**ORIGINAL
ARTICLE**

Plant species richness–environment relationships across the Subantarctic–Patagonian transition zone

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ABSTRACT

Aim To evaluate the relative importance of climate, productivity, environmental heterogeneity, biotic associations and habitat use by cattle to account for the species richness of trees, shrubs and herbs across the Subantarctic–Patagonian transition.

Location An area of *c.* 150 × 150 km, within the transition zone between the Subantarctic and Patagonian subregions on the eastern slope of the Andes (*c.* 39–42° S, 70–72° W).

Methods All vascular plants found at each one of 50 (10 × 10 m) sampling plots were counted to estimate the local tree, shrub and herb species richness. Path analysis was used to evaluate the relationship between the richness of the three life-forms and plant cover, dried litter biomass, mean annual temperature, annual precipitation, daily temperature range, substrate heterogeneity and number of faecal pats. Principal coordinates of neighbour matrices was used to model the spatial autocorrelation of the data.

Results Total plant species richness showed a unimodal pattern of spatial variation across the transition. Richness responded positively to indirect effects of precipitation mediated through plant cover, but there was a negative overall effect of precipitation on richness towards the west of the transition, most strongly for trees. An increase in substrate heterogeneity promoted a local increase in herb and shrub richness; the richness of trees increased in sites with steeper slopes. Canopy closure had a direct negative impact on herb richness; it also increased the local accumulation of litter, which negatively affected shrub and herb richness. The impact of habitat use by cattle negatively affected herb richness in areas to the east of the biogeographical transition.

Main conclusions We suggest that the importance of indirect climatic effects mediated by vegetation cover can account for species richness patterns across this transition, most strongly for woody species, which supports the productivity hypothesis. The southern temperate forests towards the west may represent a deviation from the predictions of the water–energy dynamics hypothesis. Dissimilar spatial patterns of variation in the richness of woody and herbaceous species, and their different responses to climatic and heterogeneity variables across the transition, suggest that plant life-form influences the plant species richness–environment relationships.

Keywords

Eastern Andes, eigenvector-based spatial filtering, floristic diversity, longitudinal gradient, partial regression, path analysis, precipitation, productivity, vegetation cover, water–energy dynamics.

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Journal of Biogeography

INTRODUCTION

Transition zones between biomes or biogeographical regions can be ideal systems for understanding the relationship between geographical variation in species richness and the current environment. Most often, these regions coincide with gradients in environmental conditions that span a wide range of variation, and are associated with pronounced species richness gradients, high turnover of species or a combination of both (e.g. Williams *et al.*, 1999; Smith *et al.*, 2001; Araújo, 2002; see also Ruggiero & Ezcurra, 2003). If the range of environmental variation sampled along a biogeographical transition is sufficiently high, then associated richness–climate relationships found there can be representative of the kind of present-day environmental conditions that might be necessary for extant species to persist (see also O'Brien, 2006). Understanding the variety of richness–environment relationships that occur across biogeographical transition zones may contribute to the development of a general hierarchical theory of diversity (e.g. Whittaker *et al.*, 2001; Willis & Whittaker, 2002) and may also provide information relevant to local biodiversity conservation planning.

We analysed the relationship between plant species richness and several environmental variables across the transition zone between the Subantarctic and Patagonian biogeographical subregions of the Andean region (Morrone, 2002) in southern South America. This transition zone is structured across one of the most pronounced environmental gradients in the world. The presence of the Andean Cordillera in the west acts as a topographic barrier to the humid winds from the Pacific, causing intense rainfall on the western (Chilean) side of the Cordillera, and an exponential decline of precipitation with distance from the Cordillera on the eastern (Argentinean) side (e.g. Barros *et al.*, 1983). Here, major climatic, soil and biotic differences along this biogeographical transition generate three distinct dominant physiognomic units from west to east: forests, shrublands and steppes (Fig. 1), that together present exceptional floristic diversity (Cabrera, 1976; Ezcurra & Brion, 2005). We analysed the spatial variation in local species richness of different plant life-forms to evaluate their association with several environmental variables representative of climate, productivity, local environmental heterogeneity, biotic associations and impact of habitat use by cattle. We analysed whether the richness variation of herbs, shrubs and trees showed a different response to environmental change. The morphological, phenological and ecological traits of different life-forms can be affected by environmental conditions, which can therefore affect the number of species that can occur in a given area (O'Brien, 1993). For example, in Patagonia the growing period of annual herbs requires rainfall during spring, whereas shrubs rely on deeper water stored during autumn (Sala *et al.*, 1989; Golluscio & Sala, 1993). Given that precipitation also affects grasses and shrubs in a different fashion, the environmental conditions that maximize the production of one do not necessarily maximize the other (Soriano & Sala, 1983; Jobbágy & Sala, 2000).
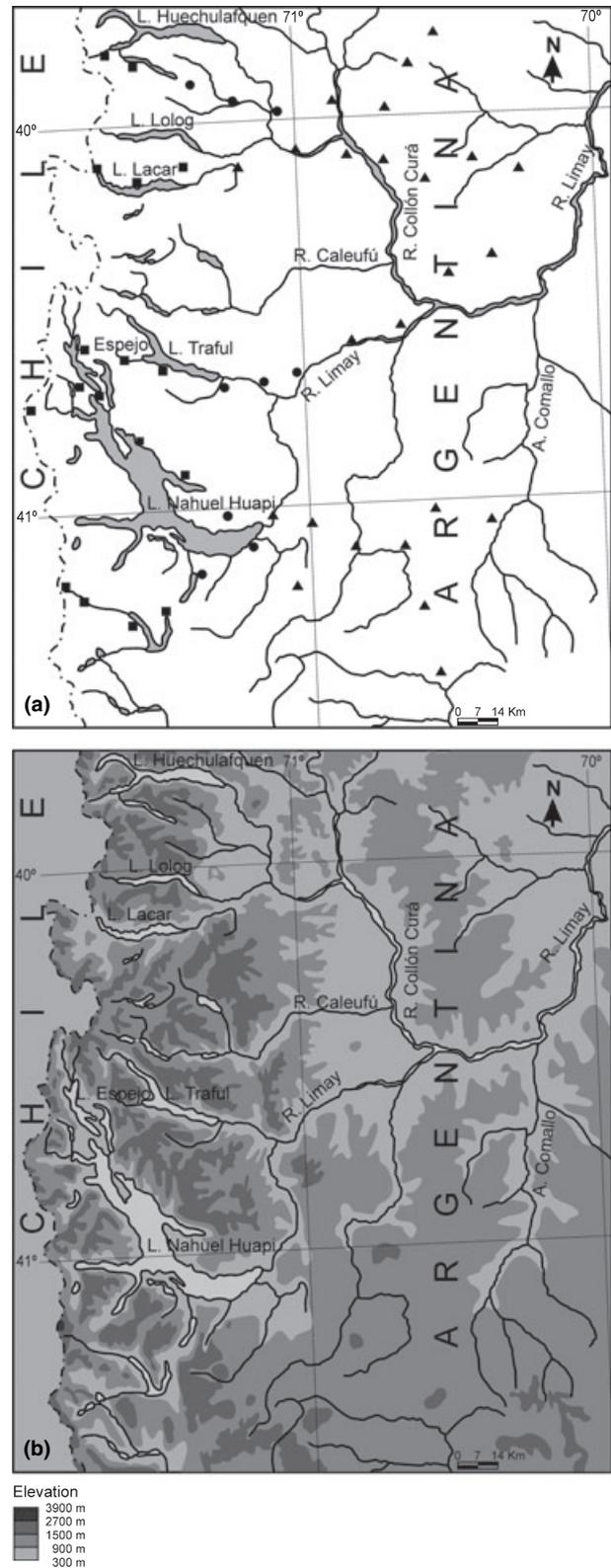

Elevation
3900 m
2700 m
1500 m
900 m
300 m

Figure 1 Map of the study area across the Subantarctic–Patagonian transition, showing (a) locations of sampling plots within the forests (black squares), shrubland (black circles) and steppe (black triangles) and (b) details about the topography and hydrology of the area. Note the presence of the highest elevations and several glacial lakes in the west.

