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Beetle abundance–environment relationships at the Subantarctic–Patagonian transition zone

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Abstract. 1. The spatial variation in the abundance of individuals may be associated with the variation in environmental variables. The productivity hypothesis proposes that climate affects plant productivity, which may limit the abundance of beetles. The thermal-limitation hypothesis proposes the direct effect of ambient temperature may limit beetle abundance. We analysed the abundance of epigaeic beetles at the Subantarctic–Patagonian transition to test for these abundance–environment relationships.

2. We collected beetles using 450 pitfall traps within a ~150 × 150 km area representative of the Subantarctic–Patagonian transition. We used path analysis to evaluate the relationships between beetle abundance and plant cover, litter biomass, averaged minimum and daily temperature range, and mean annual precipitation. We used principal coordinates of neighbour matrices to model the spatial autocorrelation of the data.

3. The abundance of beetles increased strongly with tree canopy cover and less strongly with herb cover. The increase in shrub cover had a positive effect on beetle abundance in areas to the east of the transition, within the scrubland-steppe, but it has a negative effect on beetle abundance in areas to the west of the transition, within the forests. The association between beetle abundance and minimum daily temperature was negative or weak throughout. Increased temperature variation had a negative effect on beetle abundance.

4. We suggest that indirect positive climatic effects mediated through plant cover are important to account for the variation in beetle abundance, which favours the productivity hypothesis. Thermal limitation may operate locally through variation in daily temperature range.

Key words. Eigenvector-based spatial filtering, epigaeic beetles, Patagonian steppe, path analysis, productivity, Subantarctic forests, thermal limitation.

Introduction

Productivity and climate may regulate the geographical variation in the abundance of individuals through different mechanisms (Hawkins *et al*., 2003; Currie *et al*., 2004; Evans *et al*., 2005; Clarke & Gaston, 2006 for review). The amount of resources available to organisms, e.g. plant biomass, is known to limit local abundance and, in general, areas with greater resources support more individuals (e.g. Srivastava & Lawton, 1998; Hurlbert, 2004). However, the ambient temperature alone, or combined with water availability, may also be a key direct climatic determinant of the abundance of individuals (e.g. Turner *et al*., 1996; Clarke & Gaston, 2006 for discussion and examples). Nonetheless, few studies have focused on the analysis of these abundance–energy relationships (but see: Srivastava & Lawton, 1998; Kaspari *et al*., 2000; Hurlbert, 2004; Botes *et al*., 2007), and the evidence in support of a positive causal relationship from energy to the abundance of individuals at large spatial scales is not consistent (e.g. Currie *et al*., 2004). In the present study, we contributed to this area of research with evidence of the association of local beetle abundance with climate and productivity, at the transition between the Subantarctic and Patagonian subregions, in southern South America.

The transition zone between these biogeographical subregions represents one of the most pronounced environmental gradients in the world (Barros *et al*., 1983) with three distinct, dominant physiognomic units from west to east: forests, scrublands and steppes (Fig. 1) (Paruelo *et al*., 1998b). Changes in beetle composition and abundance parallel these environmental changes

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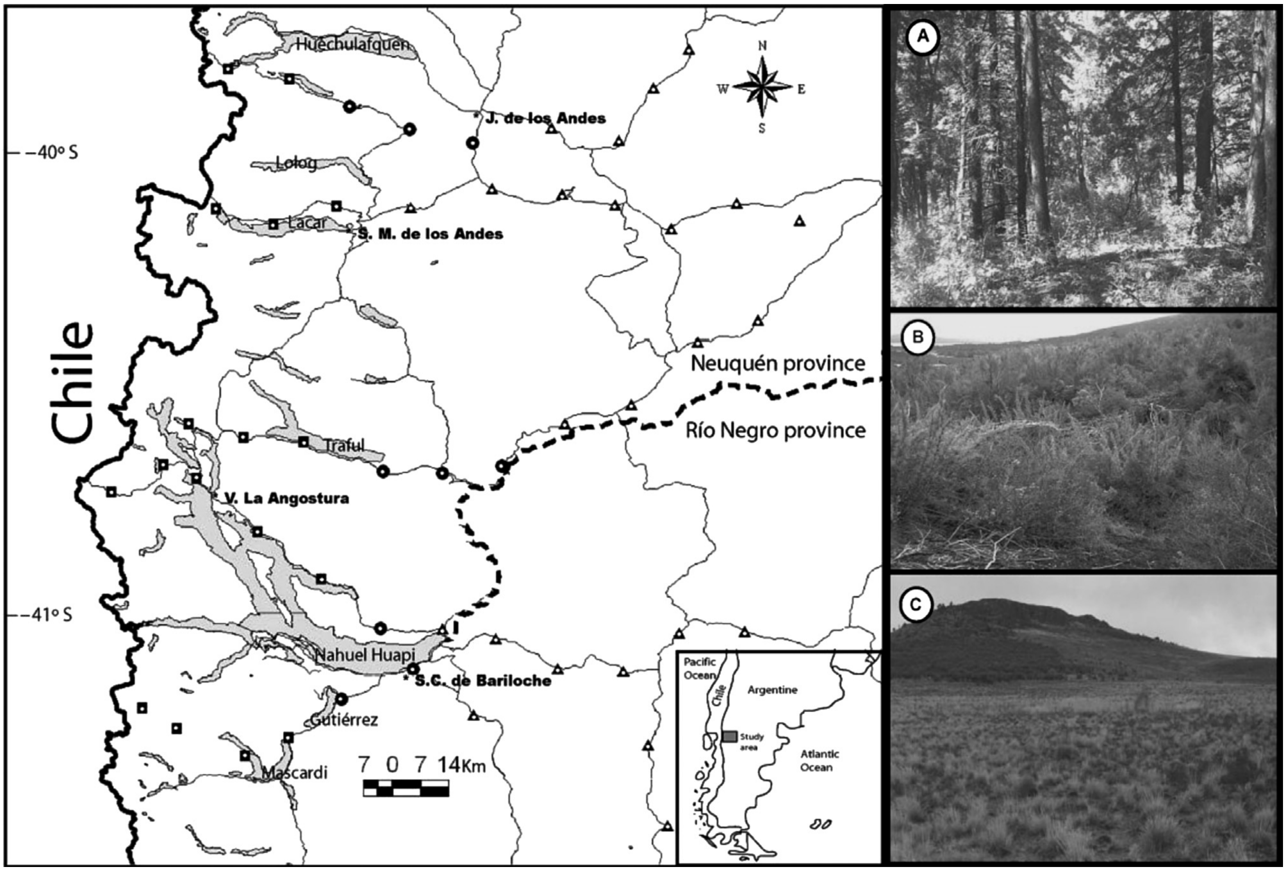


Fig. 1. Map showing locations of sampling plots within the (A) forests (black squares), (B) scrubland (black circles) and (C) steppe (black triangles). Note the presence of several glacial lakes in the west. The dashed line indicates the political limit between the Rio Negro and Neuquén provinces in Argentina. Other lines are roads.

