



Original article

Distribution of functional traits in subtropical trees across environmental and forest use gradients

Cecilia Blundo ^{a,*}, Lucio R. Malizia ^b, Mario González-Espinosa ^c^a CONICET, Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán, CC 34, Yerba Buena, 4107, Tucumán, Argentina^b Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 45, San Salvador de Jujuy, 4600, Jujuy, Argentina^c Departamento de Conservación de la Biodiversidad, El Colegio de la Frontera Sur (ECOSUR), Carretera Panamericana y Periférico Sur s/n, Barrio de María Auxiliadora, San Cristóbal de Las Casas, Chiapas, 20290, Mexico

ARTICLE INFO

Article history:

Received 21 April 2015

Received in revised form

22 September 2015

Accepted 23 September 2015

Available online xxx

Keywords:

Demographic rates

RLQ analysis

Seasonal premontane forests

Shade tolerance

Tree functional types

Tree morphology

ABSTRACT

The relationship between functional traits and environmental factors contribute to understanding community structure and predicting which species will be able to elude environmental filters in different habitats. We selected 10 functional traits related to morphology, demography and regeneration niche in 54 subtropical premontane tree species to describe their main axes of functional differentiation. We derived species traits, environmental variables and species abundance data from 20 1-ha permanent plots established in a seasonal subtropical premontane forest in northwestern Argentina. We analyzed the relationship between species functional traits and environmental factors through RLQ and fourth-corner analyzes. We found an axis of structural differentiation that segregates understory from canopy species, and an axis of functional differentiation that segregates species that maximize resource acquisition from those that promote resource conservation. Environmental and forest use gradients operate hierarchically over subtropical premontane tree species influencing the distribution of demographic and morphological traits. The interaction between climatic and topographic factors influences the distribution of species functional traits at the regional scale. In addition, the history of forest use seems to operate at the landscape scale and explains the distribution of species traits reflecting a trade-off between resource acquisition and resource conservation strategies in secondary forests across different successional stages. Our results support the idea that functional traits may be used to analyze community structure and dynamics through niche differentiation and environmental filtering processes.

© 2015 Elsevier Masson SAS. All rights reserved.

1. Introduction

Several mechanisms have been proposed to explain species coexistence within local communities. Niche assembly mechanisms such as habitat segregation, functional differentiation of species and biological interactions imply some degree of spatial and temporal differentiation in resource utilization among plant species (Wright, 2002; Silvertown, 2004). In opposition, neutral assembly mechanisms assume that species are competitively equivalent and plant communities result from random local processes associated to seed dispersal (Hubbell, 2001; Chave et al., 2002). Actually, both niche and neutral processes are considered as determinants of species diversity and distribution (Chase, 2005; Leibold and

McPeck, 2006), but their relative contribution may vary with the scale of analysis (Ricklefs, 2004).

In forest ecology, the functional approach that classifies pioneer/ climax tree species explains species coexistence within local communities (Swaine and Whitmore, 1988; Wright, 2002). Variation in plant ecological strategies determines whether species functional types show advantages in different environmental conditions (Grime, 2006; Westoby and Wright, 2006). It has been proposed that correlations between morphological and functional traits related to capture, use and release of resources reflect a trade-off between resource acquisition and conservation (Díaz et al., 2001; Poorter et al., 2006). While some species have high tissue turnover and growth rates, reflecting faster resource acquisition, other have little or slow tissue turnover and high survival rates, promoting resource conservation (Reich, 2014).

Inter-specific variation in morphological traits has been used to define plant strategies (Reich et al., 2003; Easdale et al., 2007a), and

* Corresponding author.

E-mail addresses: ccblundo@gmail.com (C. Blundo), luciomalizia@gmail.com (L.R. Malizia), mgonzalez@ecosur.mx (M. González-Espinosa).

classify functional groups of species in different communities (e.g. Müller et al., 2007; Saldaña-Acosta et al., 2008; Souza et al., 2014). Some basic features related to leaves and stems (or trunks), maximum height and seed size, are key to define functional plant strategies (Westoby, 1998). Other features such as dispersal mode and environmental conditions required to recruitment also contribute to define how plants use resources (McIntyre et al., 1999; Lavorel and Garnier, 2002). Additionally, functional classifications based on species demographic patterns reflect intrinsic characteristics and integrate the physiological response to different environmental and biological factors (Condit et al., 1996; Easdale et al., 2007b).