The present study is part of a wider project we developed to elucidate the environmental correlates of spatial variation in the richness and abundance of different taxonomic groups (beetles, ants and plants) across the same transition zone (e.g. abundance of beetles; Ruggiero *et al.*, 2009). Here, we adopt a comprehensive comparative approach to show the role of abiotic and biotic factors that at present may interact with biogeographical history to maintain patterns and processes, and the persistence of high biological diversity in dynamic transitional regions (e.g. Smith *et al.*, 2001; Araújo, 2002). We show how local-scale analysis of ecotones between biomes can further our understanding of larger geographical patterns and relationships. We also show the importance of considering shifts that may occur across biogeographical transitions in the effect of environmental variables on richness, and the influence of plant life-form on plant species richness–environment relationships.

Hypotheses regarding the association of plant species richness with the abiotic environment

We distinguished three kinds of hypotheses associated with the effects of abiotic components of the environment on species richness: (1) energy–productivity, (2) water–energy dynamics, and (3) environmental heterogeneity. These parameters play an important role in determining the species richness of animals and plants at large scales of spatial analysis (Brown & Lomolino, 1998; Hawkins *et al.*, 2003; O'Brien, 2006; Field *et al.*, 2009), although their effects on richness may be through different mechanisms.

Energy–productivity hypothesis

The energy–productivity hypothesis proposes that the available energy in the environment indirectly affects plant species richness through an intermediate step that involves the increase in plant biomass (Hawkins *et al.*, 2003; Evans *et al.*, 2005; Clarke & Gaston, 2006). In general, the more energy available for plants (solar energy mediated by precipitation), the more individuals and higher local species richness that the environment can maintain (Wright, 1983; Currie & Francis, 2004; Evans *et al.*, 2005; Clarke & Gaston, 2006). We used vegetation cover as a surrogate variable for above-ground net primary production (ANPP). Vegetation cover is a good predictor of green biomass, ANPP and total biomass in the Patagonian steppes (Flombaum & Sala, 2007). We predicted that climate (represented here by mean annual temperature, annual precipitation and daily temperature range) affects plant cover, which in turn has a positive influence on plant species richness.

The water–energy dynamics hypothesis

The interaction between water and energy is fundamental for understanding the capacity of environments to support greater plant species richness (e.g. O'Brien, 1993, 1998; Whittaker & Field, 2000; Whittaker *et al.*, 2001). As outlined in O'Brien (2006), water, especially in the liquid state, is inherently dynamic

and mechanistically related to biotic dynamics via its unique physical properties. The west to east gradient of decreasing precipitation across the Subantarctic–Patagonian transition is one of the main ecological controls of the differences between the forests in the west and the steppes in the east (Cabrera, 1976; Paruelo *et al.*, 1998a). Water availability also controls much of the variability in plant species richness and cover in the Patagonian steppes (Jobbágy *et al.*, 1995, 1996). Although water–energy dynamics theory emphasizes the role of liquid water in richness, we tested the direct association of precipitation and temperature with plant species richness. Although at high altitudes in the Andes most of the precipitation is in the form of snow, the decreasing continentality of southern South America buffers these latitudes from temperature extremes (see Veblen *et al.*, 1998, p. 296). Thus, within our study area (Fig. 1) winter precipitation at *c.* 850 m is mostly rainfall (Table 1). Given that our sampling plots were settled at elevations of < 1200 m, we considered it reasonable to assume that precipitation is a good proxy for rainfall, because the proportion of rainfall out of the total amount of precipitation is high.

Environmental heterogeneity hypothesis

Climatic effects on richness may operate not only through changes in mean values but also through intra-annual climatic variability. Thermal seasonality is known to be negatively associated with the richness of woody species (O'Brien, 1993, 1998). In our study area, thermal seasonality is correlated with daily variations in heat and light (Spearman rank correlation coefficient, $r_s = 0.72$, $P < 0.05$, data not shown), both of which are fundamental to photosynthesis and biological activity. We predicted a negative association between daily temperature range and richness because constant habitats may promote the coexistence of specialist species that have lower extinction risks, and this would contribute to increasing species richness (O'Brien, 1993, 1998; Cowling *et al.*, 1994; Brown & Lomolino, 1998; O'Brien *et al.*, 2000).

Habitats with a physically diverse structure promote specialization within distinct environmental conditions, which facilitates the coexistence of a greater number of species (Brown & Lomolino, 1998; Scheiner & Willig, 2005). The size of substrate fragments and the slope of the terrain are two aspects of environmental heterogeneity that are positively associated with variation in plant species richness in Patagonia (Jobbágy *et al.*, 1996; Ferreyra *et al.*, 1998). Here we tested whether sites with more heterogeneous substrates or steeper slopes have higher species richness.

Biotic associations and effects of the impact of habitat use by cattle

Association between life-forms

Local species richness is affected by biotic interactions such as competition, predation or mutualism, which promote coexistence and specialization (Brown & Lomolino, 1998). Although

Table 1 Differences between the eastern and western portions of the Subantarctic–Patagonian biogeographical transition, in number of days with rainfall (R), snow (S) and precipitation (P) during the three rainiest months in our study area. Data on total Pp (rainfall and/or melted snow in mm) and rainfall (rain excluding snowfall) are also provided when available. We compared the available data recorded during the same 10 years at two meteorological stations: (a) Bariloche aerodrome (41.15° S, 71.16° W) is at the eastern semi-arid portion of the biogeographical transition; (b) Pampa Linda, Río Manso Superior (41.15° S, 71.45° W) is at the western humid portion of the transition. Both stations are located at an elevation of *c.* 850 m.

| | (a) Bariloche aerodrome | | | | | | | | | | | | (b) Pampa Linda | | | | | | | | | | | |
| | June | | | | July | | | | August | | | | June | | | | July | | | | August | | | |
Years	Pp (mm)	R	S	P	Pp (mm)	R	S	P	Pp (mm)	R	S	P	Rain (mm)	R	S	P	Rain (mm)	R	S	P	Rain (mm)	R	S	P
1997	174.5	16	7	18	139.4	19	8	20	111.3	14	1	15	286.5	20	11	24	280.9	18	21	28	162.6	9	1	9
1996	80.0	5	3	7	34.8	6	0	6	137.4	15	8	16	92.1	11	2	11	81.9	13	0	13	188.5	19	6	19
1995	224.0	16	9	20	156.5	11	13	18	122.4	15	11	18	332.4	22	11	23	236.5	23	31	31	232.0	18	31	31
1994	202.2	19	3	20	227.8	13	5	13	33.8	10	1	10	247.4	22	4	22	248.8	16	9	20	127.8	12	1	12
1993	246.9	21	8	23	152.6	10	10	15	46.0	7	6	8	481.6	25	6	26	370.6	17	31	31	136.4	13	12	18
1992	82.0	16	8	18	12.9	10	7	13	44.5	8	4	9	291.8	23	20	28	142.1	15	31	31	108.6	15	15	24
1991	50.8	11	5	15	284.5	18	7	21	108.5	9	4	11	68.5	16	13	22	175.4	22	21	28	167.0	13	16	20
1990	91.9	10	0	10	32.3	9	2	11	45.0	10	0	10	223.5	16	4	16	83.6	12	8	15	163.1	19	2	19
1989	189.5	15	2	17	158.7	10	3	11	111.3	13	11	20	208.7	19	2	19	170.1	20	13	28	257.3	23	13	24
1988	70.36	9	1	9	6.1	3	2	5	82.8	13	5	16	245.1	17	7	20	46.1	8	18	23	210.1	20	5	21
Average	141.2	13.8	4.6	15.7	120.6	10.9	5.7	15.7	84.3	11.4	5.1	13.3	247.8	19.1	8	21.1	183.6	16.4	18.3	24.8	175.3	16.1	10.2	19.7

