to the summit of each mountain. We used multi-model selection and the Akaike information criterion to find the best ecological explanation for species richness and abundance variation.

Results The AER was hump-shaped in four mountains and negative in one; the SRER was negative in one case, humped in two cases, and either low-plateau or humped in the remaining two. Across the full gradient, the increase in vegetation cover, mainly associated with the presence of forests, predominately accounted for SRERs and AERs. In the forests, energy variables combined with precipitation, soil attributes and environmental heterogeneity accounted for richness and abundance. In the steppes, potential evapotranspiration and plant productivity were important.

Main conclusions We confirmed different forms in the shape of SRERs, and the predominance of hump-shaped patterns in AERs. Vegetation type (forests versus steppes) accounted for most of the variation in species richness and abundance on all mountains. Associations with local environmental factors were rather more variable and changed with the spatial extent of analysis, thus confirming the spatial dependence of the species richness/abundance–environment relationships.

Keywords
Biogeographical transition, Coleoptera, diversity, hump-shaped pattern, productivity, soil suitability.

INTRODUCTION

In recent years, there has been renewed interest in the species richness–elevation relationship (SRER). Although the pattern may follow multiple forms (Rahbek, 2005; McCain, 2007, 2009, 2010; Nogués-Bravo *et al.*, 2008), there is a predominance of hump-shaped over linear decreasing patterns in arthropods (Werenkraut & Ruggiero, 2011). Nonetheless, there is considerable idiosyncratic variation across arthropod taxa, precluding general conclusions on such a diverse taxonomic group (Werenkraut & Ruggiero, 2011). We assessed the shape of the SRER in epigaeic beetles inhabiting temperate mountains in South America, where detailed ecological analyses of large insect species assemblages are scant.

We also evaluated the shape of the abundance–elevation relationship (AER). Although it is often assumed that richness

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and abundance are functionally associated (e.g. Evans *et al.*, 2005), the AER has been studied less than the SRER. Some evidence suggests no consistent trends in AERs (e.g. Lawton *et al.*, 1987; Suren, 1994). Moreover, SRERs and AERs may be driven by different environmental components (e.g. Wettstein & Schmid, 1999). We assessed whether the shapes of AERs and SRERs are similar and, if so, whether they are driven by similar environmental factors.

Multiple factors may influence SRERs and AERs: air temperature, atmospheric pressure, peak solar radiation, area of bioclimatic belts, seasonality, precipitation, isolation and history (e.g. Körner, 2000, 2007; McCain, 2007, 2009, 2010). Some of these are always tightly correlated with elevation (temperature, pressure, peak solar radiation, area of bioclimatic belts) and the others are not, or are only unpredictably so. The existence or particular shape of SRERs and AERs will thus be determined by which factors have dominant effects and the degree of interactions among effects. Here, we address this issue showing how local environmental variation interacts with the elevational replacement of vegetation types to influence the SRER and AER on five elevational gradients that shared the same regional fauna (Werenkraut & Ruggiero, 2013).

Hypotheses proposed to account for the SRER and AER

Thermal limitation

Elevational decrease in temperature is often associated with a decrease in the richness and abundance of arthropod species (e.g. Kaspari *et al.*, 2000a,b; Sanders *et al.*, 2003, 2007; Almeida-Neto *et al.*, 2006; Botes *et al.*, 2007; Garibaldi *et al.*, 2011). Temperature may influence the population density and species richness of ectotherms across geographical gradients primarily through its effects on the biochemical kinetics of metabolism (Allen *et al.*, 2002). This predicts an inverse relationship between population density and temperature, and an increase in species richness with higher temperature. We tested the association of temperature and slope exposure with the richness and abundance of beetles.

Physiological functions of insects are sensitive not only to variation in temperature means but also to temperature variability (Chown & Terblanche, 2006). Diurnal thermal variation is expected to be greater in the Andean steppes with semi-desertic climatic conditions than in the forests where canopy cover may favour more stable temperature conditions at ground level. We evaluated whether diurnal thermal variation was a significant factor affecting SRERs and AERs.

Productivity

Areas of high productivity usually support more individuals and more species, because an increase in productivity raises the overall availability of food for individuals in the consumer trophic level, promoting the coexistence of a high number of species (Kaspari *et al.*, 2000b; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Evans *et al.*, 2005). We indirectly tested this hypothesis using a satellite-derived enhanced vegetation index (EVI), designed to distinguish the ‘green’ photosynthetically active signal of vegetation activity (Huete *et al.*, 2002). Vegetation indexes are often used as a surrogate for plant productivity in studies of animal and plant species diversity (Cusens *et al.*, 2012), but above-ground net primary productivity may be also correlated with vegetation cover (see Evans *et al.*, 2005) or total plant biomass (Flombaum & Sala, 2007). We tested the association between EVI and vegetation cover, and then evaluated whether they influence positively the abundance and richness of beetles; however, the presence of dense vegetation at ground level is also known to reduce ground-dwelling insect catches (e.g. Melbourne, 1999). Thus, an alternative prediction was that an increase in herb cover might negatively influence the richness and abundance of beetles.

Litter is also an essential part of nutrient cycling in forest ecosystems (Sayer, 2006), which may positively influence insect diversity, through increasing the availability of shelter and/or additional resources for some species (e.g. carabid beetles: Koivula *et al.*, 1999); however, it may also be an impediment to beetle mobility, reducing insect catches (Rickard & Haverfield, 1965). We evaluated the association of litter with the richness and abundance of beetles.

Water–energy dynamics

Availability of liquid water and optimal energy conditions are necessary and fundamental to biotic dynamics (i.e. changes in the form and location of living organisms) and vary over space in a systematic fashion. Differences in the abiotic capacity of the environment to support species may lead over time to geographical gradients in species richness (O’Brien, 2006). Indeed, water–energy dynamics accounts for richness patterns in a wide variety of animal and plant taxa (e.g. Hawkins *et al.*, 2003; O’Brien, 2006). We tested whether local variation in precipitation and potential evapotranspiration accounts for the local variation in richness and abundance of beetles.

Environmental heterogeneity

Plant species richness may represent different resources and generate different microhabitats that may promote the coexistence of specialist insects, and thus high species richness on a local scale (e.g. Otte, 1976; Siemann *et al.*, 1998; but see Hawkins & Porter, 2003a,b). Although the angle of slope does not create spatial heterogeneity directly, it affects the amount of solar radiation intercepted by land surfaces, the amount of water runoff and infiltration, and soil formation processes (Bennie *et al.*, 2008); thus, we considered the angle of slope as a measure of the strength of micro-environmental gradients occurring at each sampling plot. We evaluated how plant species richness and the angle of slope are associated with the richness and abundance of beetles.