The relationship between functional traits and environmental factors contribute to understand community structure and predict which species will be able to elude environmental filters in different kinds of habitats (Díaz et al., 2001). These relationships may be the result of evolutionary processes related to adaptation to particular conditions (e.g. climatic seasonality) or ecological processes that reflect a trade-off between survival and growth (e.g. gap dynamics) (Reich et al., 2003; Reich, 2014). Climate and disturbance regimes are important broad scale environmental filters predicting ecosystem dynamics (McIntyre et al., 1999). In forest systems, land-use patterns may also influence vegetation responses through species turnover, changes in relative abundance or changes in species traits (Raevel et al., 2012). Understanding how functional traits are distributed across environmental gradients allow for a better prediction of changes in species composition in response to global changes (McGill et al., 2006).

Seasonal subtropical premontane forests in northwestern Argentina are deciduous forests distributed at low-elevations of the subtropical Andean mountain range. Currently, these ecosystems exhibit some degree of anthropogenic intervention, mainly due to selective logging of valuable timber species (Brown et al., 2001). In this paper, we test the hypothesis that changes in environmental conditions originated by disturbances favor differential establishment and survival of tree species in relation to demographic and morphological attributes. Demographic traits associated to species occupying areas subjected to recent disturbances will include fast growth and tree turnover rates due to higher resource availability. These species will tend to present large leaf size, low wood density and high recruitment in gaps. Moreover, species of older forests with continuous canopies, will exhibit opposite demographic and morphological traits; i.e. slow growth and tree turnover rates, small leaf size, high wood density and low recruitment rate (Westoby, 1998; Reich, 2014). We selected 10 functional traits related to morphology, demography and regeneration niche for 54 subtropical premontane tree species to describe functional differentiation axes, and to analyze the relationship between species functional traits and environment and forest use.

2. Materials and methods

2.1. Study area

Seasonal subtropical premontane forests in northwestern Argentina represent the southernmost extension of Andean Neotropical montane forests. Climate is subtropical with a marked dry season and occasional frosts during May–August (Brown et al., 2001). Annual rainfall range is 800–1000 mm, concentrated in summer months (~80% of rain between November–March), when temperature can exceed 40 °C (Bianchi and Yáñez, 1992). The tree flora is relatively well known, with more than 79% deciduous tree species (Digilio and Legname, 1966; Legname, 1982; Killen et al., 1993). Along the altitudinal range (400–900 m), premontane

forests are distributed on flat and hilly areas with up to 40% slope. During the last century, large areas of forest in the flatlands have been replaced by agriculture (e.g. sugar cane, citrus, soybean), while the remaining forest is generally used for timber extraction through selective logging (Brown et al., 2001).

2.2. Tree species census

We established 20 1-ha (20 × 500 m) permanent plots between 2002 and 2009, distributed across 8000 km² of subtropical premontane forests (22–24° S and 63–65° W). All plots were corrected for slope to include 1 ha. In each plot we obtained a full inventory of trees ≥10 cm diameter at breast height (dbh). We marked trees with numbered aluminum tags, measured their dbh (at 1.30 m height, avoiding trunk irregularities) and identified them to species or morphospecies whenever field identification was not possible. We also collected voucher specimens of all species and morphospecies to control against voucher specimens identified by specialists at the University of Jujuy herbarium. Five years after the establishment of the plots, we measured again 17 out of the 20 plots.