we did not examine the role of biological interactions, we tested for associations among variables that might be indicative of such interactions. For instance, trees are expected to relate negatively with herbs since trees out-compete herbs for light (Anderson *et al.*, 2001; Balandier *et al.*, 2006). Hence, we explored whether canopy closure was negatively associated with herb richness. Also, the accumulation of plant litter, and especially tree leaves, is known to inhibit the germination and establishment of species, which in turn suppresses plant diversity in productive habitats (e.g. Xiong & Nilsson, 1999, and references therein). Here we explored whether the accumulation of litter affects the richness of different life-forms. Lastly, shrubs usually interact positively with herbs in the arid Patagonian steppes, being fertile refuges that favour herb settlement through mechanisms that include seed recruitment and protection against winds and excessive sun (Aguiar *et al.*, 1992; Belsky & Canham, 1994; Soriano *et al.*, 1994; Páez & Marco, 2000). We tested whether an increase in shrub cover promotes an increase in herb richness in the arid steppes.

The impact of habitat use by cattle

The introduction of cattle to Patagonia since the beginning of 19th century has changed the structure and composition of local plant communities (Veblen *et al.*, 1992, 1996; Relva & Veblen, 1998; Vazquez, 2002; Ezcurra & Brion, 2005). In general, cattle grazing has a negative impact on plant species richness (Bisigato & Bertiller, 1997; Perelman *et al.*, 1997; Cingolani *et al.*, 2003; Tadey, 2006). Although our study area was mostly pristine, some areas of it showed evidence of cattle grazing. We evaluated whether the impact of use by cattle was negatively associated with local plant species richness.

MATERIALS AND METHODS

Area of study

The study was conducted on the eastern slope of the Andes in Argentina (39–42° S, 70–72° W; Fig. 1) at the transition zone between the Subantarctic and Patagonian subregions. The area includes the Nahuel Huapi and Lanín national parks, and represents a pronounced environmental gradient (Barros *et al.*, 1983) with three distinct dominant physiognomic units from west to east: forests, shrublands and steppes (Fig. 1; Paruelo *et al.*, 1998a). The southern Andes act as a barrier to the humid westerlies causing a greater amount of 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.*, 1998a,b). Annual precipitation ranges from *c.* 3000 mm in the west to 500 mm in the east, and falls mostly in winter (Barros *et al.*, 1983). Landforms and sediments created by glacial processes are also evident throughout the region (Clapperton, 1993; Fig. 1).

Fieldwork

We sampled the vegetation in 50 plots, each 100 m^2 (10 × 10 m) *c.* 15 km apart within a *c.* 150 × 150 km area representative of the Subantarctic–Patagonian transition (Fig. 1). Such plots were large enough for sampling trees and understorey plants, without impeding sampling or replication within the study area. All plots were placed away from wet meadows and urban areas, in places that ranged from 893 to 1154 m in elevation, i.e. to avoid the confounded effects of altitude–environment relationships on richness, and lacked signs of recent fire, overgrazing or other

anthropogenic disturbances. In each plot we surveyed the vegetation and also collected data on environmental variables during spring (November 2004).

Estimation of species richness and vegetation cover

Species richness

We examined three sets of vascular plant species: (1) herbs (all vascular plants < 0.30 m in height); (2) shrubs (all woody vascular plants between 0.30 and 2 m in height and trunks < 10 cm in diameter at breast height) and (3) trees (all woody vascular plants > 2 m in height and trunks > 10 cm in diameter at breast height). Species richness was estimated by counting the total number of species of trees (TREERICH), shrubs (SHRUB-RICH) and herbs (HERBRICH) in each 10×10 m plot.

Vegetation cover

We used a concave spherical densiometer to estimate the proportion of tree canopy cover. We visually divided each 10×10 m plot into four quadrants to make four densiometer readings facing each of the four cardinal directions. These values were averaged to estimate canopy cover (TREECOV) for each plot. We estimated shrub cover (SHRUBCOV) at each plot as the averaged diameter of individual shrubs, estimated visually, multiplied by the total number of shrubs of each species counted at each plot. We 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 m^2.

Choice and estimation of environmental variables

Climatic variables

The mean annual temperature (TEMP) and annual precipitation (PREC) for each plot was taken from layers with a spatial resolution of 1 km^2, developed by Hijmans *et al.* (2005), available in the WorldClim database (http://www.worldclim.org/current.htm). We mounted one HOBO H8 logger (Onset Computer Corporation, Bourne, MA, USA) on a pole fixed at the centre of each sampling plot to record the temperature at ground level every 2 h during the entire sampling season. We obtained a total of 745 readings spread over 62 days during spring–summer. We extracted the maximum and minimum temperatures recorded each day and estimated the mean daily temperature range (TVAR) for each plot.

Local environmental heterogeneity

The slope (SLOPE) of each plot was estimated with a clinometer. We estimated visually the overall diameter of

rocks, gravel and stones found on the ground, and assigned a value of substrate heterogeneity (SUBST) to each plot according to the interval scale: 0 = no rocks; 1 = rocks < 1 cm in diameter; 2 = rocks between 1 and 10 cm, 3 = rocks between 10 and 30 cm, and 4 = rocks larger than 30 cm.

Plant litter biomass

Nine 9-cm diameter samples (separated *c.* 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).

Impact of habitat use by cattle

We counted the number of cattle faecal pats (FEC) within the limits of each plot; this has been previously used as an index of habitat use by herbivores in north-western Patagonia (Relva & Veblen, 1998).

Analysis of data

Test of species richness–environment relationships

We summarized the relationships among variables derived from hypotheses proposed at the beginning of the present analysis in a unique causal scheme (i.e. path diagram), that included the following effects.

1. Productivity hypothesis: we tested for the direct effects of TEMP, PREC and TVAR on SHRUBCOV, HERBCOV and TREECOV. We also tested for the effects of these three latter variables on SHRUBRICH, HERBRICH and TREERICH. Indirect effects of PREC, TEMP and TVAR on richness were estimated by multiplying the path coefficients involved in all the steps from climatic to richness variables. The resultant values from these multiplications were summed to calculate total indirect effects of PREC, TEMP and TVAR mediated through more than one 'causal' or endogenous variable.

2. Water–energy hypothesis: we tested for the direct effects of PREC and TEMP on SHRUBRICH, HERBRICH and TREE-RICH.

3. Environmental heterogeneity hypothesis: we tested the direct effects of TVAR, SUBST and SLOPE on SHRUBRICH, HERBRICH and TREERICH.

4. Associations between life-forms: we tested the direct effects of TREECOV on SHRUBRICH, TREECOV, SHRUBCOV and SHRUBRICH on HERBRICH, and LITTER on SHRUBRICH and HERBRICH.

5. Effect of habitat use by cattle: we tested the direct negative effects of FEC on SHRUBRICH, HERBRICH and TREERICH.

We used the PROC CALIS statement in SAS 9.1 for Windows to statistically test for the relationships between variables proposed by our model (Hatcher, 1994; SAS Institute Inc., 2004). CALIS allows one to specify the proposed theoretical model as a system of multiple linear equations that express the relationships among variables. We assumed all

relationships between variables to be linear throughout. Path coefficients are standardized 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 1-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). To 'test' indirectly the hypotheses proposed, we compared the sign (positive/negative) and the magnitude of direct and indirect associations estimated by path coefficients (hereafter called 'effects') with the predictions derived from each hypothesis. We standardized all variables prior to analysis.

We tested the fit of our model first for all plots (i.e. hereafter 'the whole biogeographical transition'; $n = 50$ plots), and then separately for the forests ($n = 17$) and shrubland–steppes ($n = 33$); the steppe and shrubland plots had a great similarity in floristic composition that justified combining them in a single dataset (see Speziale, 2006, for a detailed analysis).