(e.g. Sackmann *et al.*, 2006; Sackmann & Farji-Brener, 2006). Yet, detailed ecological analyses of the spatial variation in beetle abundance along this biogeographical transition are lacking. Epigaeic beetles may significantly respond to environmental changes associated with productivity gradients at the transition between biogeographical units (e.g. tenebrionids: Krasnov & Shenbrot, 1998). We examined the spatial variation in beetle abundance along the Subantarctic–Patagonian transition to test for ecological associations predicted by the productivity and thermal limitation hypotheses.

Hypotheses on abundance–environment relationships

The *productivity hypothesis* (Kaspari *et al.*, 2000; see also Hawkins *et al.*, 2003; Currie *et al.*, 2004) postulates that net primary productivity limits the abundance of individuals in the consumer trophic level, and climate strongly affects net primary productivity. As productivity is difficult to measure directly, we used vegetation cover as a surrogate to analyse the relationship between the abundance of beetles and net primary productivity. In general, vegetation cover provides a good measure of plant biomass (e.g. Mueller-Dombois & Ellenberg, 1974) that correlates strongly and positively with net primary productivity (e.g. Evans *et al.*, 2005). Flombaum & Sala (2007) tested the validity of these relationships for several plant species in the Patagonian steppes and showed that, here, vegetation cover is a good predictor of green biomass, aboveground net primary production, and total plant biomass. Variation in the amount of leaf litter may also have an effect on ground-dwelling beetles, influencing the availability of refuges from predation, foraging success, and providing additional resources for some herbivores (e.g. Stapp, 1997; Koivula *et al.*, 1999; Antvogel & Bonn, 2001; Sippola *et al.*, 2002; Laussau *et al.*, 2005; Mazía *et al.*, 2006). Together, vegetation cover and leaf litter biomass represent aspects of the productivity of habitats that may have a significant positive impact on beetle abundance (e.g. Niemelä & Spence, 1994; Antvogel & Bonn, 2001; Laussau *et al.*, 2005). Therefore, we expected an overall positive effect of vegetation cover and leaf litter biomass on the abundance of beetles.

The *thermal limitation hypothesis* (Kaspari *et al.*, 2000) proposes that the direct effect of temperature on insect development, growth, and behaviour regulates the abundance of individuals in an assemblage (e.g. *Strophingia*: Hodkinson *et al.*, 1999;

ground-nesting ants: Kaspari *et al*., 2000; ground-dwelling beetles: Mazía *et al*., 2006; Botes *et al*., 2007 and references therein). Here we expected an overall positive effect of increasing minimum daily temperature (T_{MIN}, see methods for a definition) on the abundance of beetles. We also explored whether temperature variability (T_{VAR}, see methods for a definition) affects beetle abundance. Because individuals would need to have either wider physiological tolerances or the ability to escape the extreme climatic conditions to withstand temperature variability (e.g. Addo-Bediako *et al*., 2000), we predicted that a local decrease in temperature variability might promote an increase in the local abundance of beetles.

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 Andes act as a barrier to the humid westerly airflow at these temperate latitudes causing greater amount and lower variability in precipitation in the Andean Cordillera compared to the eastern extra-Andean zones (Barros *et al*., 1983; Jobbágy *et al*., 1995; Paruelo *et al*., 1998a). The west–east gradient of precipitation is one of the main ecological controls of the change in the physiognomy of the vegetation from west to east. This involves the replacement of forests of *Nothofagus* species that grow at 1500–3500 mm of annual precipitation by semi-arid scrub vegetation and forests of *Austrocedrus chilensis* and *Nothofagus antarctica* that grow along the foothill zone at 1400–1800 mm of annual precipitation, and steppes, mainly composed of xerophytic shrubs and herbs that grow at 600–800 mm of annual precipitation towards the east (Cabrera & Willink, 1980; Paruelo *et al*., 1998a). Landforms and sediments created by glacial processes are also obvious throughout the region (Clapperton, 1993; Fig. 1).

Estimation of abundance and choice of environmental variables

Beetle abundance. We collected beetles using 450 plastic pitfall traps (diameter 9 cm, depth 12 cm) arranged in 50, 100-m^2 grid plots of nine traps. The plots were ~15 km apart, within a ~150 × 150 km area representative of the Subantarctic–Patagonian transition (Fig. 1). The geographical position of each plot was recorded using a global positioning system (GPS).

We nested two traps one inside the other to minimise ground disturbance while emptying traps, which can affect pitfall catches (e.g. carabid beetles: 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 8 days during three sampling periods in the southern spring and summer seasons (November 2004, January and March 2005). The temperature conditions in the Patagonia region during January and March (2005) were typified as 'normal' when compared to a long-term 1961–1990 temperature data (*Boletín Climatológico*, Volumen Anual 2005 at http://www.smn.gov.ar). There was, however, a deficit in precipitation during January 2005 (e.g. 3.2 mm of precipitation were recorded in Bariloche, compared to 22.2 mm recorded in the 1961–1990 data; *Boletín Climatológico*, Volumen XVII at http://www.smn.gov.ar). Our catches obtained over the beginning, middle, and end of the plant growing season, which included the main period of beetle activity, allowed minimising the effects of those extreme weather conditions.

To estimate the abundance of beetles at each of the 50 plots, we tallied the number of individuals caught per pitfall trap at each site and sampling event and calculated averages for each site over the three sampling periods (ABUND). Because a few traps were broken, we averaged the abundance estimation at each site over the total number of pitfalls that remained functional at the end of each sampling period.

Vegetation cover. We distinguished herbs (all vascular plants < 0.30 m in height), shrubs (all woody vascular plants between 0.30 and 2 m in height and < 10 cm in diameter breast height) and trees (all woody vascular plants > 2 m in height and > 10 cm in diameter breast height). We used a concave spherical densiometer to estimate the proportion of tree canopy cover in the 17 forest and 9 scrubland plots (i.e. the 24 steppe plots had no trees). 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. Then for each plot, we summed the four herb-cover values for a total of herb cover per metre squares.

Plant litter biomass. To obtain equivalent samples of litter biomass at each plot, we removed litter as much as was necessary to dig in the pitfall traps. We stored the removed litter in paper bags, and dried them to constant mass in a forced convection oven at 60 °C and weighed to estimate dry litter biomass (LITTER).