2.3. Environmental factors

We obtained climatic, topographic and logging history data for all plots. Climatic data were derived from local precipitation and mean monthly temperature models from a map surface developed by Bianchi et al. (2008) for NW Argentina. Both models were generated based on data from 450 meteorological stations, recorded between 1934 and 1990. We measured slope in 25 (20 × 20 m) subplots within each 1-ha plot using a clinometer; we then used mean slope to characterize topography in each plot. Since plots were established in forests that have been affected by selective logging in the past, we considered the year of the last intervention (data reported by landowners) as a measure of forest successional age after major disturbance (3–30 years without previous logging at the time of plot establishment) and basal area of stumps as a measure of disturbance intensity (0–8.5 m² ha⁻¹).

2.4. Species functional traits

We developed a matrix of species-traits including four morphological traits (maximum height, wood density, leaf length and dispersal mode), four demographical traits (growth, mortality, recruitment and tree turnover rates), and two regeneration niche traits (shade tolerance and affinity to soil fertility) (Appendix A, Table A.1). We measured height with a clinometer for a minimum of 25 trees within each permanent plot and then we estimated height for the rest of the censused individuals using the clinometer measures as a reference. Maximum height for each tree species was estimated as the average height of all adult trees censused in the permanent plots. We derived species wood density from INTI native species database (available at <http://www.inti.gob.ar/maderaymuebles/index.php?seccion=maderasnativas>). We used leaf length values reported by Legname (1982) as a measure of leaf size. We classified tree species according to propagule dispersal mode (fruits or seeds) based on descriptions reported by Legname (1982) and field observations. Species were grouped as anemochorous (fruits or seeds with winged appendages), zoochorous (fleshy fruits or seeds with an aril), and autochorous (fruits or seeds that fall by gravity under the parental tree).

All demographic variables were computed using the data generated from the repeated measurement of 17 permanent plots. We calculated relative growth rate as the change in dbh (natural

logarithm) between the first and second measurement in species with at least 10 individuals measured twice. Mortality and recruitment rates were calculated for each species; all demographic formulas followed Condit et al. (2004). Finally, we calculated annual turnover rates for each tree species as the mean between losses due to mortality and gains due to recruitment.

We characterized regeneration niche using tree sapling abundance and soil data measured in 14 out of the 20 1-ha permanent plots. Ten samples (sapling and soil) were obtained every 40–60 m at each plot, using point transects along the 500-m. At each sample point we recorded sapling abundance per species (1–5 cm dbh) within 5×5 m regeneration subplots (140 regeneration subplots). Additionally, we collected four pooled topsoil (0–20 cm depth) samples within a 3×3 m area for each subplot. Soil samples were analyzed using standardized protocols from the Instituto Nacional de Tecnología Agropecuaria (INTA- Cerrillos, Salta, Argentina). We considered 10 physical and chemical characteristics of the soil (content of sand, silt or clay, pH, salinity, water saturation capacity, organic matter, C, N and P); to describe sapling distribution along edaphic gradients we performed a weighted averages analysis, following Easdale et al. (2007a). For each species, we calculated the average value of each soil variable in the subplot where the species occurred, weighted by sapling abundance in this same subplot. Then, we analyzed the weighted averages matrix with 10 edaphic variables and 54 tree species with a Principal Component Analysis (PCA). The first principal component explained 48% of the total variance, summarizing species differential affinities to organic matter, C, N and water saturation capacity (loadings: 0.45, 0.45, 0.43 and 0.40, respectively). Texture components (sand, silt and clay), pH, salinity and P showed loadings <0.25 on the first axis, indicating that species affinities to these variables were independent from their affinities to the first variables and that they had no weight on this axis. We used species scores along axis 1 as the measure of their affinity to soil fertility. Finally, we estimated shade tolerance as the species capacity to support sapling populations under closed canopy cover, following Easdale et al. (2007a). For each species we computed the quotient between sapling frequency (1–5 cm dbh) in 5×5 m regeneration subplots, and adult tree frequency (dbh > 10 cm) in 20×20 m subplots containing each regeneration subplot. Therefore, the more shade tolerant the species, the more likely that its saplings would be found under the forest canopy. In opposition, juvenile trees that are capable of growing in bright light conditions (e.g. pioneers) tend to have low survivorship under adult trees and closed canopy.