We assumed that models had a good fit if the proportion χ^2/degrees of freedom (χ^2/d.f.) was lower than 2 and the values of the following indices were higher than 0.9: normed Bentler and Bonett index (NFI), Bentler's comparative fit index and goodness of fit index (GFI) (see Hatcher, 1994, for a formal definition).

Modelling of spatial variation in species richness

We used sam v. 3.0 (spatial analysis in macroecology; Rangel *et al.*, 2006) to identify significant spatial patterns of variation in species richness. 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 (i.e. spatial autocorrelation) of a dataset 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 (here recorded by a global positioning system) to construct a matrix of Euclidean distance among sites. Then, it applies a principal coordinates 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 sine 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 (see Borcard & Legendre, 2002, for a formal description of the method; Diniz-Filho & Bini, 2005; Rangel *et al.*, 2006). We conducted a separate PCNM analysis on the richness data for trees, shrubs and herbs.

The inclusion of spatial filters and environmental variables in a partial regression

We partitioned the variation in species richness into: (1) Local environmental effects – the fraction of the richness variation explained by the environmental descriptors independently of any spatial structure. (2) Regional spatially structured environmental variation – the amount of spatial variation in the richness data shared by environmental variables. This shared variation might be due to direct causal or non-causal relationships between environmental variables and richness due to their separate relationships with some external (unidentified) space-structuring process. (3) Spatial variation in richness not shared by our environmental variables – the spatial variation in the richness data that might reflect some biological process that is independent of the environmental variables that were included in our analysis. (4) Unexplained variation – the fraction of the richness variation explained neither by the spatial coordinates nor by environmental data (see Borcard *et al.*, 1992; Boone & Krohn, 2000).

RESULTS

The spatial variation in local species richness

The variation in local plant species richness across the biogeographical transition followed a unimodal pattern and peaked in the shrublands, where an average of 26 species were recorded locally in the 10×10 m plots (Fig. 2a,b). SHRUBRICH and HERBRICH also increased in the shrublands, with an average of 18 and 37 species, respectively, recorded locally (Fig. 2c–f). TREERICH showed less local variation, with an average of three species coexisting locally in the forests (Fig. 2g,h).

Test of species richness–environment relationships

Our model adequately fitted the data and accounts for the associations between richness and environment across the whole biogeographical transition (χ^2/d.f. = 1.38; NFI = 0.93; GFI = 0.90; Fig. 3; see Table 2 for basic statistics of variables). Here, we found an overall (= direct + indirect) consistent positive effect of PREC on TREERICH, SHRUBRICH and HERBRICH; the total effect of TEMP on richness was weak throughout, and TVAR had a negative effect only on TREERICH (Fig. 3, Table 3). However, the richness of the three life-forms analysed separately showed a rather different response to the effect of other environmental variables across the whole biogeographical transition. An increase in PREC promoted an increase in SHRUBCOV and TREECOV that, in turn, translated into an increase in SHRUBRICH and TREE-RICH (Fig. 3, Table 3); the indirect positive effect of PREC on
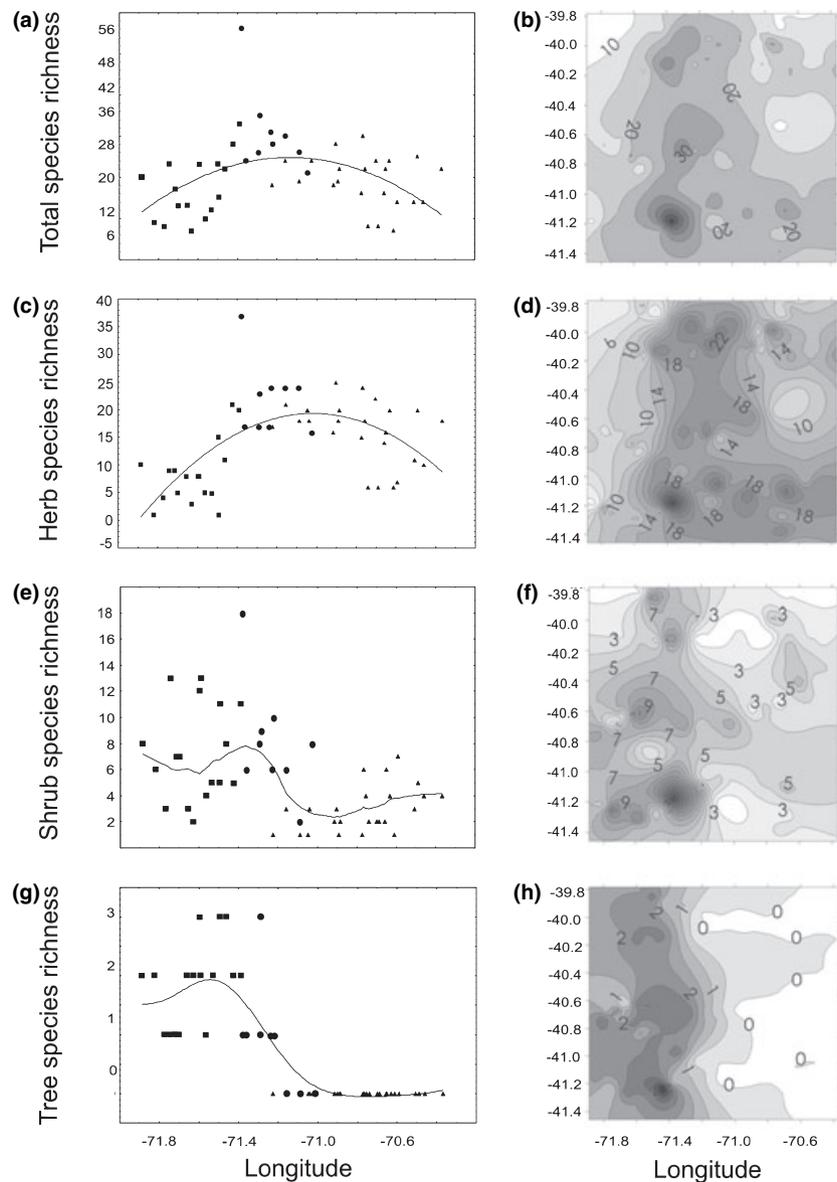
Figure 2 The spatial variation of total (a,b), herb (c,d), shrub (e,f) and tree (g,f) species richness across the Subantarctic–Patagonian biogeographical transition. To guide the eye for an easy interpretation of trends, we fitted a second-order polynomial on the total (a) and herb (c) richness, a LOWESS smoothing on shrub richness (e) and distance-weighted least-squared smoothing on tree richness (g). Isoline maps (b,d,f,h) were constructed after interpolation of data over the total extent of the study area.

TREERICH and SHRUBRICH was higher than its direct effect that negatively affected TREERICH (Table 3). In contrast, HERBRICH responded positively and more strongly to the direct effect of PREC (Fig. 3, Table 3). As expected, the local variation in HERBRICH was also positively associated with HERBCOV. SHRUBRICH and HERBRICH increased locally with the increase in substrate heterogeneity but this association was not found in TREERICH; there was a negative, although rather weak, effect of SLOPE on HERBRICH which contradicted our original prediction (Fig. 3, Table 3). An increase in TREECOV had a positive effect on SHRUBRICH and negatively affected HERBRICH; SHRUBRICH and HERBRICH decreased with the increase in LITTER. The negative effect of FEC was evident only on HERBRICH (Fig. 3, Table 3).

The division of data into the forests ($n = 17$) and shrubland–steppes ($n = 33$) showed that our ecological model fitted

the data from the shrubland–steppe (χ^2/d.f. = 0.64; NFI = 0.93; GFI = 0.92). A climatic model fitted the forest data only after the exclusion of SLOPE, SUBST and FEC (χ^2/d.f. = 0.35; NFI = 0.96; GFI = 0.96). Thus, in the forests we could evaluate only the role of climate and associations between life-forms.