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Soil characteristics

Local variation in beetle species richness and abundance may be associated with variation in soil characteristics. For example, in South Dakota, sandy soils support a higher abundance of Tenebrionidae than clayey soils (Calkins & Kirk, 1975). In South African mountains, tenebrionid species density is positively associated with clay percentage and soil pH. Differences in soil type and pH also explain variations in carabid abundance (Hosoda, 1999; Botes *et al.*, 2007). In general, soils rich in nutrient minerals with high water retention capacity usually contain a more numerous, more diversified mountain fauna than those with few minerals and low water retention capacity (Mani, 1968). We evaluated how the richness and abundance of beetles were associated with water pH, NaF pH, texture, bulk density, gravel percentage, organic matter percentage and soil moisture.

MATERIALS AND METHODS

Area of study

The study was conducted within the Nahuel Huapi National Park in north-western Patagonia (Argentina) (41º08′ S, 71º02′ W; Fig. 1). Average temperature during the summer season is 18 °C and, during winter, 4 °C. Most precipitation within the region occurs during the autumn and winter and strongly decreases along the west–east gradient, which accounts for the presence of Subantarctic forests towards the west, and the Patagonian steppes towards the east (Paruelo *et al.*, 1998). Similarly, above 1600 m a.s.l. changes in plant species composition and the physiognomy of plant communities are associated with the transition between the Subantarctic forests and the high Andean steppes.

We selected five mountains: (1) La Mona, located towards the western humid end of the precipitation gradient; (2) Pelado and (3) Challhuaco, towards the eastern drier end; and (4) López and (5) Bayo, in an intermediate position (Fig. 1).

Beetle sampling

We collected beetles using 486 plastic pitfall traps (diameter 9 cm, depth 12 cm), arranged in fifty-four 100 m² grid plots of nine traps. In each mountain, 9 to 12 plots were established at intervals of about 100 m of elevation, which allowed sampling of ≥ 90% of the total elevational range on each mountain. The geographical position of each plot was recorded using Global Positioning System (GPS) technology.

Pitfall traps were filled with diluted propylene glycol (40%) and a drop of soap. Traps were operative for 7 days during four sampling periods (January and March 2005 and 2006) in the southern summer season, resulting in a total of 28 trap days. Our catches were obtained during the middle and end of the plant growing season, which included the main period of insect activity (see Ruggiero *et al.*, 2009; Garibaldi *et al.*, 2011). Pitfall traps are useful to estimate relative activity-density of species rather than absolute abun-

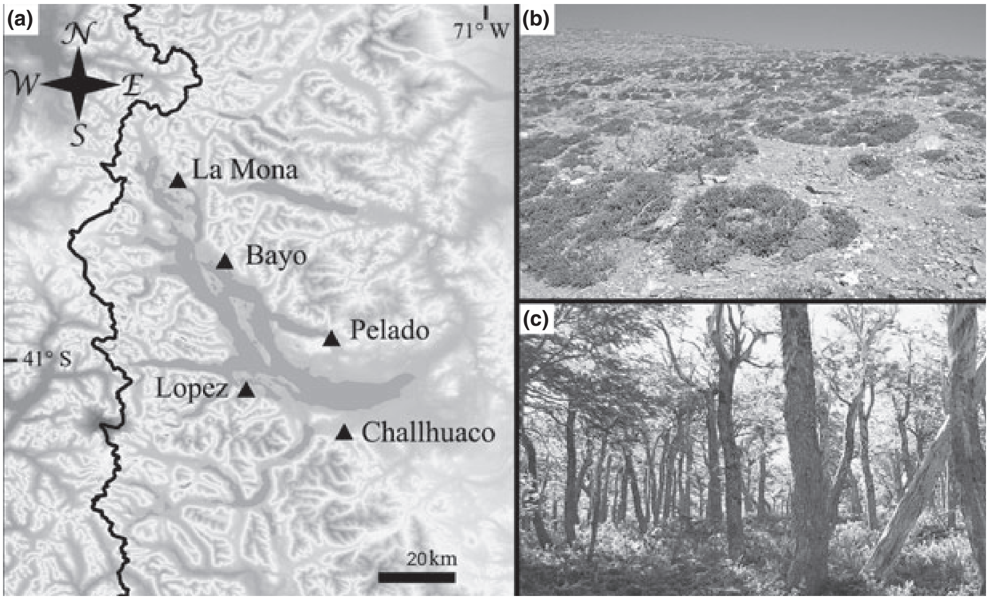

Figure 1 (a) Map of the study area in north-western Patagonia indicating the location of the five mountains: Pelado (40º56′ S, 71º20′ W, mean annual precipitation at the base, PP: 1220 mm, sampled elevation range, SER: 800–1800 m, proportion of the total elevational gradient sampled: 100%, number of 10 m × 10 m sampling plots, *n* = 11); Challhuaco (41º13′ S, 71º19′ W, PP: 1100 mm, SER: 900–2000 m, 95%, *n* = 12); Bayo (40º45′ S, 71º36′ W, PP: 1650 mm, SER: 900–1782 m, 100%, *n* = 9); López (41º05′ S, 71º33′ W, PP: 1730 mm, SER: 800–1800 m, 90%, *n* = 11); and La Mona (40º34′ S, 71º42′ W, PP: 1930 mm, SER: 800–1800 m, 100%, *n* = 11). (b) Example of a high Andean steppe habitat. (c) Example of a forest habitat.

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dance; hence, to obtain reliable, comparable estimates of relative abundance in different habitats we employed the recommended strategy of using the sum of pitfall catches over the whole period of beetle activity in different years (Baars, 1979). Within each plot, we pooled the contents of the nine pitfalls into one sample. We preserved all samples in 80% ethyl alcohol for taxonomic identification. Whenever possible, we identified beetles to species, otherwise to morphospecies. Taxonomic identifications were checked by expert taxonomists (see Acknowledgements and Appendix S1a in the Supporting Information).

Estimation of species richness and abundance of individuals

The local beetle species richness (RICH_{raw}) denotes the total number of species caught on each plot over the four sampling periods. We used EcoSim 7.72 (Gotelli & Entsminger, 2006) to compute individual-based rarefaction ($\text{RICH}_{\text{rare}}$) within the 'forests' ($n = 36$ plots, including the forests and moist shrublands, rarefied to 73 individuals), and the 'steppes' ($n = 18$ plots, including the high-Andean steppes and dry shrublands, rarefied to 16 individuals) (see Werenkraut & Ruggiero, 2013, for habitat details). We counted all individuals captured on each plot over the four sampling periods ($\text{ABUN}_{+\text{Staph}}$), and the total number of individuals per plot excluding Staphylinidae ($\text{ABUN}_{-\text{Staph}}$). We did not interpolate the presence of beetle species between the highest and lowest elevations at which they were collected because this could suggest a mid-elevation peak in species richness where it does not exist (Grytnes & Vetaas, 2002).