2.5. Data analysis

We performed a Principal Coordinate Analysis (PCoA) for a matrix of eight traits and 54 species to explore the main patterns of morphological and demographic differentiation among tree species. We used Gower distance for the similarity matrix, a proximity measure that allows combining quantitative and qualitative variables (Gower, 1971). As many of the variables did not fit normal distributions and some of them had natural outliers, we used Spearman correlations to explore the associations of (1) morphological to demographic traits, (2) PCo axes to morphological and demographic traits, and (3) PCo axes to regeneration niche variables. Shade tolerance and affinity to soil fertility were correlated to the PCo axes, because they represent species responses that depend on their morphological and demographic traits (e.g. species with large leaves and rapid growth should tend to regenerate in sites with greater light availability). We used the *k*-means method to define the optimal number of Trees Functional Types (TFT) along the first PCo axes.

We simultaneously analyzed matrices of species traits ($Q_{(q \times m)}$, 54 species by 10 functional traits), environmental variables ($R_{(n \times p)}$, 20 1-ha plots by five climatic, topographic and logging history variables), and tree species abundance ($L_{(n \times q)}$, 20 1-ha plots by abundance of 54 species) to describe distribution of species functional traits across environmental and forest use gradients. We performed RLQ analysis (Dolédéc et al., 1996) and fourth-corner analysis (Legendre et al., 1997) to summarize the relationships between species traits and environmental factors in a $D_{(m \times p)}$ matrix. RLQ is an extension of co-inertia analysis that searches simultaneously for linear combinations of variables in *Q* and lineal combinations of variables in *R*, maximizing covariance and weighting per *L* matrix (Dolédéc et al., 1996). Finally, we computed permutation tests to evaluate significant relationships in matrix *D*. According to Dray and Legendre (2008), in order to reject the null hypothesis that there is no relationship between *Q* and *R* using fourth-corner, one must first check that there is no relationship between *L* and *Q* nor between *L* and *R*. Generally, RLQ and fourth-corner analyses are jointly used to analytically and graphically identify groups of species traits under certain environmental conditions (e.g. Lienin and Kleyer, 2011; Raavel et al., 2012). We performed all analyses using R statistical software (R Development Core Team, 2013) using packages *vegan* (*vegdist* function), *stats* (*cmdscale* function) and *ade-4* (*dudi.pca*, *dudi.coa*, *rlq* and *fourth-corner* functions).

3. Results

3.1. Functional differentiation in subtropical premontane trees

We found two main differentiation axes for the 54 tree species analyzed, based on eight morphological and demographic traits. First, a structural differentiation axis segregated canopy species, generally wind-dispersed, with low mortality and tree turnover rates, from sub-canopy or understory species, in general zoochorous or autochorous, with high mortality and turnover rates. PCo 1 supported this result, explaining 37.9% of the total variance. Maximum height, dispersal mode, mortality and turnover rates explained distribution of tree species along PCo 1 ($\rho > 0.70$, Table 1). A second functional differentiation axis segregated species that maximize resource acquisition from those with a strategy of resource conservation. Species with medium to long leaves, high growth rates and low to intermediate wood density were separated from species with small leaf length, low growth rates and high wood density. PCo 2 showed this functional differentiation explaining 23.7% of the total variance. *K*-means analysis over the scores on the PCo axes allowed identifying four TFTs: sub-canopy or understory species (TFT 1) and canopy species (TFT 2), both with faster resource acquisition strategy, and understory (TFT 3) and large-sized trees (TFT 4), both with resource conservation strategy (Fig. 1).

