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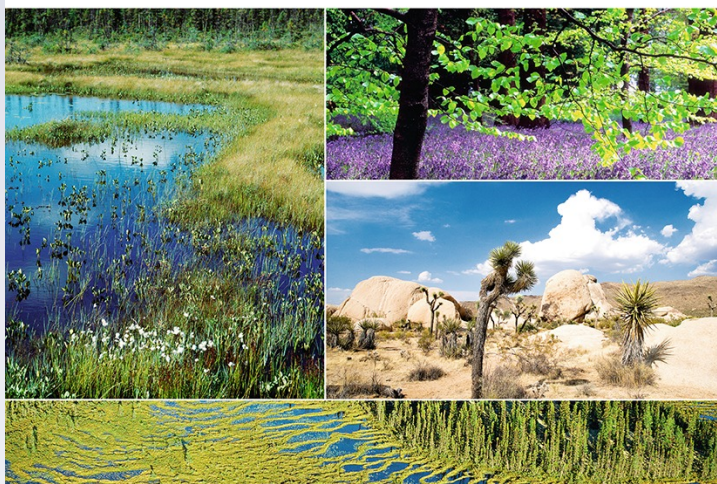
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# Relative contribution of niche and neutral processes on tree species turnover across scales in seasonal forests of NW Argentina

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**Abstract** Environmental heterogeneity and dispersal limitation influence tree species distribution, but their relative contributions change with the spatial scale of analysis. We analyzed tree species turnover using twenty 1-ha permanent plots to quantify variation in floristic similarity explained by environmental factors and geographical distance at regional (among plots) and local (within plots) scales in seasonal premontane forests of northwestern Argentina. We related floristic similarity (Bray–Curtis) with environmental variation and geographical distance using specific regression models

(regression of distance matrix and mixed-effects models at regional and local scales, respectively). Floristic similarity decreased with distance at both spatial scales but its relative contribution was significant only at the regional scale (18 and <1 % at regional and local scale, respectively). Dispersal limitation may be a relevant process at biogeographical scale where dispersion at large distances become infrequent for some species. In addition, we identified that regional climatic and topographic gradients and local edaphic variation contribute to explain floristic similarity across scales in seasonal premontane forests. Environmental heterogeneity explained about the same variance in floristic similarity at regional and local scales (7 and 8 %, respectively). We conclude that quantitative aspects of floristic patterns, such as the relative contribution of niche and neutral processes to explain species distribution, can strengthen conservation strategies at different spatial scales, and therefore could be a useful tool in conservation planning.

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## Introduction

Understanding the processes that determine species distribution and abundance within space and time is a central question in plant ecology. Historical processes determine the regional species pool in a particular

ecosystem, while environmental factors such as climate, soil, and disturbance determine which species can coexist in local communities (Steege and Zagt 2002; Ricklefs 2004). On one hand, niche assembly mechanisms like the water-energy dynamics hypothesis (Wright 1983), and historical factors or processes (Ricklefs 1987), explain global or regional patterns of species diversity and distribution. The underpinning of these ideas is that regional patterns of species distribution respond to differences in the physical environment, such as climate (present in the first and historical in the second hypothesis). In addition, habitat segregation, species functional differentiation and biological interactions have been proposed to explain species distribution within local communities (Wright 2002; Silvertown 2004). On the other hand, neutral assembly mechanism supposes that species are competitively equivalents and plant communities result from local random processes associated with seed dispersal (Hubbell 2001; Chave et al. 2002). Currently, both niche and neutral processes are considered as determinants of species diversity and distribution (Gilbert and Lechowicz 2004; Chase 2005; Leibold and McPeck 2006; John et al. 2007), but their relative contribution may vary with the spatial scale of analysis (Condit et al. 2002; Ricklefs 2004).