Climatic variables. We mounted one HOBO H8 logger (Onset Computer Corporation, MA, USA) on a pole fixed at the centre of each 10 × 10-m sampling plot to record the temperature at ground level every 2 h during the entire sampling season. A total of 745 readings spread over 62 days were obtained from the loggers. We extracted the maximum and minimum temperatures recorded each day to estimate the average minimum daily temperature (TMIN), and the average daily temperature range (TVAR) for each plot. We also estimated mean annual precipitation (PREC) for each plot by an interpolation from an isoline regional map (Barros *et al*., 1983).

Analyses of data

The mapping of the spatial variation in abundance and environmental variables. We generated isoline maps to model the spatial variation of each variable. We used the known values of each

Table 1. Variables associated with and predication of + (positive) or – (negative) relationships between ABUND and environment derived from the hypotheses considered by our model.

	Thermal limitation	Temperature variability	Productivity				
	TMIN	TVAR	TMIN	PREC	TREECOV	SHRUBCOV	HERBCOV
Direct	+	–	+ (on plant cover)		+	+	+
Indirect			+	+			
			Indirect > direct				

Direct, direct causal covariation; indirect, indirect causal covariation. See main text for variable definition.

variable at the 50 plots to generate a continuous surface of interpolated data over the total extent of the study area with the tension spline interpolation method applied by the Spatial Analyst extension of ARCVIEW 3.3. Note, however, that interpolated data were used here exclusively for visualisation purposes. All subsequent statistical analyses were conducted on the original data points. The total of 50 sampling plots was used for the analyses focused on the whole biogeographical transition. Separate analyses were conducted on the forests plots ($N = 17$); because the total number of plots within the scrubland ($N = 9$) was rather low, they were combined with the steppe plots ($N = 24$) to get a scrubland-steppe data set ($N = 33$) that was also analysed separately. The steppe and scrubland plots had a great similarity in floristic composition that also justified combining them in a single data set (see Speziale, 2006 for detailed analysis).

Test of abundance–environment relationships. A path diagram was used to summarise the relationships among variables derived from hypotheses proposed at the outset of the present analysis in a unique causal scheme. To 'test' indirectly the hypotheses proposed, the sign (positive/negative) and the magnitude of direct and indirect associations estimated by path coefficients (hereafter called 'effects') between the environmental variables and ABUND were compared with the predictions derived from each hypothesis. Specifically, the effects predicted by the hypotheses (summarised on Table 1) included in our path model were the following:

1 *Productivity hypothesis*: we tested for an effect of TMIN, TVAR and PREC on TREECOV, SHRUBCOV, HERBCOV and LITTER to represent changes in temperature and water availability that drive the spatial and temporal variation in primary productivity along the biogeographical transition (Paruelo *et al.*, 1998a, 1998b; Jobbágy *et al.*, 2002). Our model tested for the positive direct effect of TREECOV, SHRUBCOV, HERBCOV and LITTER on ABUND. We also tested for the direct positive effect of PREC on ABUND because this hypothesis predicts that the bottom-up control of PREC on ABUND through plant cover should be higher than its direct effects.

We did not test for reciprocal influences between climatic variables and plant cover because TMIN and TVAR had weak associations with TREECOV ($r_{\mathrm{TMIN}}^2 = 0.14$), SHRUBCOV ($r_{\mathrm{TMIN}}^2 < 0.01$, $r_{\mathrm{TVAR}}^2 = 0.10$) and HERBCOV ($r_{\mathrm{TMIN}}^2 = 0.07$, $r_{\mathrm{TVAR}}^2 = 0.21$). The only strong relationship of TREECOV with TVAR ($r^2 = 0.76$) along the whole gradient reflects an effect of macrohabitat because the steppes lack trees; however, the association was weak or absent within the forests ($r_{\mathrm{TVAR}}^2 < 0.01$).

2 *Thermal limitation hypothesis*: we tested for a direct positive effect of TMIN on ABUND, and a negative effect of TVAR on ABUND.

We assumed that TMIN, TVAR and PREC may be correlated. Because we did not have a priori hypotheses of the relationships between TREECOV, SHRUBCOV, HERBCOV, and LITTER, we included direct associations between them only if the analysis of covariance structure suggested that including such associations would significantly ($P < 0.05$) improve the fit of our model (e.g. a positive effect of TREECOV on LITTER, see results).

We used the PROC CALIS statement in SAS 9.1. for Windows to statistically test for relationships between the abundance of beetles and the environmental variables as proposed by our model (Hatcher, 1994; SAS Institute Inc., 2004). The CALIS procedure allows specifying the proposed theoretical model (path model) as a system of multiple linear equations (structural equations) that express the relationships among variables. Path coefficients are standardised regression coefficients that are estimated by the maximum likelihood method, and represent the magnitude of 'effect' or rate of change in a dependent variable that is associated with a one-unit change in another variable within the system while holding the other variables constant. The CALIS procedure determines whether the proposed theoretical model successfully accounts for the actual relationships observed among variables in the sample data (see e.g. Hatcher, 1994, SAS Institute Inc., 2004). We tested our model first for all plots (i.e. the entire biogeographical transition), and then separately for the forest and scrubland-steppe. We standardised all variables before analysis. Analyses based on raw variables produced the same qualitative results as those using $\log_{10}$-transformed ABUND, although the latter improved the pattern of distribution of the residuals to approach normality. Thus, below we present the results based on $\log_{10}$ (ABUND).

Modelling the spatial variation in beetle abundance. To identify significant spatial patterns of variation in beetle abundance and environmental variables, we used SAM version 3.0. (Spatial Analysis in Macroecology: Rangel *et al.*, 2006). We applied principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2002; Diniz-Filho & Bini, 2005; Rangel *et al.*, 2006), which takes into account the neighbourhood relationships among the sites to reveal the spatial structures (=spatial autocorrelation) of a data set over the whole range of scales encompassed by the sampling design (Borcard & Legendre, 2002). PCNM can be used with irregularly spaced data taken from sites that provide good coverage of the geographical sampling area, as in the present study. The PCNM method uses the spatial coordinates of the sampling sites to construct a matrix of Euclidean distance among the sites. Then, it applies a principal coordinate analysis on a modified distance matrix to derive principal coordinates – i.e. Euclidean components – of the neighbourhood relationships of the modified distance matrix. These components are eigenvector-based 'spatial filters', associated with positive eigenvalues. The spatial filters derived from PCNM are a combination of sinus and cosine waves that allow the decomposition of the whole spatial structure in the data into spatial patterns at different spatial scales, i.e. components with large eigenvalues are representative of broad-scale spatial patterns and those with low eigenvalues are representative of fine-scale spatial patterns (Borcard & Legendre, 2002 for a formal description of method; Diniz-Filho & Bini, 2005; Rangel *et al*., 2006). We conducted a separate PCNM analysis for beetle abundance data and each of the environmental variables. SAM version 3.0, also allows obtaining eigenvector-filtered variables that represent the residual variation in the original (raw) variables after they were 'filtered' by the components derived from PCNM. The eigenvector-filtered variables lack significant spatial autocorrelation. We used both the spatial filters that modelled the beetle abundance variation and the eigenvector-filtered (abundance and environment) variables in two further complementary analyses explained below.