In the forests, some species richness–environment associations differed from those observed across the whole biogeographical transition (Fig. 4). For instance, there was an overall negative effect of PREC on TREERICH and HERBRICH, although it was very low on SHRUBRICH (Table 3). There was a tendency for SHRUBRICH to increase with TEMP. There was also a positive direct effect of TVAR on TREERICH and SHRUBRICH that contradicted our original predictions (Fig. 4, Table 3). We found a strong positive *a posteriori* (i.e. not included in our original conceptual model but suggested by the results) correlation between TREERICH and HERBCOV
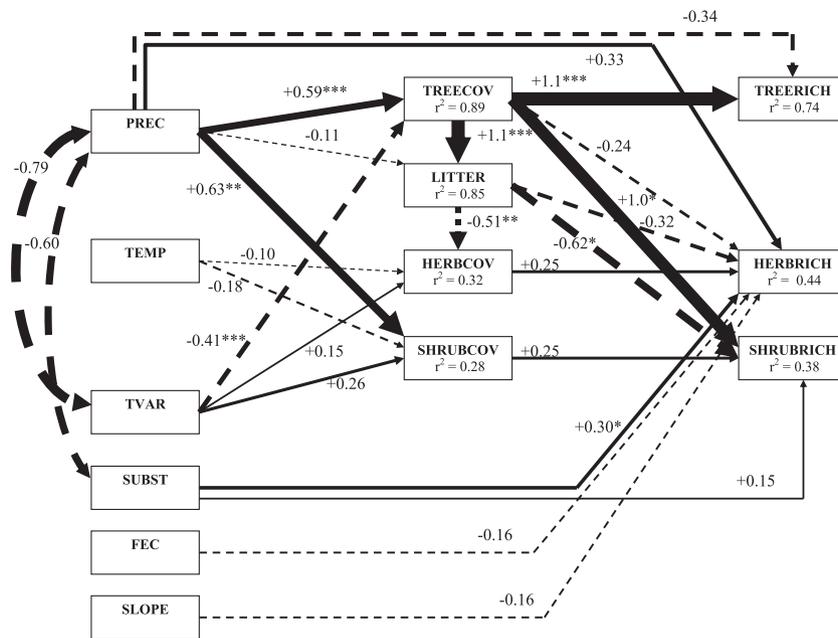
Figure 3 Path analysis to test direct and indirect relationships among the variables hypothesized to explain the variation in plant species richness across the whole Subantarctic–Patagonian biogeographical transition. Continuous single-headed arrows or dashed single-headed arrows indicate positive and negative direct effects, respectively. Two-headed arrows represent correlations between variables. We show only path coefficients ≥ 0.10. The line thickness of the arrows 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. TREERICH, tree richness; HERBRICH, herb richness; SHRUBRICH, shrub richness; TREECOV, tree cover; LITTER, dried litter biomass; HERBCOV, herb cover; SHRUBCOV, shrub cover; PREC, precipitation; TEMP, mean annual temperature; TVAR, daily temperature range; SUBST, substrate heterogeneity; FEC, number of faecal pats; SLOPE, slope of the terrain in each plot; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2 Descriptive statistics of variables used in the present study of the Subantarctic–Patagonian biogeographical transition, including mean values (Mean) and standard error of the mean (SE), minimum (Min) and maximum (Max). Definition of variable names is given in the caption to Fig. 3.

	Whole transition ($n = 50$)			Forest ($n = 17$)			Shrubland–steppe ($n = 33$)		
	Mean (SE)	Min	Max	Mean (SE)	Min	Max	Mean (SE)	Min	Max
TEMP (°C)	8.6 (1.1)	7.2	10.5	8.3 (1.6)	7.2	9.6	8.5 (1.4)	7.5	10.5
TVAR (°C)	26.7 (1.7)	7.7	46.3	12.06 (0.99)	7.7	25.7	32.7 (1.4)	15.3	46.26
PREC (mm)	867.2 (56.7)	337.0	1660.0	1346.0 (51.7)	973.0	1660.0	620.6 (34.6)	337.0	964.0
TREECOV (%)	29.3 (4.8)	0.0	85.8	70.84 (2.74)	43.5	85.8	7.8 (2.9)	0.0	60.2
SHRUBCOV (%)	26.2 (2.6)	1.2	84.8	35.1 (5.6)	6.5	84.8	21.6 (2.2)	1.2	59.1
HERBCOV (%)	35.7 (3.2)	0.0	94.0	18.4 (4.0)	0.0	62.0	44.6 (3.5)	18.0	94.0
LITTER (g)	48.2 (8.1)	0.0	187.4	113.0 (10.4)	24.9	187.4	14.8 (4.5)	0.0	111.2
SUBST	1.3 (0.2)	0.0	4.0	0.06 (0.06)	0.0	1.0	1.9 (0.2)	0.0	4.0
SLOPE (°)	8.6 (1.0)	0.0	30.0	1.3 (1.9)	2.0	30.0	6.6 (0.9)	0.0	20.0
FEC	3.3 (0.6)	0.0	14.0	1.5 (0.5)	0.0	6.0	4.3 (0.8)	0.0	14.0

that suggested that high richness of trees occurred in sites with high herb cover, although we could not identify a causal directional effect between them (Fig. 4, Table 3). On the other hand, other effects, such as the negative influence of LITTER on SHRUBRICH and HERBRICH, remained the same, as did the negative effect of SHRUBCOV and TREECOV on HERB-RICH (Fig. 4, Table 3).

In the semi-arid shrubland–steppe, an overall local increase in PREC promoted a strong increase in TREERICH, SHRUBRICH and especially in HERBRICH (Table 3). However, once again, we found differences in the extent to which the three life-forms supported our original predictions (Fig. 5). As predicted, the positive effect of PREC on TREERICH was mediated through TREECOV. There was also a positive effect of increasing

Table 3 Direct (Dir) and indirect (Ind) positive (+) or negative (−) effects of environmental variables on plant species richness in the Subantarctic–Patagonian biogeographical transition. Indirect effects correspond to the effects of climatic variables mediated through plant cover (TREECOV, SHRUBCOV and HERBCOV) and litter. We highlight in bold the positive effects of environment on richness. Effects whose magnitudes were lower than 0.10 are not shown. Definition of variable names is given in Fig. 3.

| | Direct causal covariation (Dir) | | | | | | | | | | Indirect causal covariation of climate mediated through plant cover and litter (Ind) | | | Total climatic effects (Dir + Ind) | | |
| | Climate | | | Plant cover and litter | | | | Heterogeneity | | Habitat use by cattle | Climate | | | Climate | | |
	TEMP	TVAR	PREC	TREECOV	SHRUBCOV	HERBCOV	LITTER	SUBST	SLOPE	FEC	TEMP	TVAR	PREC	TEMP	TVAR	PREC
Biogeographical transition																
TREERICH			−0.34	**+1.1**								−0.45	**+0.65**		−0.45	**+0.31**
SHRUBRICH				**+1.0**	**+0.25**		−0.62	**+0.15**					**+0.47**			**+0.47**
HERBRICH			**+0.33**	−0.24		**+0.25**	−0.32	**+0.30**	−0.16	−0.16						**+0.33**
Forests																
TREERICH		**+0.10**	−0.52	**+0.19**											**+0.14**	−0.44
SHRUBRICH	**+0.16**	**+0.34**	**+0.10**				−0.71					−0.18	−0.16	**+0.16**	**+0.16**	−0.06
HERBRICH				−0.45	−0.37	**+0.16**	−0.25					−0.21	−0.53		−0.21	−0.53
Shrubland–steppe																
TREERICH	−0.14		**+0.25**	**+0.80**				−0.12	**+0.24**		−0.15	−0.31	**+0.48**	−0.29	−0.31	**+0.48**
SHRUBRICH				−0.17	**+0.34**		**+0.46**	**+0.16**				−0.12	**+0.29**		−0.12	**+0.54**
HERBRICH		**+0.18**	**+0.94**	**+0.28**		−0.22	−0.62	**+0.21**		−0.55		**+0.10**	**+0.10**		**+0.28**	**+1.0**