Estimation of environmental variables

Thermal limitation

Summer minimum daily temperature (TMIN) and summer mean daily temperature range (TVAR) were estimated at each plot using 54 HOBBO H8 loggers (Onset Computer Corporation, MA, USA). Slope exposure (SUN) at each plot represented the local variation in sunshine exposure, from high to low sunshine exposure: SUN = N > NW > NE > W > E > SW > SE > S (see Appendix S1b).

Productivity

Data on enhanced vegetation index (EVI) at 250 m × 250 m pixel resolution was obtained every 16 days during the 2005–06 growing seasons from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite (ORNL DAAC, 2008). We estimated the aboveground cover of herbs (HERBCOV), shrubs (SHRUBCOV), tree canopy cover (TREECOV), and litter biomass (LITTER) on each 10 m × 10 m plot.

EVI showed a positive correlation with TREECOV across the entire elevational gradient ($n = 54$, Spearman's rank correlation coefficient, $r = 0.59$, $P = 2.27 \times 10^{-6}$), being less correlated with SHRUBCOV ($r = 0.29$, $P = 0.03$), and LITTER ($r = 0.40$, $P = 0.02$); it was not correlated with HERBCOV ($r = 0.20$, $P = 0.14$). Within habitats, EVI was not correlated with plant cover variables with the exception of HERBCOV in the steppes ($r = 0.50$, $P = 0.03$). Hence, we conducted separate tests based on vegetation cover (productivity-1) or satellite derived vegetation index (productivity-2) (see Appendix S1b).

Water–energy dynamics

We extracted total potential evapotranspiration (PET) and summer (December–March) precipitation (PREC) at each plot from high resolution (30 arc-seconds) digital databases (PET based on the Hargreaves method: Trabucco & Zomer, 2009; PREC: Hijmans *et al.*, 2005). In our study area, a considerable proportion of precipitation falls in the form of snow during winter, mainly at high elevations (> 1200 m a.s.l.). The water–energy dynamics hypothesis emphasizes the role of water in the liquid state; we therefore used summer precipitation as a proxy for rainfall (see Appendix S1b).

Environmental heterogeneity

We counted the number of species of trees (TREESP), shrubs (SHRUBSP) and herbs (HERBSP), and the angle of slope (SLOPE) at each 10 m × 10 m plot (see Appendix S1b).

Soil characteristics

We estimated water pH (PH.H2O), NaF pH (PH.VOLC), texture (TEXTURE), bulk density (BULDEN), gravel percentage (GRAVEL%), organic matter percentage (OM%) and soil moisture (HUM%) for each 10 m × 10 m plot (see Appendix S1b).

Analysis of data

Assessment of the SRER and AER

We identified the shape of the SRER based on data from the five mountains taken together (regional), and also separately for each mountain. We regressed data of richness (y) on elevation (x), and evaluated the likelihood of the data, given four different models: (1) linear decreasing (DEC) pattern, ($y = a - bx$) where a is the intercept and $-b$ is the slope; (2) a low-plateau pattern (L-PL; rather constant high richness at low elevations followed by a decrease in richness), $y = a + bx^2$ and $b < 0$; (3) hump-shaped pattern (H-SH), $y = a + bx + cx^2$, where a is the intercept, and b and c are regression coefficients, and $c < 0$; and (4) lack of an elevational pattern (NP), $y = a$ (details in Werenkraut & Ruggiero, 2011).

The model with the lowest AIC_c (Akaike's information criterion corrected for small samples; Burnham & Anderson, 2002) was the best model supported by the data. We compared the size of the increments of information loss for each i remaining

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model to the estimated best model ($\Delta_i = \mathrm{AIC}_{c(i)} - \mathrm{AIC}_{c(\min)}$); models with $\Delta_i > 2$ of the best model have considerably less support, and those with $\Delta_i < 2$ of the best model were equally likely (Burnham & Anderson, 2002).

We also identified the SRER visually following McCain's (2009) criteria. We applied a loess smoothed fit on each dataset at 0.5 degrees of smoothing and two steps to verify whether the shape of the SRER was indeed unimodal or linear (Cusens *et al.*, 2012). We looked for a consensus between the visual, statistical and loess smoothed fit methods to identify the final shape (Werenkraut & Ruggiero, 2011). Because we lack a priori predictions of the AER, we applied only the loess smoothed fit to the abundance data.

Associations of species richness and abundance of individuals with environmental variables

We tested the associations predicted by the hypotheses for the full gradient (54 sampling plots), then separately for the steppes and the forests, for all estimations of richness and abundance ($\mathrm{RICH}_{\mathrm{raw}}$, $\mathrm{RICH}_{\mathrm{rare}}$, $\mathrm{ABUN}_{+\mathrm{Staph}}$ and $\mathrm{ABUN}_{-\mathrm{Staph}}$). We followed three steps:

1. Selection of the best model to represent each single hypothesis. We conducted an exhaustive search of the best statistical model (with the lowest AIC_c) for each of the six environmental hypotheses and each dataset (full gradient, forests, steppes) (Burnham & Anderson, 2002).

2. Selection of the best variables within each hypothesis. We conducted model averaging and used the Akaike weight (w_i) to estimate the relative importance of each i predictor variable within each hypothesis (Burnham & Anderson, 2002).

3. Elaboration of a final composite ecological model. For each dataset, we elaborated a composite model, combining the most important variables ($w_i > 0.5$) in the best single hypothesis supported by the data with the single most important variable, i.e. the one with the highest w_i, of each of the other hypotheses (for details see Appendix S2).

We used SAM 4 (Rangel *et al.*, 2010) to evaluate whether the presence of spatial autocorrelation in our original data introduced statistical bias in the overall statistical analysis (Diniz-Filho *et al.*, 2003; Appendix S3). We conducted variation partitioning to quantify the proportion of the richness and abundance variation explained by: (1) environmental factors independently of elevation; (2) shared effects of environmental factors and elevation; this would indicate whether environmental factors are related to elevation just as richness and abundance are, hence the direct causal links between environmental factors and beetle richness and abundance could not be untangled; (3) 'effects' of elevation alone, which represent the effect of other unmeasured factors; and (4) unexplained variation (e.g. Borcard *et al.*, 1992; Appendix S3).