The inclusion of spatial and environmental descriptors into a partial regression. We included the (raw) environmental variables and the spatial filters obtained from PCNM analysis of the abundance data in a partial regression to partition the variation in beetle abundance into: (i) local environmental effects, which was the fraction of the abundance variation explained by the environment descriptors independently of any spatial structure; (ii) regional spatially structured environmental variation, which was the amount of spatial variation in the abundance data shared by environmental variables [note that this shared variation might be due to direct causal or non-causal relationships between environmental variables and abundance due to separate relations of both (spatial and environmental) sets of variables with some external (unidentified) space-structuring process]; (iii) spatial variation in beetle abundance not shared by our environmental variables, which was the spatial variation in the abundance data that might reflect some biological process that has no apparent relation to the environmental variables that were included in our analysis; and (iv) unexplained variation, which was the fraction of the abundance variation explained neither by the spatial coordinates nor by environmental data (see Borcard *et al*., 1992; Boone & Krohn, 2000).

Verification of the ecological model. To evaluate the extent to which the spatial autocorrelation in the data affected the ecological associations, we conducted a second and complementary path analysis that tested the ecological relationships originally proposed, although based on the eigenvector-filtered variables (i.e. abundance and environmental variables). This provides a test of the magnitude of direct and indirect effects of the environment on beetle abundance after removing the effect of spatial autocorrelation or, in other words, to examine the magnitude of local ecological relationships that are independent of spatial autocorrelation.

Results

We caught a total of 12 579 individuals during the study. The most abundant families in our sample were Staphylinidae (N = 4561 individuals), Carabidae (N = 3958), Leiodidae (N = 1524), Tenebrionidae (N = 634), Curculionidae (N = 193) and Scarabaeidae (N = 179). We also captured beetles from 42 other families with very low abundances that taken altogether represented only 11.9% of individuals captured.

We considered it reasonable to assume that our abundance data were sufficiently diverse at family level to infer conclusions about community-level patterns in the abundance–environment relationships.

Spatial variation in beetle abundance and environmental variables

The spatial variation in ABUND, TREECOV, and LITTER over the whole study region showed geographical patchiness within the forests, and a gradient of decreasing abundance towards the east (Fig. 2). PREC also showed a strong west–east gradient. In contrast, SHRUBCOV showed geographical patchiness to the west but a west–east gradient was apparent only in the southwest (Fig. 2). HERBCOV and TVAR peaked in the scrubland-steppe. TVAR increased to the east, and TMIN showed geographical patchiness over the whole study area (Fig. 2).

The beetle abundance–environment relationships

Our models explained a greater proportion of mean variation in beetle abundance across the whole biogeographical transition ($r^2 = 0.81$; Fig. 3) and in the forests ($r^2 = 0.74$; Fig. 4) than in the scrubland-steppe ($r^2 = 0.44$; Fig. 5). Some of the variables used to test the plant productivity hypothesis explained well the spatial variation in beetle abundance, either when the analysis focused on the whole biogeographical transition (Fig. 3a; Table 2) or, after the division of data into macro-habitats, on the forests (Fig. 4) or scrubland-steppe (Fig. 5). Across the whole gradient and within the forests, ABUND responded positively and strongly to TREECOV and less strongly to HERBCOV (Figs 3 and 4; Table 2). We detected a positive indirect effect of climate – i.e. PREC and TMIN – on ABUND, mediated through the effect of TREECOV and HERBCOV, which was stronger within the forests (Table 2). Within the scrubland-steppe, ABUND increased with SHRUBCOV and, more strongly, with HERBCOV (Fig. 5; Table 2). PREC consistently showed positive indirect effects on ABUND – mediated through plant cover – across the entire biogeographical transition, in the forests and in the scrubland-steppe, which contrasted with its weak positive or negative direct effects (Figs 3–5; Table 2).

Some findings were not consistent with the productivity hypothesis, however. Although LITTER increased with PREC as predicted, LITTER had a weak negative effect on ABUND across the whole gradient and almost no effect within the forests