SHRUBCOV on SHRUBRICH, although direct and indirect effects of PREC were equally associated with the increase in SHRUBRICH (Table 3). In contrast, HERBCOV was negatively associated with HERBRICH, which in turn was positively and directly influenced by the increase in PREC (Fig. 5, Table 3). SHRUBRICH decreased with the increase in TEMP; the increase in TVAR had a negative effect on TREERICH and SHRUBRICH, as expected, but it had a positive influence on HERBRICH (Fig. 5, Table 3). SHRUBRICH and HERBRICH increased with the increase in SUBST; TREERICH responded negatively to the increase in SUBST but responded positively to the increase in SLOPE (Fig. 5, Table 3). The increase in TREECOV promoted a decrease in SHRUBRICH but had a positive influence on TREERICH and HERBRICH. In contrast to our original prediction, we did not find a positive effect of SHRUBCOV on HERBRICH (Fig. 5, Table 3). The accumulation of LITTER was associated with an increase in SHRUBRICH but had a negative effect on HERBRICH, which was also negatively affected by FEC (Fig. 5, Table 3).

Spatial decomposition of variation in plant species richness across the biogeographical transition

The PCNM analysis revealed that TREERICH and SHRUBRICH somewhat shared spatial patterns of autocorrelation, explained by the same two spatial filters (Fig. 6), although the total proportion of spatial autocorrelation explained by three significant filters ($P < 0.05$) was greater for TREERICH (Table 4). HERBRICH showed different spatial patterns of autocorrelation, modelled by two spatial filters (Table 4, Fig. 6).

Partition of plant species richness variation

The full regression model (including the spatial filters and raw environmental variables) explained a greater proportion of the total variation in TREERICH than in SHRUBRICH and HERBRICH. The spatially structured component of environmental variation explained a similar proportion of the total variation in TREERICH than local environmental effects independent of spatial structure; it explained a lower proportion of the variation in SHRUBRICH, and a slightly higher proportion of the variation in HERBRICH. The proportion of variation explained by the spatial descriptors not shared by our environmental variables was rather low (Table 4), suggesting that significant tests of our models were valid and little affected by residual autocorrelation. This also indicated that the environmental descriptors we included in the models adequately described the structure of the variation in plant species richness across our study region.

DISCUSSION

The unimodal pattern in species richness

The spatial variation in total plant species richness across the Subantarctic–Patagonian transition followed a unimodal
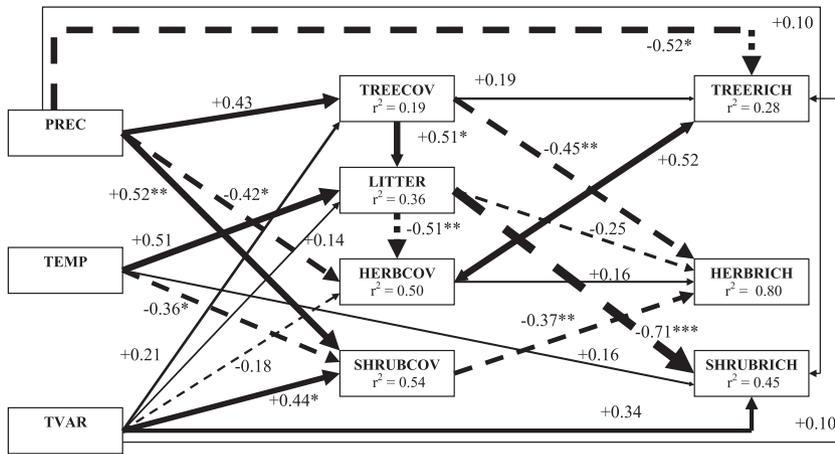
Figure 4 Path analysis to test direct and indirect relationships among variables hypothesized to explain the variation within the forest in the western part of the Sub-antarctic–Patagonian biogeographical transition. Presentation as in Fig. 3.

pattern, and suggested the value of using measures of water and energy to account for within-region plant species richness patterns, as previously suggested for the global scale (e.g. O'Brien, 1993; Whittaker & Field, 2000). In our study, precipitation and daily temperature range were the two main climatic drivers of local plant species richness. We found that the strong association between the richness of woody plants and precipitation was mediated through plant cover, which supports the productivity hypothesis. Productivity is one of the outcomes of biotic dynamics that vary as a function of available liquid water and optimal energy conditions (O'Brien, 2006). An increase of plant cover coupled with higher allocation to woody biomass, to increase the height and to have an advantage in competing for light, often occurs when water stress decreases and carbon fixation is enhanced across precipitation gradients (Schulze *et al.*, 1996; Holmgren *et al.*,

1997; Austin & Sala, 2002). In western Patagonia, the strong west–east gradient in precipitation explains more than 60% of the spatial variation in ANPP, which varies from c. 2500 kg ha^{-1} in the wettest portion (i.e. forests) to c. 500 kg ha^{-1} in the driest extreme (i.e. steppe) of the biogeographical transition (see Golluscio *et al.*, 1998; Paruelo *et al.*, 1998a). Thus, the unimodal pattern in richness shown in our study is consistent with current models of a climate-driven productivity–richness relationship that predict a general increase in local richness from less productive environments to intermediate ones, and an inflexion point with a subsequent decay in richness for the most productive environments (e.g. Sarr *et al.*, 2005; Scheiner & Willig, 2005).

The spatial variation and effects of precipitation and daily temperature range on richness run in opposite directions across the Subantarctic–Patagonian transition: precipitation
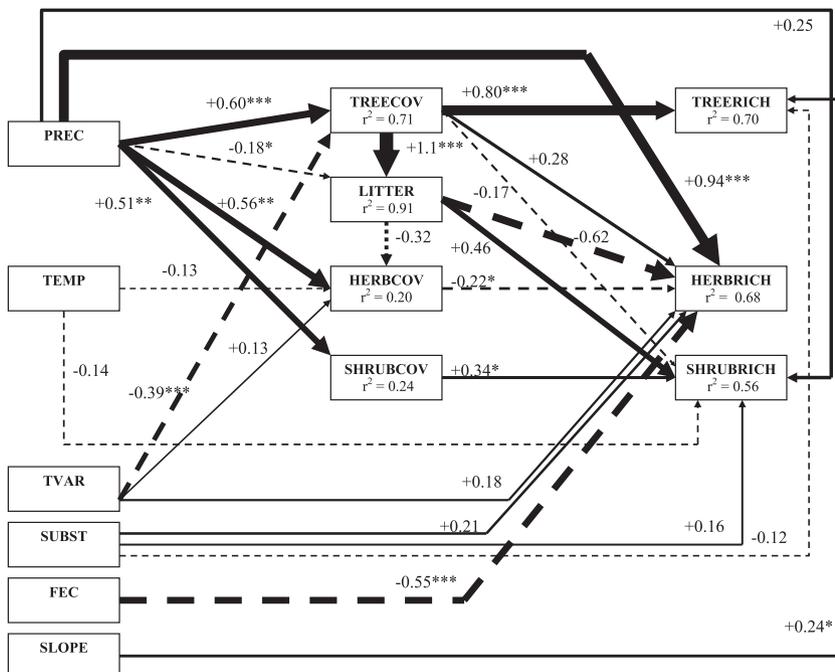

Figure 5 Path analysis to test direct and indirect relationships among variables hypothesized to explain the variation within the shrubland–steppe in the eastern part of the Subantarctic–Patagonian biogeographical transition. Presentation as in Fig. 3.

increases strongly towards the west whereas daily temperature range increases towards the east. The peak in species richness suggests the place where water–energy dynamics is less strongly limiting biological activity (O'Brien, 1993, 1998, 2006) and where the presence of intermediate climatic conditions, in terms of daily temperature range and precipitation, may facilitate species coexistence.