Shade tolerance was associated with the two PCo axes, showing that species with positive scores on PCo 1 and negative scores on PCo 2, were those with highest shade tolerance in the recruitment stage; i.e., species that had greater sapling abundance under adult trees (Table 1, Fig. 1). Affinity to soil fertility did not associate to any PCo axes nor to species traits, exhibiting only a low negative correlation to shade tolerance ($\rho = -0.27$, $P < 0.05$, Fig. 2). On the one hand, this relationship reflects that few premontane tree species presented high shade tolerance (~15% of species analyzed; mostly understory species with high wood density of TFT 3, e.g. *Piper tucumanum*, *Sebastiania brasiliensis*, *Trichilia clausenii*, *Eugenia uniflora*). On the other hand, few species (~17% of species analyzed; generally canopy species of TFTs 2 and 4, e.g. *Caesalpinia*

Table 1

Spearman correlation coefficients with $P \leq 0.05$ between: (a) morphological traits, (b) demographic and morphological traits, (c) PCo axes and species traits, and (d) regeneration niche, morphological and demographical traits. H = maximum height (m), WD = wood density (g cm^{-3}), D = dispersal mode (1: anemochory; 2: zoochory; 3: autochory), L = leaf length (cm), M = mortality rate (%), R = recruitment rate (%), TT = tree turnover rate (%), G = growth rate (mm year^{-1}), ST = shade tolerance (frequency of sapling, frequency of adult-tree $^{-1}$), ASF = affinity to soil fertility (PCA scores).

	Morphology				Demography				Regeneration	
	H	WD	D	L	M	R	TT	G	ST	ASF
(a) H										
WD	0.36									
D	-0.62									
L		-0.37								
(b) M	-0.54	-0.47	0.35							
R		-0.25								
TT	-0.52	-0.50	0.36		0.91	0.46				
G	0.25	-0.35		0.63		0.27				
(c) PCo 1	-0.79	-0.61	0.74	0.26	0.70	0.31	0.75		0.35	
PCo 2	0.50	-0.27	-0.39	0.81		0.25		0.79	-0.35	
(d) ST	-0.35		0.39	-0.26		0.40	0.30			
ASF									-0.27	

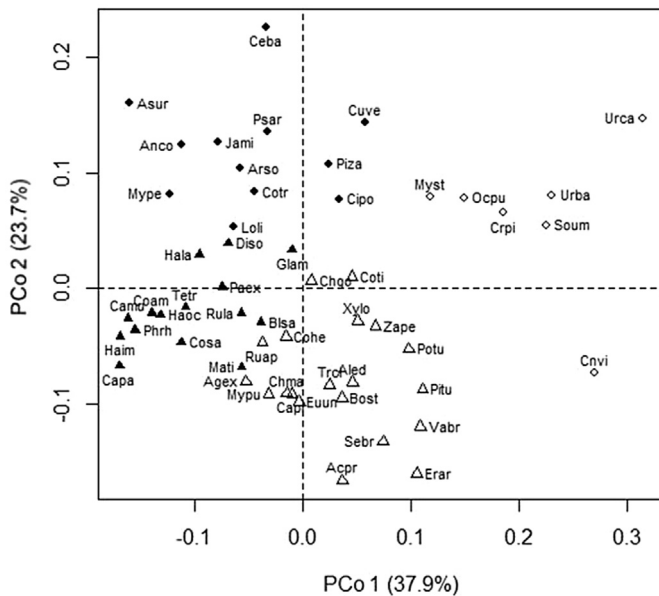


Fig. 1. Ordination of 54 tree species on the multivariate space based on eight morphological and demographic traits. Symbols represent each TFT determined by k -means analysis. Black symbols represent canopy trees and white symbols represent sub-canopy or understory trees. Circles and triangles correspond to species that maximize resource acquisition or conservation, respectively. Species codes are given in Appendix A, Table A1.

paraguariensis, *Maclura tinctoria*, *Pseudobombax argentinum*) exhibited high affinity to soil fertility, recruiting in soils with $>5.5\%$ of organic matter content (organic matter content in soil samples ranged from 3% to 10%).