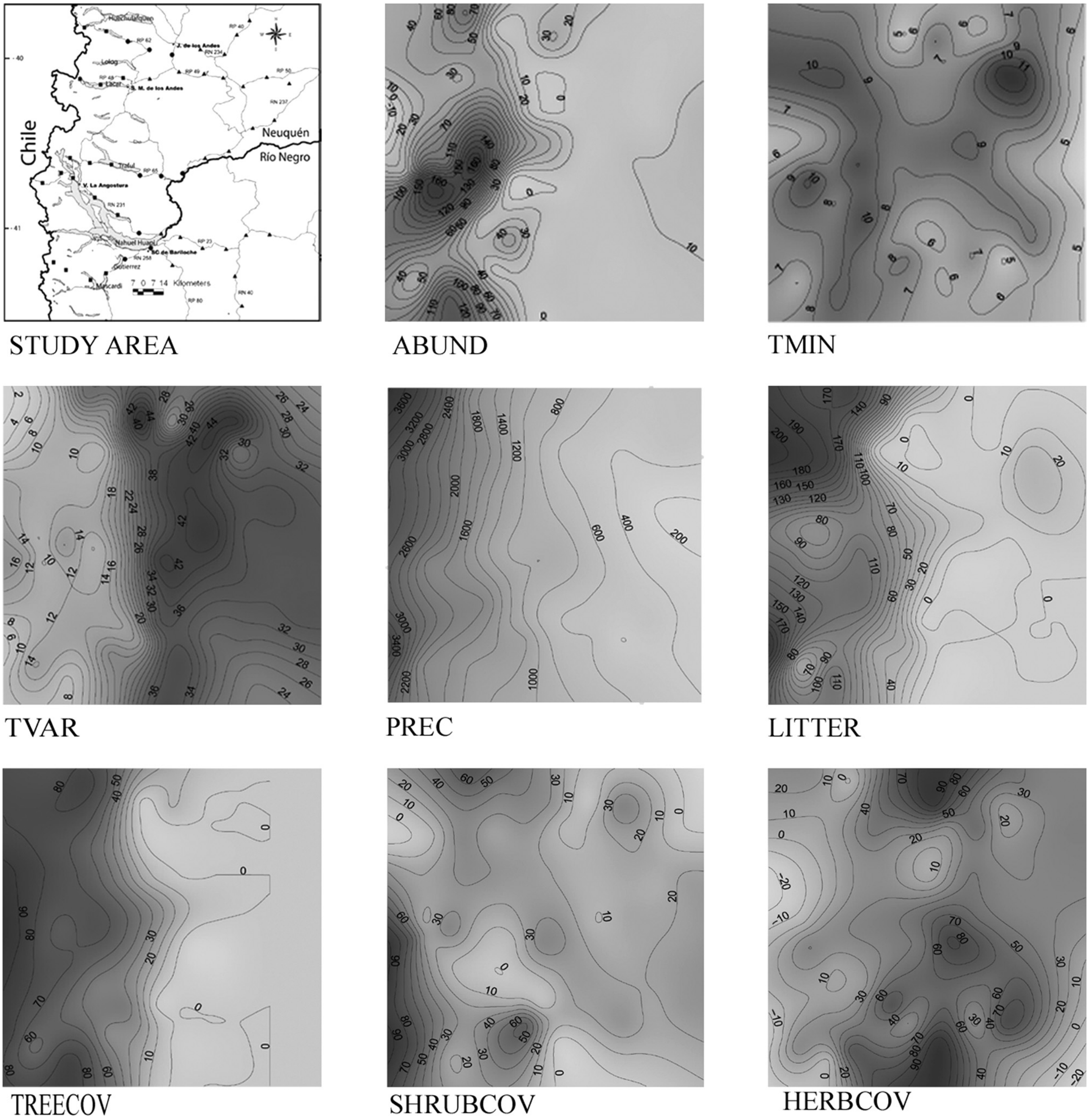


Fig. 2. The spatial variation of variables under study. Isoline maps were constructed after interpolation of data over the total extent of the study area. ABUND, beetle abundance; TMIN, minimum daily temperature; TVAR, daily temperature range; PREC, mean annual precipitation; LITTER, dried litter biomass; TREECOV, canopy cover; SRUBCOV, shrub cover; HERBCOV, herb cover.

(standardised path coefficient, $r = +0.03$) or within the scrubland-steppe ($r = -0.03$; Figs 3–5; Table 2). Within the forests, the local increase in SHRUBCOV had a strong negative effect on ABUND (compare Figs 4 and 5; Table 2).

There was a weak overall negative effect of TMIN on ABUND along the biogeographical transition, which was stronger within the forests (Figs 3–5, Table 2; see below). However, as predicted, ABUND decreased with increasing TVAR, and more strongly within the scrubland-steppe rather than within the forests (Figs 3–5; Table 2).

Spatial decomposition of the beetle abundance variation

The PCNM analysis applied on abundance data revealed two significant eigenvectors ($P < 0.05$), representing broad-scale

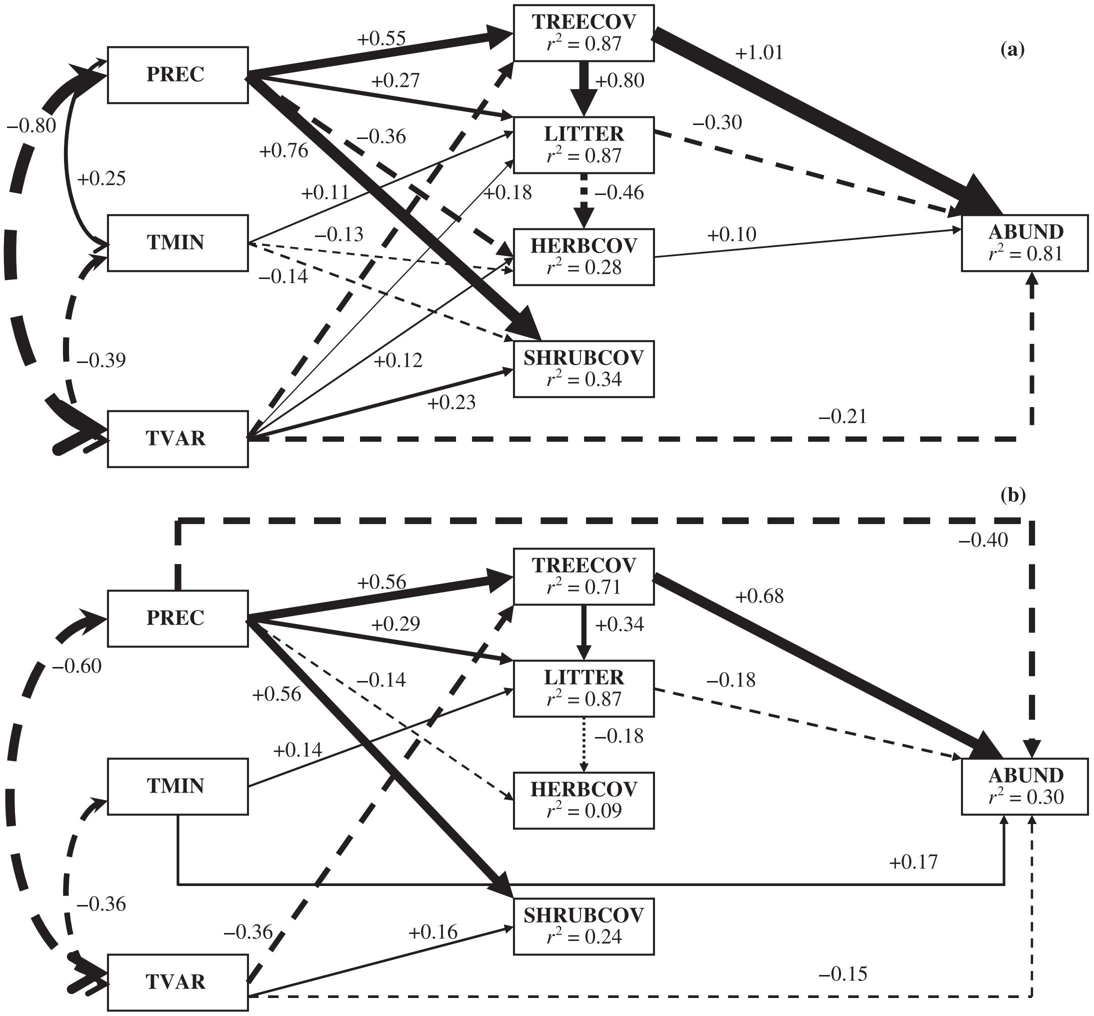


Fig. 3. Path analysis to test direct and indirect relationships among (a) original variables and (b) eigenvector-filtered variables, i.e. which lack significant spatial autocorrelation, hypothesised to explain the variation in beetle abundance across the biogeographical transition. Continuous single-headed arrows or dashed single-headed arrows indicate positive and negative direct effects, respectively. Two-headed arrows represent correlations between variables. We show only path coefficients greater or equal to 0.10. The arrow line thickness is proportional to the magnitude of each path coefficient or 'effect'. r^2, coefficient of determination, indicating the proportion of variation of each variable explained by the model. Definitions of variable names are given in Fig. 2.