Many studies have used geographic distance between sites as a proxy for seed dispersal ability and have considered the main environmental gradients according to the spatial scale of analysis to explain tree species distribution and community structure. Such studies incorporate environmental and spatial information using powerful multivariate methods than can separate the effects of environment and dispersal (Vellend et al. 2014). For example, climatic gradients were associated with floristic patterns at the regional scale (Oliveira-Filho and Fontes 2000; Pyke et al. 2001), while at the landscape scale species composition was associated with topography (Clark et al. 1999), edaphic variation (Phillips et al. 2003; Tuomisto et al. 2003; Gilbert and Lechowicz 2004), and human disturbance (Williams-Linera and Lorea 2009). When tree species communities were analyzed at the local scale, species turnover was related to light availability (Webb and Peart 2000), topographic location (Valencia et al. 2004; Baldeck et al. 2012), and soil fertility (Silva et al. 2011). Many of the cited studies attribute the rapid decline in floristic similarity

with distance between samples to dispersal limitation or other neutral processes.

Seasonal premontane forests are deciduous montane forests distributed at low elevations in northwestern Argentina and southern Bolivia. We studied floristic similarity patterns among and within twenty 1-ha permanent plots to identify environmental factors that explain tree species turnover at regional and local scales, and to analyze the relative contribution of niche and neutral processes on floristic similarity across spatial scales. We predicted that changes in species abundance and dominance among permanent plots (i.e., regional scale) would result from climatic, topographic, and forest-use gradients. However, local environmental conditions (e.g., slope, soil texture, and soil fertility) influence tree species turnover within 1-ha plots across hundreds of meters. Distance would also be an important factor limiting seed dispersal of some species mainly at the regional scale.

## Methods

### Study area

Fieldwork was carried out in seasonal premontane forests of NW Argentina (22–24°S and 63–65°W), between 400 and 900 m a.s.l. (Fig. 1), at the southernmost extension of Andean Neotropical Montane Forests (Cabrera and Willink 1980). In the study area, these forests are distributed across two mountain ranges located from northeastern foothills to southwestern foothills. Climate is defined as subtropical with a marked dry season and occasional frost during cold months. Annual rainfall range is 800–1000 mm concentrated in summer months (~80 % rainfall from November to March). Rainfall varies across mountain ranges decreasing from northeastern foothills to southwestern foothills (with about 175 mm of difference in annual rainfall between foothills). During the rainy season, temperature may exceed 40 °C (Brown et al. 2001). The tree flora of the study area is relatively well known (Legname 1982). Due to soil fertility and water availability, large, flat forested areas have been replaced by agriculture (e.g., sugar cane, citrus, soybean), while remaining forests are generally used for timber through selective logging (Malizia et al. 2012).

**Fig. 1** Extent of the study area and location of the twenty 1-ha permanent plots in seasonal premontane forests of northwestern Argentina. *Black symbols* = permanent plots established in the Northeastern foothills and *white symbols* = permanent plots established in the Southwestern foothills. *Squares* = slope <5 %, *triangles* = 5–10 % slope, and *circles* = slope >10 %



### Permanent plots

We established twenty 1-ha permanent plots between 2002 and 2009 distributed in an area of approximately 8000 km<sup>2</sup> of premontane forest (Fig. 1). Nine plots were established in the northeastern foothills (22.1–22.9°S and 63.8–64.1°W), and 11 plots were established in the southwestern foothills (22.6–24.1°S and 64.4–64.9°W). All plots were 20 × 500 m (25 subplots of 20 × 20 m) corrected for slope to cover

1 ha. The orientation of plots was perpendicular to the main slope of the land to avoid large differences in altitude within plots; difference in altitude along the 500 m was less than 205 m (a.s.l.) in all plots. A full inventory was made of all trees ≥10 cm diameter at breast height (dbh) in every plot. Trees were marked with numbered aluminum tags, measured for dbh (1.30 m, avoiding trunk irregularities), and identified to species or morphospecies if field identification was not possible. We collected voucher specimens of all

species and morphospecies sampled in the plots. Voucher specimens were distributed to taxonomic specialists or matched to specialist-identified material. Only six individuals (0.06 %) remained unidentified (e.g., trees with no leaves, database errors) and were excluded from all analyses.