3.2. Relationship between species traits and environmental factors

Species traits, environmental factors and species abundances

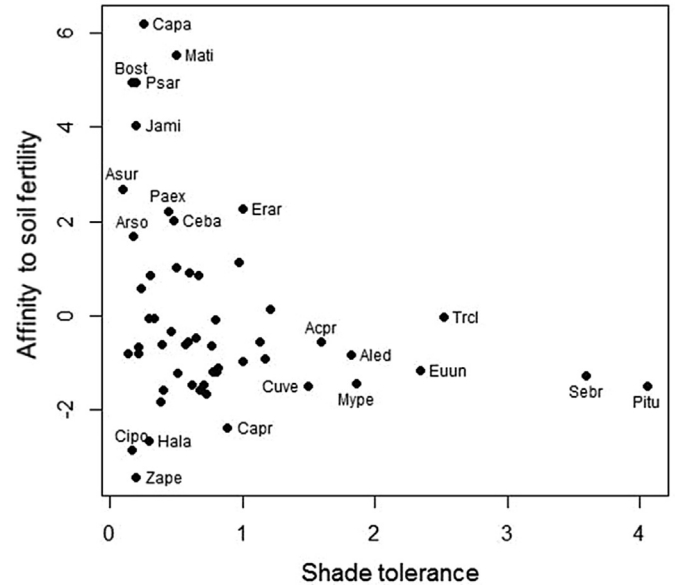


Fig. 2. Shade tolerance vs. affinity to soil fertility in 54 species of subtropical trees. Affinity to soil fertility corresponds to PCA scores performed with weighted average analysis of edaphic variables; positive scores reflect high nutrient content (organic matter, C and N). Shade tolerance corresponds to frequency of sapling. Frequency of adult-tree $^{-1}$; higher values reflect high shade tolerance. Species codes are given in Appendix A, Table A1.

were highly correlated (RLQ, $P < 0.001$), suggesting that the observed patterns are not the result of random processes and that RLQ axes represent relevant dimensions of differentiation. The major variation was captured by the first RLQ axis (81%), reflecting the distribution of plots along climatic gradients (Table 2, Fig. 3 b and d). Species traits associated to axis 1 were maximum height, wood density, dispersal mode, as well as turnover, mortality and recruitment rates. Functional traits related to regeneration niche, however, were weakly correlated to RLQ 1. Relationships between

Table 2

Summary of RLQ analysis showing correlations of both axes with environmental factors and species traits.

	RLQ 1	RLQ 2
Eigen value	0.48	0.08
Variance explained (%)	81	14
Temperature	0.75	0.38
Rainfall	−0.88	−0.22
Topographic slope	−0.36	−0.87
Years without logging	0.24	−0.69
Basal area of stumps	0.25	0.56
Maximum height	0.84	0.27
Wood density	0.75	−0.15
Dispersal mode	−0.74	0.06
Leaf length	−0.16	0.62
Mortality	−0.72	−0.13
Recruitment	−0.59	0.53
Tree turnover	−0.78	0.08
Growth	−0.08	0.88
Shade tolerance	−0.50	−0.18
Affinity to soil fertility	−0.58	0.28

environmental factors and species traits included a positive correlation between rainfall and demographic traits; i.e., more annual rainfall implied higher turnover rates, given by higher mortality and recruitment (Table 3). Plots with higher rainfall (negative RLQ 1 in Fig. 3) were characterized by tree species with low maximum height, low wood density, low affinity to soil fertility, and zoochory

and autochory as predominant dispersal modes. Mean annual temperature showed an inverse but weaker pattern; i.e., plots with higher mean annual temperature (positive RLQ 1 in Fig. 3) were characterized by species with high maximum height and high affinity to soil fertility, and predominantly wind-dispersed (Table 3, Fig. 3c and d).

The second RLQ axis explained considerably less variance (14%), and ordered the plots along topographic and forest use gradients (Table 2). On the one hand, plots with negative scores on axis 2 were characterized by high topographic slopes (i.e. plots established in hilly areas) and generally included older secondary forests with more than 20 years without selective logging. Species traits associated to these environmental characteristics were short leaves and low growth and recruitment rates. On the other hand, plots with positive scores on axis 2 were located on flat areas (slope <5%), and included recently logged forests (3–8 years without logging and high basal area of stumps), as well as species with higher growth and recruitment rates and longer leaves (Table 2, Fig. 3b–d). Correlations between environmental factors and species traits on RLQ 2 were weaker. However, they showed that in older secondary forests, notable species traits were high maximum height, high wood density, and high affinity to soil fertility during the regeneration stage, lower recruitment rates, and predominantly wind-dispersed (Table 3). Finally, topography had an influence over demographic traits, because plots located on hilly areas exhibited lower growth rates and higher mortality rates (Table 3).