Table 2. Direct (dir) and indirect (ind) positive (+) or negative (–) effects of climatic variables on beetle abundance. Indirect effects correspond to the effects of climatic variables mediated through plant cover (TREECOV, SHRUBCOV and HERBCOV) and litter. We highlighted in bold positive effects of environment on beetle abundance. Effects whose magnitudes were lower than 0.10 are not shown. The italicised values indicate the magnitude of the effects of environmental variables on beetle abundance after controlling for the effects of spatial autocorrelation along the biogeographical transition.

	Direct causal covariation (dir)							Indirect causal covariation mediated through plant cover (ind)			Total effects (dir + ind)		
	TMIN	TVAR	PREC	TREECOV	SHRUBCOV	HERBCOV	LITTER	TMIN	TVAR	PREC	TMIN	TVAR	PREC
Whole biogeographical transition		–0.21		**+1.01**		**+0.10**	–0.30		–0.29	**+0.22**		–0.50	**+0.28**
	+0.17	*–0.15*	*–0.40*	***+0.68***			*–0.18*		*–0.20*	***+0.32***	***+0.17***	*–0.35*	*–0.08*
Forests	–0.54	–0.13	–0.46	**+0.82**	–0.44	**+0.22**		**+0.42**		**+0.14**	–0.12	–0.12	–0.32
Scrubland-steppe	–0.13	–0.46	**+0.13**	NA	**+0.11**	**+0.32**				**+0.15**	–0.18	**–0.38**	**+0.28**

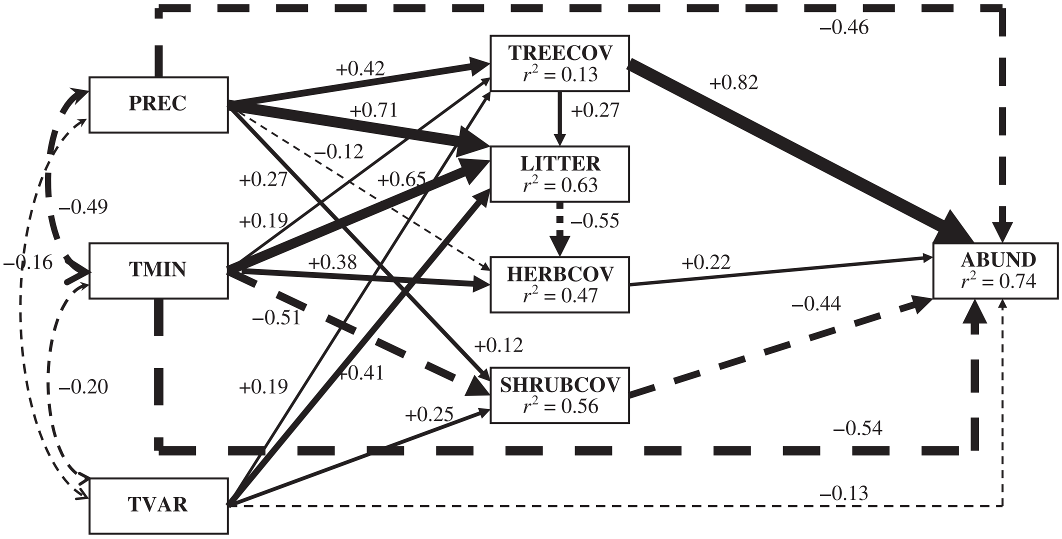


Fig. 4. Path analysis to test direct and indirect relationships among variables hypothesised to explain the variation in beetle abundance within forests. Presentation as in Fig. 3.