RESULTS

We collected 24,783 beetles. Almost half (12,365) were classified into 321 species/morphospecies and 52 families (see Appendix S1a). The remaining individuals (12,418) belonged to Staphylinidae, which could not be identified beyond family level. RICHraw ranged from 4 (1800 m a.s.l.) to 37 (1300 m a.s.l.) on López, from 10 (1700 m a.s.l.) to 38 (1400 m a.s.l.) on Pelado, from 9 (1600 m a.s.l.) to 52 (900 m a.s.l.) on Bayo, from 11 (1700 m a.s.l.) to 68 (1200 m a.s.l.) on La Mona, from 9 (1900–2000 m a.s.l.) to 30 (1400 m a.s.l.) on Challhuaco. The number of individuals ($\mathrm{ABUN}_{-\mathrm{Staph}}/\mathrm{ABUN}_{+\mathrm{Staph}}$) ranged from 24/25 (1800 m a.s.l.) to 490/1862 (1500 m a.s.l.) on López, from 16/20 (1700 m a.s.l.) to 863/1637 (1500 m a.s.l.) on Pelado, from 18/25 (1600/1700 m a.s.l.) to 548/768 (900 m a.s.l.) on Bayo, from 76/81 (1700 m a.s.l.) to 664/1865 (1200/1500 m a.s.l.) on La Mona, from 20/23 (2000 m a.s.l.) to 239/619 (1400 m a.s.l.) on Challhuaco.

Assessment of the SRER and AER

The SRER and AER on the five mountains taken together could not be easily assigned to a shape, although they tended to follow either an H-SH pattern or a low-plateau pattern (L-PL = high richness at low elevations followed by an elevational decrease; McCain, 2009) (Table 1, Figs 2 & 3). Data on the five mountains taken separately suggested that Pelado

Table 1 The shape of the epigaeic beetle species richness–elevation relationship (SRER) on five mountains in north-western Patagonia based on the statistical and visual methods and final shape after consensus. We used bold to highlight the AIC_c (corrected Akaike information criterion) values of models best supported by our data. Any model with a difference of information loss (Δ_i) < 2 of the best model was considered equally likely for a particular dataset. Number of sampling plots (n) for the Regional scale and for each mountain: Regional, n = 54; López, n = 11; Pelado, n = 11; Bayo, n = 9; La Mona, n = 11; Challhuaco, n = 12. NP, lack of an elevational pattern; DEC, linear decreasing pattern; H-SH, hump-shaped pattern; L-PL, low-plateau pattern.

	Statistical				Visual	Loess smoothed fit	Consensus
Methods	NP	DEC	L-PL	H-SH			
Regional	438.02	421.63	418.33	**413.21**	H-SH	L-PL	H-SH/L-PL
López	86.18	87.62	86.57	**81.41**	H-SH/L-PL	L-PL	H-SH/L-PL
Pelado	**84.81**	88.31	87.89	**85.34**	H-SH	H-SH	H-SH
Bayo	78.43	**70.44**	**68.97**	73.96	DEC	DEC	DEC
La Mona	98.26	90.94	**88.84**	**89.58**	H-SH	L-PL	H-SH/L-PL
Challhuaco	82.00	81.71	80.41	**75.42**	H-SH	H-SH	H-SH

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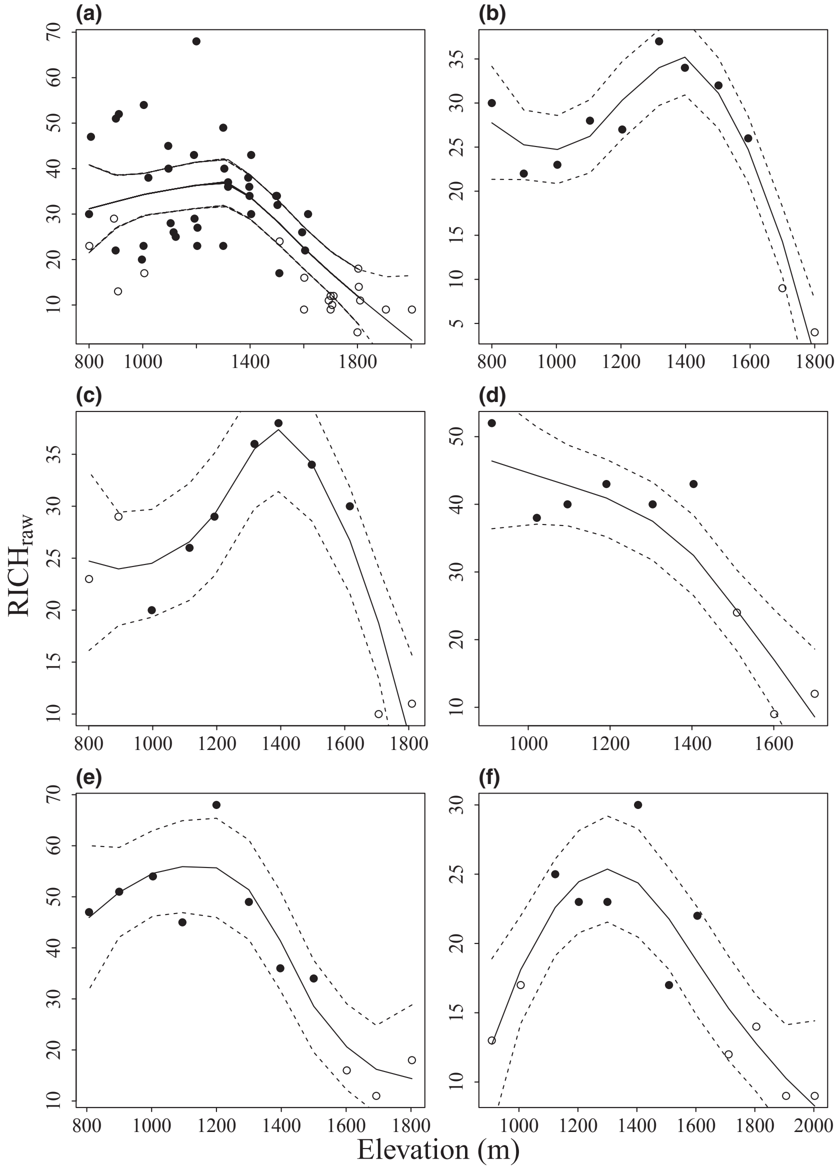