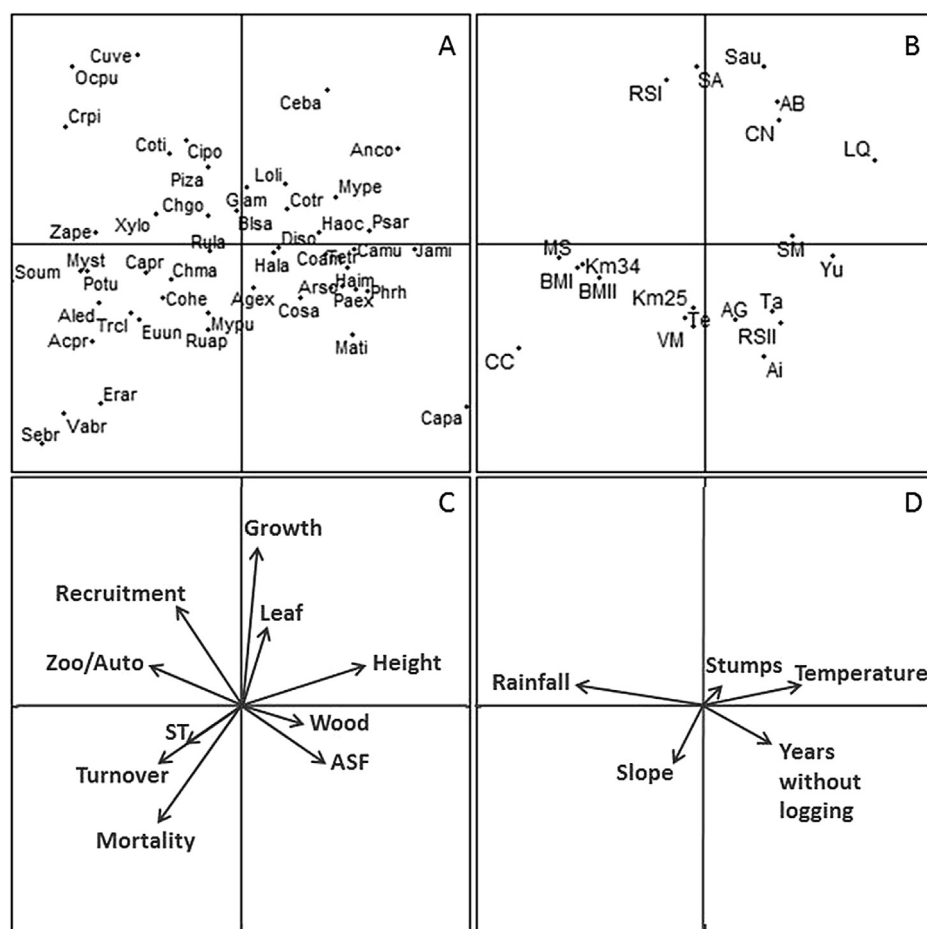


Fig. 3. Ordination graphics along RLQ axes of (A) 54 species of subtropical premontane trees, (B) 20 1-ha permanent plots, (C) 10 species functional traits, and (D) Five environmental characteristics in the 20 permanent plots. ST = shade tolerance, ASF = Affinity to soil fertility. Species codes are given in Appendix A, Table A1.

Table 3

Matrix $D_{(m \times p)}$ generated by fourth-corner analysis showing correlations between environmental factors and species traits. Significance levels: (****) $P < 0.001$, (**) $P < 0.01$, (*) $P < 0.05$.