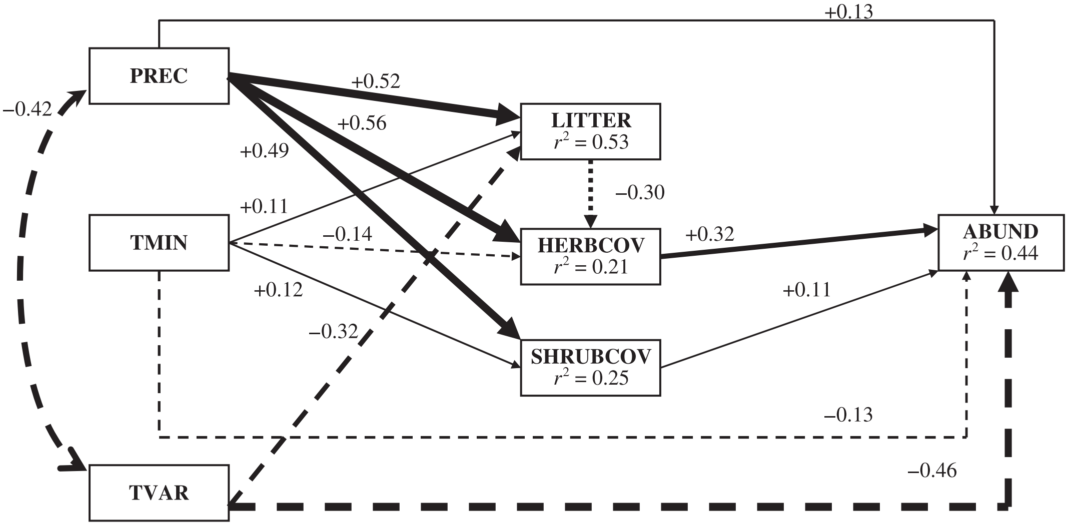
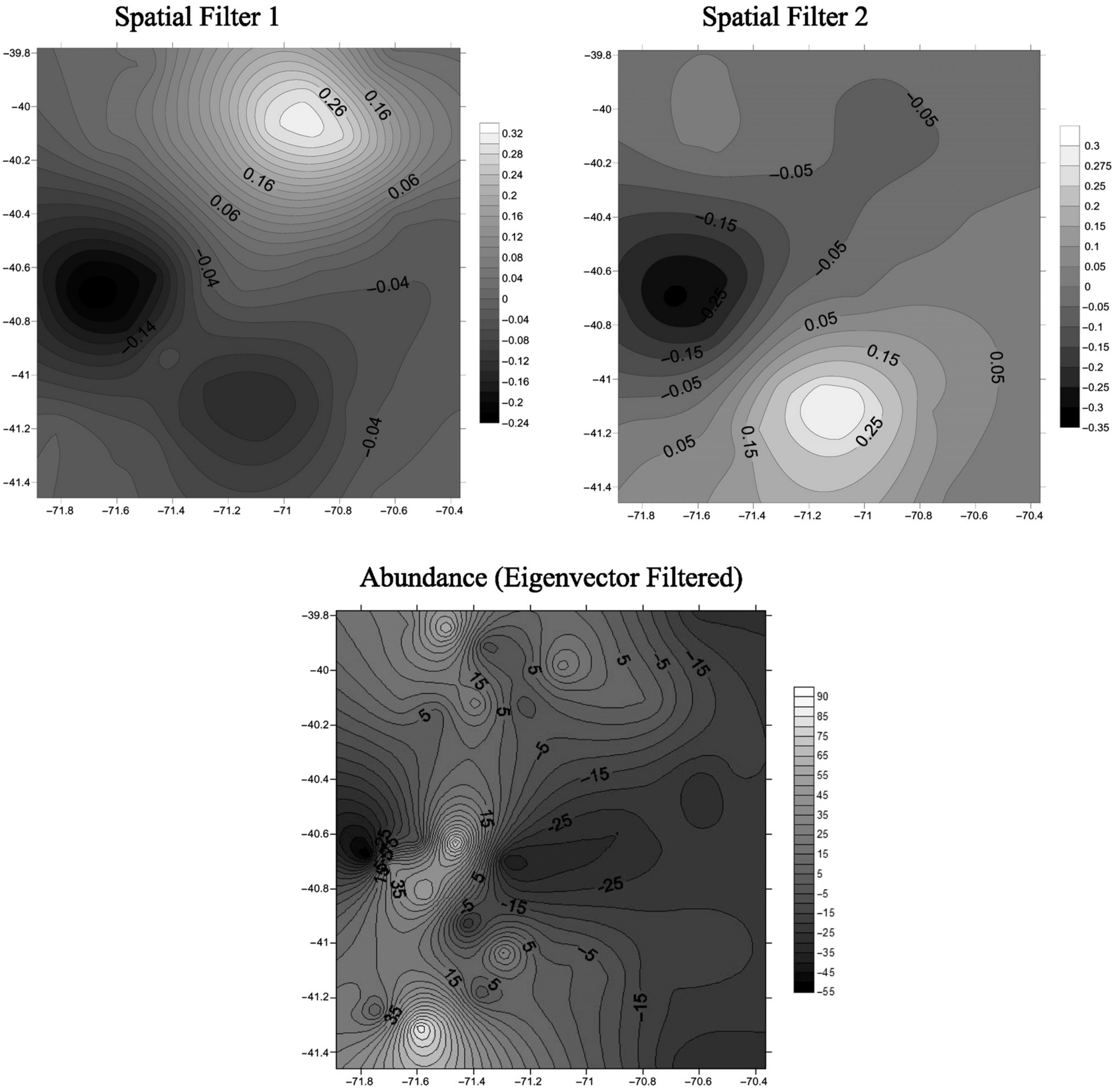


Fig. 5. Path analysis to test direct and indirect relationships among variables hypothesised to explain the variation in beetle abundance within the scrubland-steppe. Presentation as in Fig. 4.

spatial patterns, that together explained half of the mean total spatial variation in beetle abundance along the biogeographical transition ($r^2 = 0.50$; Fig. 6). SAM version 3.0 did not detect significant spatial descriptors of the spatial variation in beetle abundance in the forests or in the scrubland-steppe.

Partition of beetle abundance variation and verification of the ecological relationships

The full regression model (including the spatial filters and raw environmental variables) explained 73% of the total variation in beetle abundance across the biogeographical transition zone. The spatially structured component of environmental variation explained about 44% of the total variation in beetle abundance; local environmental effects, independent of spatial structure, explained a lower proportion of variation (24%). The proportion of variation explained by the spatial descriptors not shared by our environmental variables was rather low (5.7%), suggesting that significant tests of our model were valid and little affected by residual autocorrelation. This also indicated that the environmental descriptors we included in the model adequately described the structure of the variation in beetle abundance across the region.



Spatial Filter 1

Spatial Filter 2

Abundance (Eigenvector Filtered)

Fig. 6. Patterns depicted by spatial filters selected as significant spatial descriptors of beetle abundance within the whole biogeographical transition. Eigenvector-filtered abundance shows the variation that remains in beetle abundance data after removing the variation of spatial filters 1 and 2. Compare with ABUND in Fig. 2.

The path analysis conducted on eigenvector-filtered variables (Fig. 3b) confirmed that beetle abundance tended to increase with tree canopy cover across the biogeographical transition. In fact, the analyses confirmed that TREECOV was the most important predictor of ABUND; the influence of HERBCOV and SHRUBCOV was found not to be important (Fig. 3b; Table 2). The negative direct effect of PREC on ABUND, previously detected only within the forests (compare Fig. 3b and 4), was confirmed for the entire region. ABUND negatively responded to TVAR, and we also found a weak effect of TMIN on ABUND (Fig. 3b).

Discussion

The variation in the abundance of beetles along the Subantarctic–Patagonian transition was associated with environmental variables that supported the primary productivity hypothesis. The direct effects of minimum daily temperature on beetle abundance were negative or positive, but weak throughout, which contradicted the prediction of the thermal limitation hypothesis. However, the increase in daily temperature range predictably had a negative impact on beetle abundance, which may be considered indicative of thermal limitation (see below). Our analyses suggest that understanding the beetle abundance variation at large geographical scale demands an incorporation of both local and broad-scale factors. Although a greater proportion of the spatial variation in beetle abundance along the transition was explained by regionally spatially structured components of the environment, there were local ecological effects that affected beetle abundance after controlling for spatial autocorrelation, which can be considered independent of the strong east–west environmental gradient. Moreover, we detected differences in the beetle abundance–environment relationships between the eastern and western parts of the biogeographical transition; our ecological model explained the spatial variation in beetle abundance better within the forests than within the scrubland-steppe. In the latter, more than half of the total variation in beetle abundance remained unexplained. This suggests that the spatial variation in beetle abundance within the scrubland-steppe might be governed by different factors. In addition, the lack of significant spatial structure in the abundance data further suggests that probably in response to the greater environmental fluctuation within the scrubland-steppe, local beetle abundance might fluctuate more stochastically there.