### Environmental factors

We related floristic similarity with four regional environmental gradients: mean annual temperature, total annual rainfall, topographic slope, and years without logging (Online Resource 1). We derived climatic data from a local precipitation model and local mean monthly temperature from a map surface developed by Bianchi et al. (2008) for NW Argentina. Both models were generated from data of 450 meteorological stations from 1934 to 1990. We measured slope in 25 subplots of 20 m × 20 m within each 1-ha plot using a clinometer, and then we considered mean slope to characterize topography for each 1-ha plot. Mean slope per plot ranged from 0 to 18.7 % with a clear differentiation between flat (<5 % slope) and hilly areas (8.2–18.7 % slope). As plots were established in forests that were previously logged, we considered the year of the last intervention (data reported by landowners) as a measure of forest successional age (3–30 years without logging at the time of plot establishment). The proportion of plots established in flat or hilly areas, and in forests recently logged or older secondary forests, was as equitable as possible between foothills (see Fig. 1 and Online Resource 1).

Moreover, floristic similarity was related to local gradients of organic matter and sand content in soil, which characterize edaphic conditions, and topographic slope (Online Resource 1). Soil was sampled in 10 subplots of 20 m × 20 m (separated 40–60 m) in 14 out of the 20 plots. At each sampling point, we collected four pooled sub-samples of topsoil (0–20 cm depth) within an area of 3 m × 3 m in the subplot center. Soil samples were analyzed using standardized protocols from Instituto Nacional de Tecnología Agropecuaria (INTA-Cerrillos, Salta, Argentina).

### Data analyses

We analyzed tree species turnover using different grain sizes and extensions (i.e., inter-plot distance)

according to the resolution of environmental data. We calculated floristic similarity with tree species abundance data using Bray–Curtis measure of dissimilarity among the twenty 1-ha plots and among 10 subplots of 20 m × 20 m within each of the 14 plots with soil data. We performed analysis of variance to evaluate differences in mean floristic similarity between 1-ha plots using foothills as factor. For each environmental factor, we calculated environmental variation between sample units using Euclidean distance, i.e., environmental distance for rainfall, mean annual temperature, mean topographic slope and years without logging (among plots), and organic matter, sand content in soil, and topographic slope (among subplots within each plot). We related floristic similarity with log-transformed distance (i.e., km and m among plots and subplots, respectively) as an indirect measure of seed dispersal (Condit et al. 2002) and with environmental variation using regression models. We performed multiple regression of distance matrix (MRM, Legendre et al. 1994) to identify environmental variables that explain floristic similarity among 1-ha plots. We conducted a variation partitioning procedure (following Borcard et al. 1992) to evaluate the relative contribution of environmental factors and geographical distance, i.e., to separate the proportion explained exclusively by environment from the proportion explained exclusively by distance and the proportion of spatial autocorrelation (i.e., environmental variation spatially structured).

At the local scale, considering the hierarchical structure in the data (i.e., subplots nested within plots), we performed linear mixed-effects models LMM (Laird and Ware 1982), using the plots as a random factor. We defined fixed and random components, and selected the optimal model using the likelihood ratio test, following Zuur et al. (2009). First, we selected the optimal random structure using all explanatory variables in the fixed component centered at the plot mean (i.e., distance, organic matter, sand content in soil, and slope). Then, we dropped non-significant explanatory variables in the fixed component. Finally, we calculated proportion of variance explained within and among plots, i.e., marginal and conditional  $R^2$ , respectively, according to definitions given by Nakagawa and Schielzeth (2013). In this way, we can separate the proportion of variance explained within plots given by local environmental variation, and the proportion of variance explained among plots given by

**Table 1** Summary of MRM models (simple and multiple regression models) for floristic similarity among 1-ha plots to evaluate explanatory variables significance

Models	Intercept	<i>P</i> value	Slope	<i>P</i> value	R <sup>2</sup> adj	<i>P</i> value	VE (%)
Distance (km) (a)	0.49	0.001	−0.0013	0.001	0.32	0.001	31.8
Rainfall	0.43	0.003	−0.0004	0.003	0.14	0.003	13.8
Temperature	0.40	0.01	−0.063	0.01	0.05	0.01	5.3
Topographic slope	0.40	0.03	−0.006	0.03	0.04	0.03	3.8
Years without logging	0.38	0.07	−0.003	0.13	0.02	0.13	1.8
All environmental (b)	0.35	0.001			0.21	0.001	20.7
Rainfall			−0.049	0.002			
Temperature			−0.025	0.04			
Topographic slope			−0.027	0.02			
Full model (c)	0.35	0.001			0.39	0.001	38.8
Distance (km)			−0.072	0.002			
Rainfall			−0.017	0.21			
Temperature			−0.015	0.19			
Topographic slope			−0.026	0.02			