Figure 2 Elevational variation in the raw species richness (RICH_{raw}) of epigaeic mountain beetles (excluding Staphylinidae), shown for (a) the full gradient (n = 54 sampling plots), and for the five mountains analysed separately in north-western Patagonia: (b) López (n = 11), (c) Pelado (n = 11), (d) Bayo (n = 9), (e) La Mona (n = 11), and (f) Challhuaco (n = 12). Filled circles indicate forests, and open circles indicate steppes. On each mountain, the n 10 m × 10 m sampling plots of nine pitfall traps were established at about 100 m of elevation intervals along the total sampled elevation range (SER). Total number of individuals caught (excluding Staphylinidae) per site from the base to the summit of each mountain: López (98, 91, 223, 83, 73, 188, 390, 490, 416, 54, 24; SER = 800–1800 m), Pelado (192, 249, 318, 185, 100, 173, 332, 863, 689, 16, 39; SER = 800–1800 m), Bayo (548, 513, 266, 352, 194, 150, 63, 18, 21; SER = 900–1782 m), La Mona (466, 283, 284, 487, 664, 340, 410, 444, 116, 76, 221; SER = 800–1800 m), Challhuaco (40, 199, 85, 91, 151, 239, 87, 81, 40, 77, 53, 20; SER = 900–2000 m).

and Challhuaco supported H-SH patterns, López and La Mona supported either an H-SH or a L-PL pattern and Bayo showed a linear decreasing (DEC) pattern (Table 1, Fig. 2). The AER followed an H-SH pattern for all mountains except Bayo. Excluding or including the Staphylinidae in these analyses did not alter the overall shape of the AER (compare Fig. 3 and Fig. S3 in Appendix S1b).

At the regional scale, the variation in abundance accounted for about 60% of the variation in richness, although the relationship was nonlinear (Fig. 4a). Richness increased linearly with abundance in Bayo, La Mona and Challhuaco, but showed a weak association in López and Pelado (Fig. 4b–f).

Associations between species richness and abundance of individuals with environment

Across the full gradient, the productivity-1 hypothesis was the most supported single explanation to account for the SRER and AER, although composite models that combined productivity variables with other environmental components were better supported by our data (Table 2, compare AIC_{c} in Table S2a,b in Appendix S2). RICH_{raw} increased linearly with the increase in plant cover (TREECOV and SHRUBCOV); it decreased in sites with high LITTER, and showed an optimal (= nonlinear) relationship with EVI (Table 2, Table S2c in Appendix S2). The increase in HERBCOV, TREECOV and PET in combination with the decrease in LITTER, HERBSP and GRAVEL% most likely accounted for the increase in abundance (Table 2, Table S2a–c in Appendix S2).

In the forests, RICH_{raw} increased linearly with PREC, and showed an optimal relationship with PET as the water–energy dynamics hypothesis predicts; it also showed a negative association with PH.VOLC. $\text{RICH}_{\text{rare}}$ increased with TVAR and SHRUBSP, and showed an optimal relationship with PET (Table 2, Table S3c in Appendix S2). $\text{ABUND}_{-\text{Staph}}$ responded positively to the increase of HERBCOV and TREECOV and

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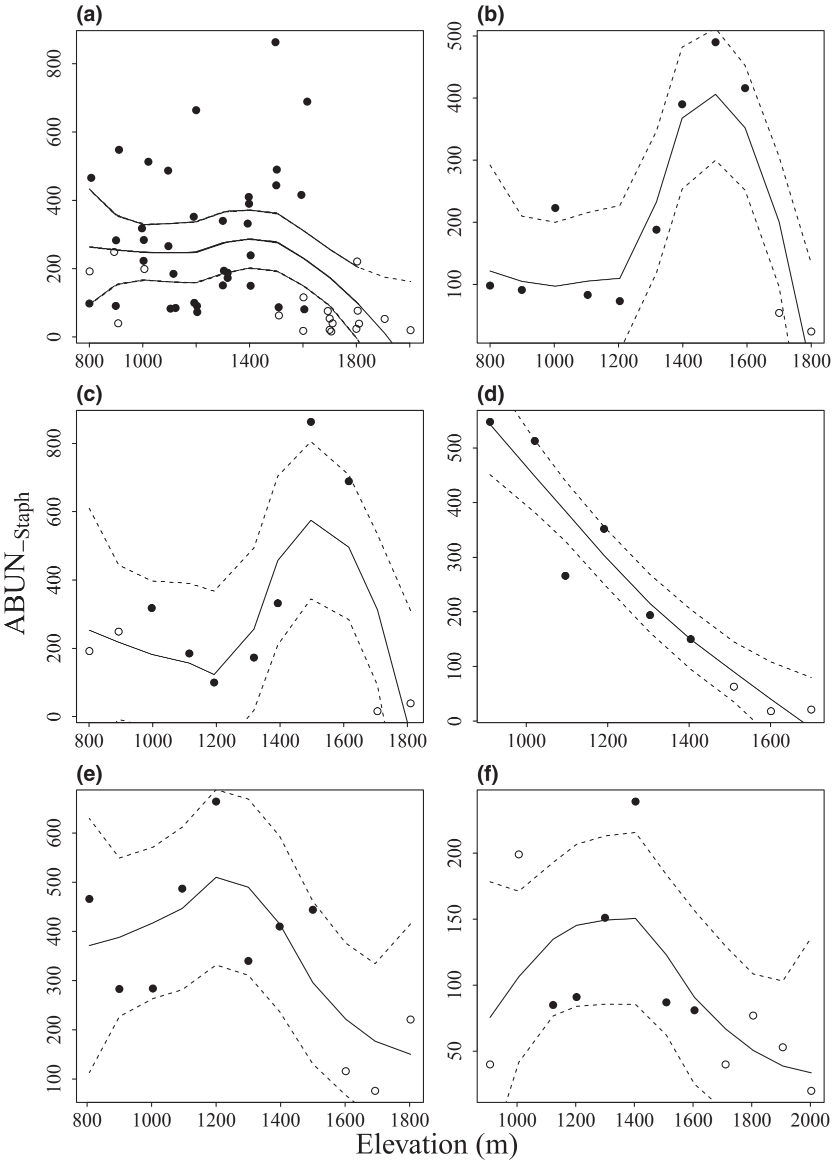

Figure 3 Elevational variation in abundance excluding Staphylinidae ($ABUN_{-Staph}$) of epigaeic mountain beetles in north-western Patagonia, shown for (a) the full gradient (n = 54 sampling plots), and for the five mountains analysed separately: (b) López (n = 11), (c) Pelado (n = 11), (d) Bayo (n = 9), (e) La Mona (n = 11), and (f) Challhuaco (n = 12). Filled circles indicate forests, and open circles indicate steppes. On each mountain, the n 10 m × 10 m sampling plots of nine pitfall traps were established at about 100 m of elevation intervals along the total sampled elevation range (SER). See Fig. 2 for number of individuals.

decreased with LITTER. The $ABUND_{+Staph}$ decreased with an increase in TVAR, TMIN and GRAVEL% (Table 2, Table S3a–c in Appendix S2).