Our results suggested a stronger effect of precipitation on plant species richness than of mean annual temperature; this was not unexpected given the strong spatial variation in precipitation along the west–east transition, whereas the narrow latitudinal and limited altitudinal extent of our study represented little variation in mean annual temperature. However, we did confirm that, within our study area, plants are sensitive to daily variations in energy regimes; the mean daily temperature range increased with the maximum daily temperature across our study region ($r = 0.96$, $P < 0.05$, $n = 50$), which suggests that, in cold regions, where energy inputs are low and likely to be limiting, higher daily temperatures may affect the richness of plants by enhancing growth.

Climatic controls of plant species richness in areas to the west and east of the transition

Although precipitation in the form of liquid water is most important for terrestrial plants in warm regions (Hawkins et al., 2003), recent evidence confirms that rainfall also accounts for tree species richness better than energy in temperate climates (Hawkins et al., 2007; see also Field et al., 2007). However, at the westernmost portion of the Subantarctic–Patagonian transition, within the forests, there were negative overall effects of precipitation on tree and herb richness and a strong direct negative effect on trees. Although a proportion of the precipitation is in the form of snow, this negative association is not merely an artefact of considering precipitation instead of rainfall in our analyses, because we restricted our study to elevations of < 1200 m, which have large amounts of rainfall in forested areas. Also, in contrast to our original predictions, the richness of woody species increased in forest sites with greater daily temperature range, which were also the warmer ones. These results suggest that, in the southern Andes, environmental conditions are generally less favourable in the forest areas with more precipitation and colder temperatures to the west, where insolation is lower and the growing season shorter. At the continental scale, evidence that excessive precipitation may limit tree richness is also found in other temperate (low-energy) regions, such as the Pacific Northwest coast in North America and north-western Europe, where trees may be unable to respond to the massive amounts of rain falling within a short growing season (Field et al., 2007; Hawkins et al., 2007). The forests towards the western portion of the Subantarctic–Patagonian biogeographical transition may represent a similar deviation of the overall richness–rainfall relationship, although in the Southern Hemisphere.
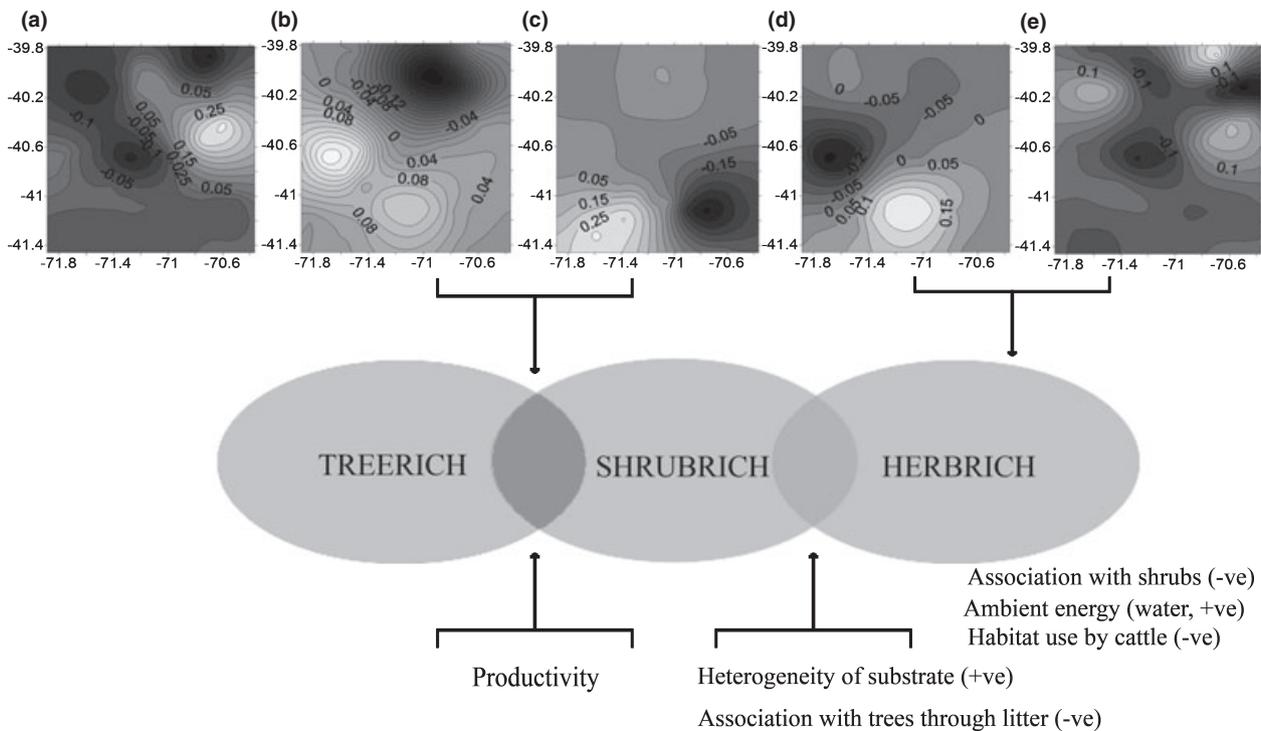

Figure 6 Patterns depicted by spatial filters selected as significant spatial descriptors of tree richness (TREERICH) (a–c), shrub richness (SHRUBRICH) (b,c) and herb richness (HERBRICH) (d,e) across the whole Subantarctic–Patagonian biogeographical transition. The overlap between ellipses is used to indicate the sharing of spatial patterns of autocorrelation and/or similar positive (+ve) or negative (−ve) association of richness with an environmental variable.

Table 4 Partition of variation in the richness of trees (TREE-RICH), shrubs (SHRUBRICH) and herbs (HERBRICH) after partial regression analysis applied on data from the whole biogeographical transition.

	TREERICH	SHRUBRICH	HERBRICH
r_f^2	0.76	0.46	0.56
r_e^2	0.74	0.38	0.44
r_s^2	0.39	0.33	0.33
Components of richness variation			
a	0.36	0.13	0.26
b	0.38	0.26	0.20
c	0.02	0.07	0.10
d	0.24	0.54	0.44

r_f^2, proportion of richness variation explained by a full regression model that included the spatial filters (shown in Fig. 6), and the raw environmental variables used in the present study, which is equal to $(a + b + c) - d$.

r_e^2, proportion of richness variation explained by the environmental model (shown in Fig. 3), which is equal to $(a + b)$.

r_s^2, proportion of richness variation explained by the spatial filters alone, which is equal to $(b + c)$.

The different sources of variation were calculated as: $a = (a + b) - b$, local environmental effects that are independent of spatial structure; $b = (a + b) + (b + c) - (a + b + c)$, spatially structured component of environmental variation; $c = (b + c) - b$, proportion of variation explained by spatial descriptors not shared by environmental variables; $d = 1 - (a + b + c)$, unexplained variation.

The deviations in the Northern Hemisphere that result in regions with fewer tree species than expected have been hypothesized to relate to other processes, such as glaciation history (Field *et al.*, 2007; Hawkins *et al.*, 2007). In the Southern Hemisphere, glaciation history could also account for the negative relationship of richness–rainfall towards the west. This pattern of lower species richness towards western sites with more precipitation has also been found in alpine areas in the southern Andes and Tierra del Fuego (Moore, 1983; Kalin-Arroyo *et al.*, 1989; Ferreyra *et al.*, 1998). In Patagonia, it has been suggested that recolonization during the Holocene, as Pleistocene glaciers retreated, began sooner in the east than in the west (Moore, 1983; Kalin-Arroyo *et al.*, 1989). The shorter time-span for forest colonization in westward areas could be a cause of their low tree richness, and the differences in this pattern for other life-forms could be related to differences in generation times, which are much longer in trees.