Multiple regression models were performed with standardized variables to allow comparable slopes

Models [a], [b] and [c] were used to calculate proportion of variance, following Borcard et al. (1992)

VE variance explained

environmental variation at larger spatial scales (e.g., differences in climate, topography, and forest use among 1-ha plots). We performed all analyses in R (R Development Core Team 2013), using *ecodist* and *nlme* packages.

## Results

We identified, measured, and marked 9390 trees belonging to 104 species, 84 genera, and 42 families (Online Resource 2). At the regional scale, floristic similarity ranged from 0.09 to 0.69; i.e., two 1-ha plots in seasonal premontane forests can share from 9 % up to 69 % tree species (with a mean of 35 % species shared). Mean floristic similarity differed between plot pairs established in the same foothill and plot pairs established in different foothills ( $F = 55.2$ ,  $P < 0.0001$ ). Thus, considering plot pairs established in the same foothill, floristic similarity ranged from 23 to 69 % species shared in the NE foothill (mean = 45 % species in common) and 14–66 % species shared in the SW foothill (mean = 41 % species in common). However, comparing plot pairs established in different

foothills, floristic similarity ranged from 9 to 58 %, with a mean of 28 % species shared.

Floristic similarity decreased with distance among 1-ha plots; distance explained the highest proportion of variance (Table 1). Similarity declined rapidly with distances up to ~30 km, where comparisons generally included plot pairs located in the same foothill. At greater geographic distances, floristic similarity decreased smoothly, and plot pairs located in the same foothill showed in average 5 % more similarity than plot pairs located in different foothills (Fig. 2a). Climatic and topographic variations contributed to explain floristic similarity at the regional scale, but not years without logging. Rainfall contributed to explain the major proportion of variance as reflected by simple regression models and the standardized slopes in multiple regressions (Table 1). Floristic similarity decreased with environmental distance (Fig. 2b), and mean similarity among plots in the same foothill (intercept = 0.64) was greater than mean similarity among plots in different foothills (intercept = 0.41). A regression model with distance and all significant environmental variables explained about 40 % of the variance in floristic similarity among 1-ha plots. After

partialling out spatial autocorrelation (14 %), geographic distance explained higher proportion of variance among plots than environmental factors (18 and 7 %, respectively).

Within the permanent plots, pairs of 20 m × 20 m subplots presented a mean of 36 % species shared. Two subplots may share up to 73 % tree species even 300 m away, or have a total species turnover (i.e., 0 % species shared) at only 40 m away. A linear mixed-effects model with random intercept and slope was better than a random intercept model ( $L$ -ratio = 20.9,  $P < 0.0001$ ). This model explained 35 % of the floristic similarity encountered within and across the 14 plots analyzed, where 27 % corresponded to variance explained among plots, mainly due to environmental differences that occur at larger spatial scales, and 8 % corresponded to variance explained within plots according to local environmental variation.