In the steppes, richness increased with PET ($RICH_{raw}$) or EVI ($RICH_{rare}$) but decreased with HUM%. $ABUN_{-Staph}$ suggested an optimal relationship with EVI, and $ABUN_{+Staph}$ increased locally with PET (Table 2, Table S4a–c in Appendix S2).

Our results were not seriously affected by the presence of spatial autocorrelation in the original variables (Fig. S4 in Appendix S3). The partition of variation confirmed that local effects of environment, independently of elevation, were important in accounting for the SRER and AER, most strongly across the full gradient and within the forests; elevational variation in richness and abundance independently of the environment was negligible, which confirmed the adequacy of the selected environmental predictors to account for the SRER and AER (Fig. 5, Table S5 in Appendix S3).

DISCUSSION

The shape of the SRER and AER

We confirmed the existence of different forms in the shape of SRERs and AERs for arthropods (Werenkraut & Ruggiero, 2011): hump-shaped patterns were unequivocally supported in Pelado and Challhuaco, and a decreasing pattern was found on Bayo. There was more idiosyncratic variation on a regional scale and on López and La Mona. Given that we applied quite standardized sampling methods throughout, and sampled over 90% of the total elevational extent these results were unlikely to have been influenced by methodological effects (Rahbek, 2005).

McCain (2007, 2009) predicts a hump-shaped SRER for dry mountains where temperature decreases linearly with elevation and water availability shows a peak at intermediate elevations, and a linear decreasing pattern for humid

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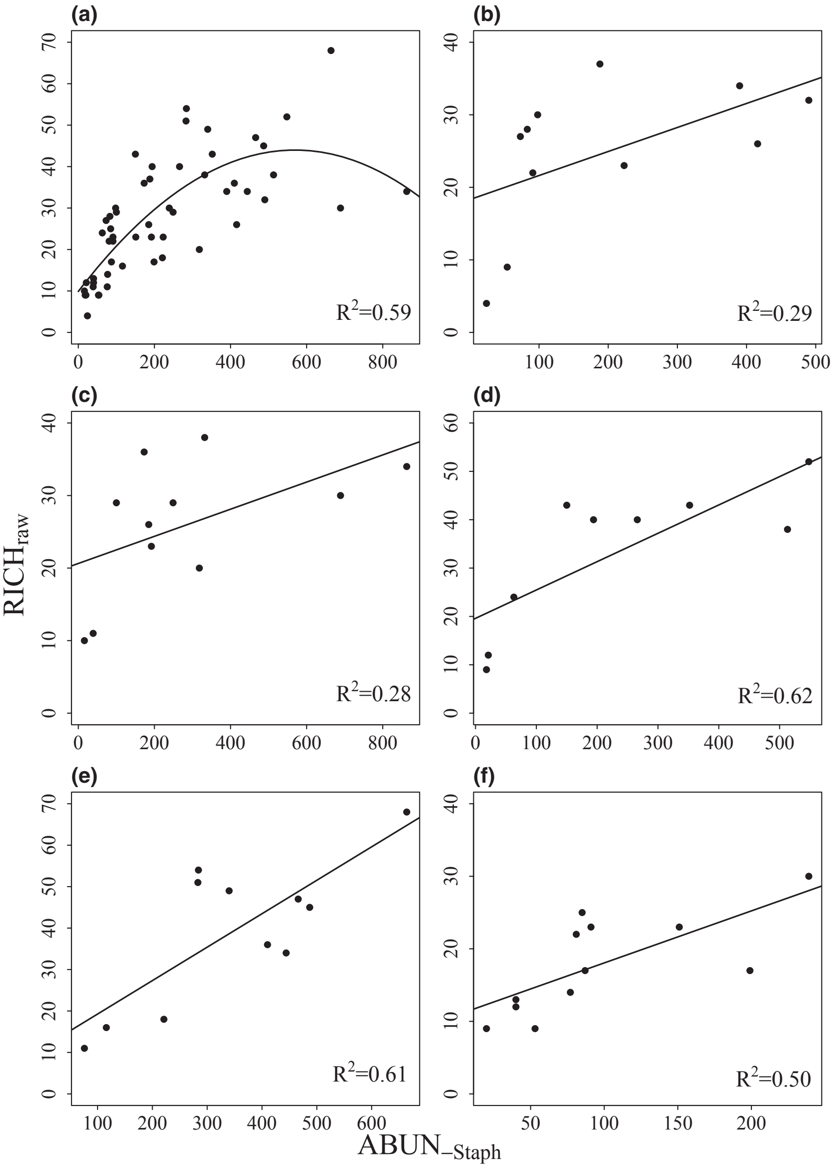

Figure 4 The relationship between abundance excluding Staphylinidae ($\text{ABUN}_{-\text{Staph}}$) and raw richness ($\text{RICH}_{\text{raw}}$) of epigaeic mountain beetles in north-western Patagonia, for (a) the full gradient (n = 54 sampling plots), and for the five mountains analysed separately: (b) López (n = 11), (c) Pelado (n = 11), (d) Bayo (n = 9), (e) La Mona (n = 11), and (f) Challhuaco (n = 12). On each mountain, the n 10 m × 10 m sampling plots of nine pitfall traps were established at about 100 m of elevation intervals along the total sampled elevation range (SER). See Fig. 2 for number of individuals.

mountains where both temperature and water decrease linearly with elevation. In our study, the elevational variation in energy and water variables was less consistent (Table 3, Fig. S1a in Appendix S1b); however, TMIN decreased with decreasing elevation on La Mona between 1000 and 800 m, and TVAR increased over this same elevational range in correspondence with the decrease in species richness; other mountains showed a low plateau or some degree of variability at the lowest elevations (Table 3, Fig. S1a in Appendix S1b). On the other hand, precipitation (PREC) decreased linearly with elevation on all mountains, probably reflecting the regional climatic conditions. The proportion of organic matter (OM%), another indicator of water availability (Bot & Benites, 2005), did show a tendency to peak at intermediate elevations on those mountains showing hump-shaped SRERs, whereas it decreased linearly where SRERs showed a negative pattern (Table 3). EVI suggested a similar hump-shaped pattern on Pelado and Challhuaco and showed a low plateau or some variability at lowest elevations on the remaining mountains (Table 3, Fig. S1 in Appendix S1b).