Human impact, seasonality and edaphic effects have also been suggested to contribute to the relationship of less tree richness in sites with more rainfall in the north-western coasts of North America and Europe (Field *et al.*, 2007; Hawkins *et al.*, 2007). In our study area human impact is low. However, seasonality in rainfall and edaphic characteristics may indeed play a role. Here, seasonality implies the occurrence of the highest levels of precipitation (snow and rainfall) in winter, i.e.

outside the warmer growing season and main period of plant activity. As a consequence, a large proportion of rainfall cannot be used by plants and simply percolates or runs off into rivers and lakes where it is not available for trees in the spring and summer. A positive linear relationship between richness and rainfall should be obtained only as long as soil remains unsaturated, but increasingly negative relationships are expected as soil becomes saturated, favouring anaerobic conditions. Although we assumed linear relationships between variables throughout the present study, future studies might consider exploring optimal richness–precipitation relationships to gain additional insight. The high rainfall conditions towards the west can also produce high soil acidity. This, together with idiosyncratic features of the tree species, related to their different optimal environmental requirements, can also affect forest composition in different areas. In the westernmost portion of the biogeographical transition, pure *Nothofagus dombeyi* rain forests are found, while more to the east, mixed forests with more mesic species of *Nothofagus* and other genera appear, which accounts for the observed pattern of 'impoverishment' towards the westernmost part of the transition.

Towards the east, in the semi-arid shrubland–steppe, we did find a strong positive effect of precipitation on the local richness of woody species, and also found the predicted negative effect of daily temperature range on the local richness of woody species. In the steppes, the maximum daily temperature recorded at ground level by our data-loggers approached 70 °C during the hottest days. Increased maximum temperature, greater daily temperature variation and water stress may be limiting factors in controlling local woody plant species richness towards the easternmost portion of the biogeographical transition.

The influence of plant life-form on species richness–climate relationships

By analysing species richness patterns for different life-forms, differences in their climatic drivers emerged that might otherwise have gone unnoticed (see Jobbágy *et al.*, 1996; Jobbágy & Sala, 2000; Oberle *et al.*, 2009). The richness of trees and shrubs shared some large-scale spatial patterns of autocorrelation and, accordingly, responded in a similar way to the effect of climatic variables. This supports the predictions of the productivity hypothesis and the role of water–energy dynamics in richness variation (O'Brien, 1993, 1998, 2006; Whittaker & Field, 2000). In our study, the increase in precipitation had a positive influence on woody species richness through an intermediate step that involved an increase in vegetation cover. The indirect effects of precipitation exceeded its direct effects throughout all the analyses performed. In contrast, herb richness showed spatial patterns of autocorrelation that largely differed from woody species, and was influenced more strongly by direct positive effects of precipitation. A weaker response of herbaceous plant species richness to regional productivity has also been

found in temperate forests of North America, which was explained by differences in lifespan and sensitivity to edaphic heterogeneity (Oberle *et al.*, 2009, and references therein). In our study area, herbs also differed from woody species in the opposite response shown to the effect of daily temperature range on richness, which further suggests that plant life-form influences the species richness–environment relationships across this biogeographical transition.

Contrasting spatial patterns in species richness and plant density between herbs and woody species are expected in the transition between forest and non-forest ecosystems, given that the average modular size of trees is orders of magnitude larger than for herbaceous and small shrub taxa (Whittaker *et al.*, 2001). Nonetheless, there are also morphological and physiological differences between these life-forms that may account for different spatial patterns of autocorrelation and species richness–environment relationship. Specifically, the morphology and phenology of herbaceous plants such as forbs are adapted to take advantage of brief and variable pulses of water input during the spring and summer in Patagonia (Golluscio & Sala, 1993). Grasses also behave opportunistically, having leaves ready to grow as soon as water becomes available, and their shallow root system is able to respond very rapidly to increments in soil water availability (Soriano & Sala, 1983). In contrast, woody species have a more clear-cut periodic pattern of growth and dormancy, and deeper roots, which have suggested they use water deeper underground (see Soriano & Sala, 1983, for detailed discussion).

The effect of local environmental heterogeneity, biotic associations and disturbance

Our study suggests that microenvironmental variability is an important factor for species richness (Jobbágy *et al.*, 1996), although woody and herbaceous genera may be sensitive to different scales of spatial heterogeneity (Ricklefs & Latham, 1992). An increase in substrate heterogeneity promoted an increase in herb richness and, less strongly, in shrub richness across the whole biogeographical transition, and in the semi-arid shrubland–steppe. The richness of trees was negatively or not associated with substrate heterogeneity, although it increased in sites with greater slopes. Herbs may take greater advantage of small-scale heterogeneity given their small size and morphological, phenological and physiological variability (Ricklefs & Latham, 1992; Golluscio & Sala, 1993). For instance, at the local scale in South Africa, perennial species richness is higher on rocky slopes, presumably because of greater heterogeneity of soil moisture conditions (Cowling *et al.*, 1994). In arid and semi-arid areas such as the Patagonian steppe, the presence of rocks on the ground may offer more microsites with shadow and humidity and may provide protection against predators (Golluscio & Sala, 1993; see also Mungía-Rosas & Sosa, 2008).

The negative direct effect of tree cover on herb richness across the whole biogeographical transition and in the forests suggests a negative association between these two life-forms, probably mediated through a biological interaction that involves competition for light (e.g. Sommer & Worm, 2002). We also found that canopy closure strongly drove the increase in the local accumulation of litter which, in turn, had a negative association with shrub and herb richness, across the whole biogeographical transition and in the forests. Litter accumulation usually inhibits germination and establishment of species, and thus suppresses plant diversity in productive habitats (e.g. Xiong & Nilsson, 1999, and references therein). However, our data showed that the effect of litter accumulation on shrub richness was positive in the shrubland–steppe. In this semi-arid habitat, litter accumulation might contribute locally to reduce evaporation, increase water retention and nutrients, and maintain more even soil temperatures, and our study suggests that this could be beneficial for shrubs rather than for herbs. In contrast to our original prediction, we did not find evidence of a positive association between shrubs and herbs in the shrubland–steppe, which could be due to the fact that facilitation can change along gradients of resource availability (e.g. Pugnaire & Luque, 2001).

As expected, the effect of habitat use by cattle was low throughout the present analysis, as we selected mostly pristine areas to establish our study plots. Lower species richness is expected in environments that are disturbed by grazing (Veblen & Lorenz, 1988; Veblen *et al.*, 1996; Díaz *et al.*, 1999), and we only found evidence of a strong negative impact of habitat use by cattle on the richness of herbs in the shrubland–steppe. This could reflect the greater pressure of cattle in the shrubland–steppe, which lacks protected areas. The national parks were established *c.* 100 years ago to protect the forests in the western part of the biogeographical transition.

In conclusion, although local or within-region climatic–richness models cannot be easily extrapolated to the global scale, substantial changes in abiotic and biotic components of the environment that occur across biogeographical transitions facilitate analysis of the role of the environment in explaining plant species richness. Our study suggests the importance of indirect climatic effects mediated by vegetation cover to account for species richness patterns across the Subantarctic–Patagonian transition – most strongly so for woody species. It points to the southern temperate forests towards the western portion of the biogeographical transition being exceptions to the overall richness–rainfall relationships predicted by the water–energy dynamics hypothesis. Finally, dissimilar spatial patterns of variation in the richness of woody and herbaceous species are associated with different responses to climatic and heterogeneity variables across this biogeographical transition, which suggests that plant life-form influences the plant species richness–environment relationships.

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Editor: Eileen O'Brien