The primary role of plant productivity

As the productivity hypothesis predicted, indirect climatic influences mediated through plant cover were more important to account for beetle abundance than direct climatic effects. This finding reinforces the predominance of the productivity hypothesis over the thermal limitation hypothesis to account for the spatial variation in ectotherm abundance, as previously suggested for ants (Kaspari *et al*., 2000), other arthropods (Perner *et al*., 2005) and lizards (Buckley *et al*., 2008). For instance, although ants are termophilic organisms, the spatial variation in their colony density can be largely explained by primary productivity (56%) whereas minimum monthly temperature only explains a small fraction (5.6%) of this variation (see Kaspari *et al*., 2000 for discussion). Beetles at the Subantarctic–Patagonian transition showed a similar pattern; plant productivity variables affected beetle abundance most strongly, whereas minimum daily temperature had only weak effects.

The distinction we made between tree canopy, shrub, herb covers and leaf litter allows a detailed examination of associations between these productivity-related variables and beetle abundance. The local abundance of beetles increased strongly with tree canopy cover and, to a lesser extent, herb cover; it was not associated with leaf litter and showed an equivocal response to the variation in shrub cover. The strong positive direct association between beetle abundance and canopy cover was confirmed after controlling for spatial autocorrelation in the data. Thus, it was indeed a local ecological effect and not merely the result of an east–west covariation of both variables along the biogeographical transition. Tree canopy cover was the most important predictor of beetle abundance. This association suggests that trees may offer foraging and oviposition sites for beetles, thus promoting a local increase in abundance. The strong positive association of canopy cover with beetle abundance could explain the high sensitivity of beetles to human-caused habitat alterations in vegetation structure (e.g. Niemelä *et al*., 1993, 2007; Elek *et al*., 2001; Spagarino *et al*., 2001; Koivula *et al*., 2004). Canopy closure has been shown to favour distinct, small-scale microhabitats at the soil surface, generating a diverse mosaic of environmental conditions that affect the abundance and distribution of ground-dwelling species (beetles: Niemelä *et al*., 1996; Butterfield, 1997; Elek *et al*., 2001; spiders: Ziesche & Mechthild, 2008). An increase in herb cover probably provides more food resources and shelter against micro-climatic variation, which may in turn increase beetle abundance. On the other hand, the effect of shrub cover on beetle abundance varied across habitats. Shrub cover affected beetle abundance positively in the shrubland-steppe but negatively in the forests. In arid and semi-arid environments like the shrubland-steppe, shrubs may act as 'keystone' structures, which beetles may actively choose, as they provide important resources of food, thermal refuges, and protection against predators (e.g. Stapp, 1997; Kitzberger *et al*., 2000; Mazía *et al*., 2006). In contrast, within temperate rain forests (e.g. *Nothofagus* forests) where vegetation is abundant and more continuous, we found a negative association between beetle abundance and shrubs. We cannot explain this intriguing pattern. Moreover, contrasting results have been reported elsewhere. For instance, forest-dwelling carabid beetles are closely associated with variation in understorey plant cover and soil properties in the Northern Hemisphere (e.g. Niemelä & Spence, 1994). Further studies would be necessary to understand the factors underlying the negative relationship between beetle abundance and shrubcover found in our study.

The influence of direct climatic effects

Our study did not find the positive association between beetle abundance and temperature found in other studies (e.g. Ahearn, 1971; Tigar & Osborne, 1997; Botes *et al*., 2007 and other references therein). The abundance of beetles did increase with the increase in minimum daily temperature after controlling for spatial autocorrelation, but this effect was only approximately 10%. The reduced latitudinal extent of our study involved a range of minimum temperature between 6 °C and 10 °C, which is narrower than the range reported in the studies cited above. This narrow temperature range may have limited our ability to detect abundance variation associated with temperature gradients. On the other hand, the association between abundance and temperature may have been affected by local environmental heterogeneity. In the forests, for instance, the strong negative relationship between minimum temperature and abundance was due to three plots that had high minimum temperature and low beetle abundance. One plot was in an *A. chilensis* forest growing within a rocky paleo-riverbed, and, in the other two plots, dead bamboo covered the ground, which probably affected the micro-environmental conditions resulting in lower abundance. When we removed these three points from the data set, the relationship between minimum temperature and beetle abundance within the forests increased from $r = 0.09$ ($N = 17$) to 0.68 ($N = 14$). However, the exclusion of these three study plots also resulted in a poorer fit of the path model to the data (e.g. the Bentler & Bonett's Non-normed index decreased from 1.00 to 0.61, the Akaike's information criterion increased from −4.03 to −1.18). A new data set would be necessary for a definite test of these effects of local heterogeneity and minimum daily temperature within the forest.

Our study suggests that thermal limitation may operate through the relationship between beetle abundance and mean daily temperature range. In all the analyses performed, the abundance of beetles decreased with the increase in mean daily temperature range, and this negative effect was stronger within the semi-arid scrubland-steppe. In general, the mean daily temperature range increased with the maximum daily temperature ($r = 0.96, P < 0.05$). In the scrubland-steppe, the maximum daily temperature recorded at ground level by our data-loggers approached 70 °C during the hottest days (data not shown). Thus, the negative effect of TVAR on ABUND may ultimately reflect the negative influence of an excessive increase in the maximum daily temperature, which might have decreased local beetle abundance and/or activity during the hottest days.

Our study also showed an equivocal relationship between beetle abundance and precipitation. The total (direct plus indirect) effects of precipitation on beetle abundance across the whole biogeographical transition and within the scrubland-steppe were positive. However, there was a strong *negative* direct effect of precipitation on beetle abundance within the forests and across the whole biogeographical transition after controlling for spatial autocorrelation, which suggests that in the most humid forest sites, towards the west of the biogeographical transition, excessive precipitation was associated with lower beetle catches. This suggests that either excessive drought in desert habitats (e.g. Ahearn, 1971) or very high precipitation in forested habitats might affect beetle behaviour, activity, and/or abundance.

In summary, the spatial variation in beetle abundance across the Subantarctic–Patagonian transition was driven by variables mainly associated with plant productivity, and canopy closure appeared to be a key ecological variable that may influence the spatial variation in beetle abundance. The thermal limitation hypothesis was only partially supported, suggesting that indirect climatic effects mediated through biological processes may be more important than direct climatic effects in accounting for local beetle abundance in temperate latitudes of the southern hemisphere.

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