The presence of sharp habitat discontinuities (forests versus steppes) may play a predominant role in accounting for differences in the shape of the SRER. It is interesting that hump-shaped patterns were found only on Pelado and Challhuaco, which harbour shrubland-steppes at the base (Fig. 2). Thus, although diversity theories rely mostly on the role of continuous variables or combinations of them to account for the SRER, these functional associations could be more difficult to establish where habitat type changes abruptly on environmental gradients; for instance, the presence of forests implies an increase in plant cover coupled with higher allocation to woody biomass, which often occurs when water stress decreases and carbon fixation is enhanced across precipitation gradients (Kitzberger, 2012). Hence, the effects of habitat type and continuous functions of environment on richness may be deeply intermingled.

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Table 2 Summary of the environmental variables included in the final ecological models to explain the elevational variation in species richness and abundance of epigaeic mountain beetles in north-western Patagonia. Bold font is used to highlight the single hypothesis most supported by our data. We indicate whether the association of each environmental predictor and richness and abundance was positive (+) or negative (−). Those associations with a sign opposite to the original prediction are shown in italics. RICH$_{raw}$ = raw species richness, RICH$_{rare}$ = rarefied species richness, ABUND$_{-Staph}$ = abundance excluding Staphylinidae, ABUND$_{+Staph}$ = total abundance, including Staphylinidae. Variables: TMIN, minimum daily temperature; TVAR, mean daily temperature range; HERBCOV, herb cover; SHRUBCOV, shrub cover; TREECOV, tree canopy cover; LITTER, litter biomass; EVI, enhanced vegetation index; PREC, summer precipitation; PET, potential evapotranspiration; HERBSP, herb species; SHRUBSP, shrub species; PH.VOLC, NaF pH; GRAVEL%, gravel percentage; HUM%, soil moisture.

Response variable	Final ecological model: hypotheses involved	Final ecological model: more important variables
FULL GRADIENT		
RICH$_{raw}$	**Productivity 1**/Productivity 2	TREECOV (+), SHRUBCOV (+), *LITTER (−)*, *EVI^2 (−)*
ABUN$_{-Staph}$	**Productivity 1**/Energy/Heterogeneity/Soils	TREECOV (+), HERBCOV (+), *LITTER (−)*, PET (+), *HERBSP (−)*, GRAVEL (−)
ABUN$_{+Staph}$	**Productivity 1**/ Heterogeneity/Soils	TREECOV (+), *HERBSP (−)*, GRAVEL (−)
FOREST		
RICH$_{raw}$	**Water–Energy**/Soils	PREC (+), *PET^2 (−)*, *PET (−)*, PH.VOLC (−)
RICH$_{rare}$	**Energy**/Thermal limitation/Heterogeneity	TVAR (+), *PET^2 (−)*, SHRUBSP (+)
ABUN$_{-Staph}$	**Productivity 1**	TREECOV (+), HERBCOV (+), *LITTER (−)*
ABUN$_{+Staph}$	**Thermal limitation**/Soils	TVAR (−), *TMIN (−)*, GRAVEL (−)
STEPPE		
RICH$_{raw}$	**Energy**	PET (+)
RICH$_{rare}$	**Soils/**Productivity 2	HUM% (−), EVI^3 (+)
ABUN$_{-Staph}$	**Productivity 2**	*EVI^2 (−)*
ABUN$_{+Staph}$	**Energy**	PET (+)

The role of climatic effects

Across the full gradient, our study reinforced the idea that indirect climatic effects mediated through biological processes (e.g. productivity) are more important than direct climatic effects (thermal limitation) in accounting for the spatial variation in the richness and abundance of epigaeic insects (e.g. beetles: Ruggiero *et al.*, 2009; ants: Kaspari *et al.*, 2000a,b; Fergnani *et al.*, 2010). Across the full gradient, species richness increased as a nonlinear function of the total number of individuals; vegetation cover, and most strongly, tree cover, were the most important factors accounting for the variation in the richness and abundance of beetles in our analyses (see also Currie *et al.*, 2004; Ruggiero *et al.*, 2009).

The replacement of vegetation types at the Subantarctic–Patagonian transition could imply a shift in the relative importance of water and energy variables, as previously shown for the latitudinal diversity gradient (Hawkins *et al.*, 2003). The forests analysed separately showed a positive effect of tree canopy cover and herb cover only on beetle abundance. Local variation in richness was better accounted for by a combination of water–energy variables in combination with soil attributes and shrub species richness. This confirms that productivity variables tend to become less explanatory with decreasing extent (Field *et al.*, 2009). The enhanced vegetation index was not associated with canopy cover within the forests. Thus, the association between canopy cover and abundance within the forests might be mediated by mechanisms other than productivity. One possibility is that an increase in forest canopy cover may promote the formation of small microhabitats at ground level, creating different environmental conditions that affect the abundance and distribution of epigaeic arthropods (e.g. Coleoptera: Niemelä *et al.*, 1996; spiders: Ziesche & Roth, 2008). In the steppes, the richness and abundance of epigaeic beetles increased linearly with potential evapotranspiration but showed more complex associations with plant productivity (EVI). Here, plant productivity was mainly associated with herb cover, suggesting that key environmental factors driving the spatial variation in the richness and abundance of epigaeic beetles may differ across major habitats.

Throughout the present analysis, the local increase in litter biomass was negatively associated with richness and abundance, as previously reported for ants (Lassau & Hochuli, 2004) and carabid beetles (Rickard & Haverfield, 1965). Litter may be an impediment to beetle mobility, associated with lower pitfall catches (Rickard & Haverfield, 1965), and this suggests that movement, and hence foraging behaviour, is more efficient in less complex habitats (e.g. Kaspari & Weiser, 1999; Lassau *et al.*, 2005). The presence of dense vegetation at ground level is also known to reduce chances of falling into pitfall traps (e.g. Melbourne, 1999); however, across the full gradient and within the forests, herb cover was positively associated with richness and abundance.