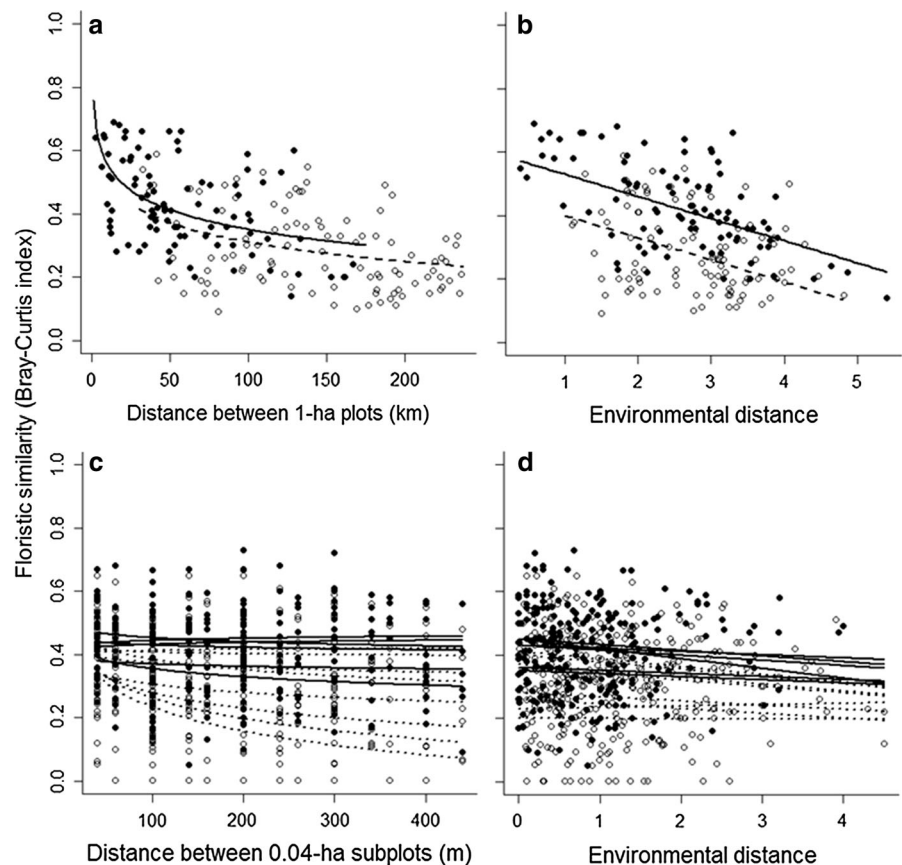
Among plots, mean floristic similarity (i.e., intercepts) was correlated with mean topographic slope across the fourteen 1-ha plots ( $r = -0.58$ ,  $P < 0.01$ ),

but not with climatic variables (temperature:  $r = -0.11$ ,  $P = 0.64$ ; rainfall:  $r = -0.33$ ,  $P = 0.15$ ). Thus, plots established in flat areas tended to present higher mean floristic similarity than plots established in hilly areas (Fig. 2c, d). Within plots, sand content in soil was the only significant environmental variable that explained floristic similarity, while distance along the plot explained a negligible variance percentage (Table 2). Although sand content in soil varied along the plots, distance explained <1 % of variance in a mixed model, and flat plots showed shorter environmental distances (i.e., higher similarity in sand content) than plots established in hilly areas (results not shown).

## Discussion

Niche and neutral assembly mechanisms help understand tree species turnover patterns at different spatial scales (Chase 2005; Leibold and McPeck 2006; John et al. 2007). We found that the relative contribution of

**Fig. 2** Distance decay of floristic similarity (Bray–Curtis index) among sample units. Similarity plotted against geographic distance and environmental distance calculated with all significant environmental variables among 1-ha plots (a, b). Black circles (solid line) = plot pairs in the same foothill and white circles (dotted line) = plot pairs in different foothills. Floristic similarity among 0.04-ha subplots within each plot (c, d). Black circles (solid line) = subplot pairs in flat plots and white circles (dotted line) = subplot pairs in plots established in hilly areas





**Table 2** Summary of the LMM for floristic similarity among 0.04-ha subplots varying intercepts and slopes by plots

Fixed effects	Estimate	SD	<i>t</i> -value	<i>P</i> value	VE (%)
Intercept	0.35	0.02	14.96	0.000	
Distance	−0.0002	0.0001	−2.04	0.01	
Sand content in soil	−0.0155	0.0080	−1.92	0.03	
Organic mater	0.0041	0.0065	0.63	0.53	
Topographic slope	−0.0008	0.0008	−0.94	0.35	
Random effects					
Intercept		0.0515			27.1
Distance		0.0003			0.2
Sandy soil		0.0152			7.9
Residuals		0.1232			64.8

Final model fitted by REML  
*SD* standard deviation; *VE*  
variance explained

distance to explain floristic similarity among sample units changes drastically with the spatial scale of analysis, reflecting different effects of dispersal limitations at regional and local scales. In addition, our results suggest that floristic similarity in seasonal premontane forests is influenced by environmental heterogeneity at regional, landscape, and local scales, and the factors operating in each scale are climate, topography, and soil texture, respectively. Topographic variation increases tree species turnover at intermediate scales, between regional climatic gradient and local edaphic variation.