Minimum temperature and daily temperature range were equivocally associated with richness and abundance. Owing to harsh winter climatic conditions and several logistic limitations, we were unable to obtain local temperature records throughout the year; however, in mountains at tropical latitudes, a positive association between temperature and

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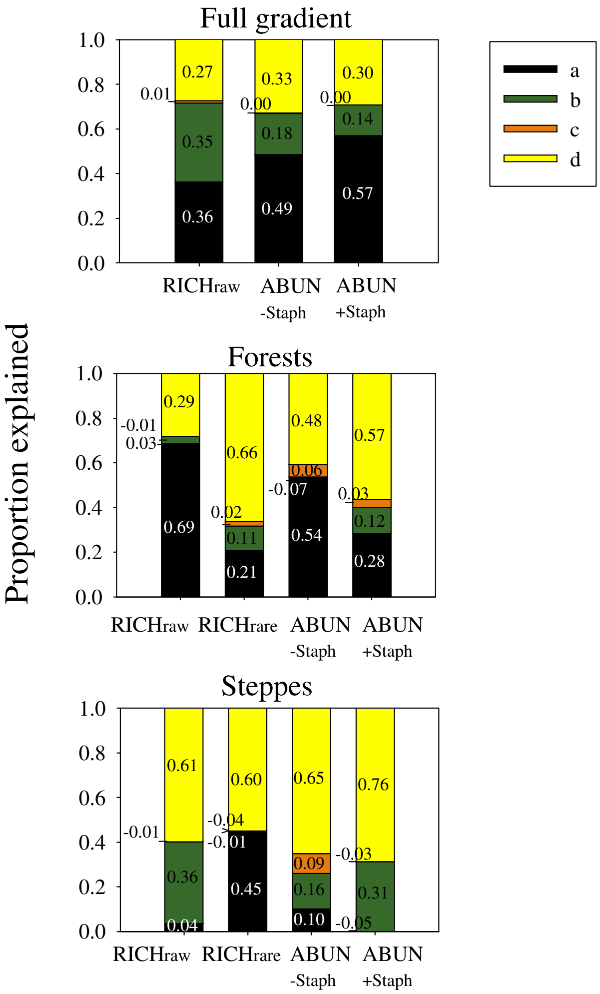

Figure 5 Proportion of richness and abundance variation of epigaeic mountain beetles in north-western Patagonia, explained by (a) the subset of environmental predictors in the best ecological model independently of elevation, (b) shared effects of elevation and environmental predictors; this component of variation may reflect either direct or indirect causal links between diversity and environment, (c) spatial variation accounted for by elevation, independently of environmental variables, and (d) unexplained variation. RICH$_{raw}$ = raw species richness, RICH$_{rare}$ = rarefied species richness, ABUND$_{+Staph}$ = abundance of epigaeic beetles including Staphylinidae, ABUND$_{-Staph}$ = abundance of epigaeic beetles excluding Staphylinidae.

Table 3 Shape of the elevational relationship for different variables on each of the five mountains studied in north-western Patagonia (Argentina). Relationships: ∩ = hump-shaped, U = u-shaped, ‾\ or _/ = low elevation plateau becoming negative or positive, \ = negative, / = positive, ~ = none or complex. Variables: TVAR, mean daily temperature range; TMIN, minimum daily temperature; TREECOV, tree canopy cover; LITTER, litter biomass; EVI, enhanced vegetation index; OM%, proportion of organic matter; HUM%, soil moisture; BULDEN, bulk density. The remaining variables showed no variability or a complex pattern on all mountains.

Variable	López	Pelado	Bayo	La Mona	Challhuaco
SRER	‾\ ∩	∩	\	‾\ ∩	∩
TVAR	~	U	_/	U	U
TMIN	‾\	‾\	\	‾\ ∩	~
TREECOV	∩	∩	\	‾\ ∩	∩
LITTER	‾\ ∩	∩	\	‾\ ∩	∩
EVI	‾\	∩	‾\	‾\ ∩	∩
OM%	~	∩	\	\	∩
HUM%	/	∩	‾\	‾\ ~	∩
BULDEN	_/ U	U	/	_/ U	U

harvestmen species richness and abundance was evident only when winter and summer temperatures were jointly analysed (e.g. Almeida-Neto *et al.*, 2006). It may be useful to consider extreme winter temperatures in future studies of insect diversity patterns in our study region.

The role of environmental heterogeneity

We found very little evidence in support of this hypothesis, which confirms its secondary importance in explaining richness gradients (Field *et al.*, 2009). Beetle species could perceive environmental heterogeneity at different spatial scales in association with differences in their body size (Levin & Pacala, 1997; Mech & Zollner, 2002). Some taxonomic groups respond more to the heterogeneity of vegetation structures (e.g. leaf type, growth type, organization of leaves) rather than to plant taxonomic diversity (e.g. Brose, 2003). Nonetheless, in *Nothofagus pumilio* forests, the elevational decrease in the abundance of folivore insects was not influenced by a shift in leaf traits but probably reflected the direct impact of decreased mean temperatures on insect populations at higher elevations (Garibaldi *et al.*, 2011). Future studies are needed to evaluate the role of plant diversity in determining the diversity of ground-dwelling beetles in these temperate habitats.

The role of soil suitability

Across the full gradient and in the forests, beetle abundance decreased with the increase in gravel percentage (GRAVEL %). The presence of gravel decreases the water-holding capacity and generates 'looser' soils (Paruelo *et al.*, 1988). Given that many coleopteran immature stages live underground, it is possible that an increase in the gravel percentage hinders the construction and maintenance of nests and/or larval survival of some species. An increase in gravel percentage could also represent an increase in environmental rugosity, which might increase the cost of moving over the ground for ground-dwelling beetles. This could result in

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lower pitfall catches, hence lower estimations of richness and abundance.

In the steppes, richness was negatively associated with soil moisture. High water content, combined with low temperatures, could have made high Andean habitats too hostile for ground beetles to survive, as previously found for termites in the Peruvian Andes (Palin *et al.*, 2010). Also, within the forests, species richness increased in sites with low volcanic influence in soil formation (PH.VOLC). This is intriguing because soils with a high volcanic influence in their formation are among the most productive in the world (Ugolini & Dahlgren, 2002). Soil acidification decreases litter decomposition rates, which may increase the available habitat and food for some insects, thus promoting an increase in species richness (e.g. Collembola: Loranger *et al.*, 2001); however, we did not find a correlation between soil acidity and organic matter, which should be corroborated in future studies.

We conclude that the replacement of low- and mid-elevation forests by the high Andean steppes plays a predominant role in accounting for the shape of the SRER and AER. A shift in the relative importance of productivity and energy variables in accounting for richness and abundance within the forests and steppes also suggests the interaction between habitat type and continuous functions of environment. Thus, decomposition of the SRER and AER into rather more homogenous subsets of data can be considered a kind of deconstruction (Marquet *et al.*, 2004), focused on macro-habitats, that could be useful in disentangling the role of different environmental factors underlying complex diversity gradients.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Taxonomic identification of taxa and estimation of environmental variables.

Appendix S2 Statistical analyses and the models fitted to the richness and abundance data.

Appendix S3 Assessment of spatial autocorrelation patterns, and variation partitioning.

BIOSKETCHES

Victoria Werenkraut is a postdoctoral researcher at Laboratorio Ecotono, INIBIOMA-CONICET/Universidad Nacional del Comahue. She is interested in spatial patterns in species richness and geographical distribution of insects in north-western Patagonia, Argentina.

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