#### Influence of geographic distance on community structure

Ecological communities are spatially structured across scales due to different factors or processes such as environmental gradients, biological interactions, and random processes (Ricklefs 2004; Borcard et al. 2011). We found that geographic distance between plots explained the largest fraction of regional variation in floristic similarity. Dispersal limitation may be a relevant factor at biogeographical scale where dispersion to great distances (e.g., >100 km) becomes infrequent for some species (Gilbert and Lechowicz 2004). According to biogeographical studies carried out in the flora of South America, Prado and Gibbs (1993) suggest that seasonal premontane forests are a remnant fragment of a greater extension of seasonal forests that characterized the central-south of South America during the dry climate of the last glacial period. In this way, premontane forests would be more

related to other deciduous or semi-deciduous forests (e.g., Caatinga, Atlantic Forest), than to the Andean Montane Forest, located above premontane forests (Prado and Gibbs 1993; Werneck et al. 2011). We found that few species with fleshy fruits probably dispersed by animals (*Myriocarpa stipitata* Benth., *Nectandra cuspidata* Nees and Mart., *Inga saltensis* Burkart, and *Muntingia calabura* L.), and with higher relative abundance in montane forests (1000–1300 m), are only present in the SW foothill. The NE foothill does not exceed the 1200 m of elevation and presents small patches of montane forests in their ridges. Probably the biogeographic origin of these species more related to montane forest could explain why they are absent in the NE foothill.

In opposition, dispersal limitation does not seem a mechanism for structuring local communities in seasonal premontane forests. The proportion of variance explained by distance within plots (<1 %) indicates no dispersal limitations at the local scale. These forests present approximately 80 % of tree species with wind dispersion of their fruits or seeds. Tree species fructify during the dry season, in concomitance with the absence of foliage, favoring dispersion. Vázquez and Givnish (1998) argue that these conditions favor dispersion several kilometers away from parental trees in dry or seasonal forests.

#### Environmental heterogeneity

Species turnover is determined by several factors acting at different spatial scales (Condit et al. 2002). Rainfall and temperature variation generates a

climatic gradient across mountain ranges where premontane forests are located. This regional gradient does not cause drastic changes in species composition but promotes changes in species abundance from one foothill to the other. The climatic control on species composition at the regional scale has been documented in many studies for tropical and temperate forests (e.g., Oliveira-Filho and Fontes 2000; Pyke et al. 2001; Svenning and Skov 2005). After variation partitioning, the fraction of floristic similarity explained by spatial autocorrelation (i.e., environmental factors spatially structured) is higher than pure environmental factors (14 and 7 %, respectively). In this way, rainfall is negatively correlated with latitude and longitude ( $r = -0.76$ ,  $r = -0.60$ ; respectively), and temperature shows an inverse and weaker pattern. In summary, the geographic gradient varies from NE to SW foothills (decreasing rainfall and increasing temperature), and determines that floristic similarity within foothills is higher than between foothills.

Topographic heterogeneity generates edaphic variation affecting drainage and nutrient deposition (John et al. 2007; Thiers and Gerding 2007). In this study, topography showed an independent effect of spatial scale. On one hand, floristic similarity decreased when topographic variation between 1-ha plots pairs increased, i.e. comparisons between one plot established in a hilly area and one plot established in a flat area. We found that some species present a higher relative abundance in flat plots decreasing their abundances in hilly areas, e.g., *Anadenanthera colubrina* (Vell.) Brenan, *Phyllostylon rhamnoides* (J. Poiss.) Taub., and *Cedrela balansae* C. DC, while other species show an inverse pattern, e.g., *Trichilia clausenii* C. DC., *M. stipitata*, and *Urera caracasana* (Jacq.) Gaudich. ex Griseb. On the other hand, subplot pairs located in flat plots shared higher proportion of species (in average 41 %) than subplot pairs within plots established in hilly areas (in average 30 %). Spatial niche differentiations related to topographic location has been documented in tropical and temperate forests as a relevant factor at local and landscape scales (Valencia et al. 2004; Thiers and Gerding 2007; Baldeck et al. 2012).

According to a multi-scale control model, secondary or minor factors at larger spatial scales may become relevant when decreasing the spatial scale of analysis (Ricklefs 2004). Within plots, local edaphic variation expressed as sand content in soil explains about 8 % of floristic similarity. We found that two neighbor subplots

(separated by 20 m) may share from 67 to only 5 % of tree species. However, this difference decreases in flat plots where two subplots 20 m away may share between 25 and 67 % of tree species. Concordantly, flat plots present higher edaphic similarity than plots established in hilly areas (i.e., lower difference in sand content in soil between subplot pairs). Along 500 m within a plot, valley or ridge topographic locations may generate changes in soil characteristics, humidity (of both environment and soil), and changes in canopy structure or direct sunlight exposure. Other factors such as occurrence of gaps and canopy cover could increase the percentage of variance explained locally.

#### Final considerations

Floristic similarity explained exclusively by environmental factors is low and about the same at both spatial scales (7 and 8 % at regional and local scales, respectively). Adding other environmental variables could increase the fraction explained by environment and change the fraction explained by distance, because these additional environmental variables also present spatial structure. However, we consider that the environment, mainly at regional scale, was described quite in detail in our study; since we include the most generally used climatic variables, we incorporate the topographic variation and also anthropic disturbance measured as years without logging intervention (the principal use of these forests).

Within 1-ha plots, variation in soil texture (expressed as sand content) seems to be more relevant than variation in nutrients. No relation was detected between floristic similarity and organic matter. We found high percentage of organic matter in the soil samples (mean =  $4.25 \pm 0.18$  %), and this result may be reflecting that it is not a limiting resource for tree species. Generally, premontane forests have been characterized by their deep and fertile soils (Brown et al. 2001; Malizia et al. 2012). As we recognized above, additional environmental factors at the local scale, such as light availability, can increase the fraction explained by environment. Biological aspects such as habitat preference (Phillips et al. 2003; Valencia et al. 2004; John et al. 2007) and species functional differentiation (e.g., gap-dependent species; Webb and Pearts 2000) may be mechanisms that contribute to explain species occurrence in local communities of seasonal premontane forests.

Other consideration about our approach at the local scale is that given the output of mixed models, we found a proportion of variance explained by “plot effect” corresponding to environmental variations at larger spatial scales. However, using this approach, we can estimate the fraction of variance explained within plots, i.e., tree species turnover across hundreds of meters. Recently, some studies have disentangled the contribution of different factors by modeling all spatial structures (from broad to fine scale) detected in plots of 25–50 ha in size (e.g., Legendre et al. 2009; Silva et al. 2011; Baldeck et al. 2012), but few studies have analyzed patterns of species turnover across scales considering different sample sizes and extensions (e.g., Karst et al. 2005).

Finally, we point two relevant aspects related to global change and the conservation of seasonal premontane forests. First, rainfall in the subtropical Andes has increased during the last three decades (Minetti and González 2006). The impact of climatic change on tree species composition and distribution has been suggested for subtropical montane forests near tree line (Grau and Veblen 2000). Here, we extend this possibility to the other extreme of the altitudinal gradient, given the relative contribution of climate (mainly rainfall) to determine floristic patterns in seasonal premontane forests. Models of species distribution recently developed determine a general trend in premontane tree species to migrate toward higher altitudes (Pacheco et al. 2010). And in second place, variations in communities' compositions according to environmental gradients at different spatial scales should be taken into account in conservation planning. For example, we found that topography is a relevant environmental factor at regional and local scales, generating changes in communities composition between flat and hilly areas. However, few patches of premontane forests in flat areas remain in well conserved status because generally are used to agriculture. It seems clear from this study, that quantitative aspects of the species distribution, such as the relative contribution of niche and neutral processes to explain floristic patterns, can strengthen conservation strategies at different spatial scales, and therefore could be a useful tool in conservation planning.

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