	Temperature	Rainfall	Topographic slope	Basal area of stumps	Years without logging
Maximum height	0.24****	−0.27****	−0.09*	0.04	0.13*
Wood density	0.09	−0.15**	−0.04	0.01	0.10*
Dispersal mode	−0.17**	0.18**	−0.02	0.01	−0.12*
Leaf length	0.04	−0.01	−0.08	0.03	−0.01
Mortality	−0.09	0.17****	0.12**	−0.04	0.02
Recruitment	−0.01	0.17**	−0.05	−0.02	−0.14**
Tree turnover	−0.07	0.20****	0.08	−0.04	−0.04
Growth	0.06	0.05	−0.15**	0.04	−0.08
Shade tolerance	−0.08	0.06	0.05	−0.01	−0.06
Affinity to soil fertility	0.20****	−0.20****	0.02	−0.04	0.12*

4. Discussion

Functional traits can be used to analyze community structure through niche differentiation and environmental filtering processes (Kraft et al., 2008; Paine et al., 2011). In this study, we found that demographic and morphological traits segregated 54 species of subtropical premontane trees across a multidimensional space in terms of tree structure and function. In addition, rainfall, temperature, topographic slope and years without logging are shown as environmental factors operating hierarchically over the regional species pool as evidenced by the first two RLQ axes. The climatic gradients of rainfall and temperature reflected along RLQ 1, and the forest use and topographic gradients reflected along RLQ 2, determine the distribution of species functional traits across the seasonal subtropical premontane forests of northwestern Argentina.

4.1. Tree classification into functional types

Distinction between pioneer and late-successional tree species has been a basic differentiation criterion in successional dynamics (Swaine and Whitmore, 1988). In premontane forests, vertical habitat segregation (understory, sub-canopy and canopy crown levels) and species longevity add complexity to this simple dichotomy. Many studies have documented the importance of tree height as an axis of differentiation in forest ecology (e.g. Loehle, 2000; Gourlet-Fleury et al., 2005). Habitat segregation through a vertical gradient of light may contribute to tree-species coexistence (Turner, 2001).

Here, we found a close relationship between tree height and dispersal mode, showing that wind-dispersal is the most frequent dispersal syndrome for canopy trees, and that zoochory and autochory are the most frequent dispersal forms for sub-canopy and understory trees. Anemochory is advantageous in seasonal dry forests, where the absence of foliage during the dry season can favor dispersal of large, canopy trees (Vázquez and Givnish, 1998). Furthermore, the higher incidence of zoochory in more humid sites, relative to drier sites, parallels a general trend found in the Neotropics, where zoochorous species disperse in the wet season and are prevalent in sites with more rain (Gentry, 1988). In subtropical Andean forests of northwestern Argentina, species with fleshy fruits fruit during the wet season (Giannini, 1999), and our results show that zoochory is predominant among tree species in plots with greater rainfall (negative RLQ 1 in Fig. 3).

The turnover dynamics of trees determine species longevity; lower recruitment and mortality were associated with longer life

cycles and consequently with higher tree longevity (Laurance et al., 2004). In montane forests, canopy species tend to have low turnover rates and to be more abundant in mature forests or in late-successional stages (Easdale et al., 2007b). Classification of trees into functional groups consider the existence of four main ecological strategies according to adult stature, longevity and light requirements in regeneration (Turner, 2001; Gourlet-Fleury et al., 2005; Poorter et al., 2006; Souza et al., 2014). Our results support this idea since we found four functional types in seasonal premontane forest: short-lived pioneers in the sub-canopy or understory, long-lived pioneers in the canopy, and understory shade-tolerant and large-sized trees, both with high wood density and a resource-conservation strategy.

A second differentiation axis in subtropical premontane trees represents the trade-off between faster resource acquisitions in opposition to resource conservation strategies. Studies in different plant communities have documented this functional differentiation that distinguishes species with fast growth rates that are competitively superior in resource-rich environments (e.g. recently disturbed sites) from species with slow growth rates that are able to persist in resource-limited environments (Reich et al., 2003; Wright et al., 2004). According to our prediction, TFTs 1 and 2 represent species with strategies of fast resource acquisition, showing high growth rates, medium to long leaves and low to intermediate wood density. Species with this strategy showed higher relative abundance in recently logged forests (e.g. *Cupania vernalis*, *Ocotea puberula*, *Cedrela balansae*, see Fig. 3a and b). On the other extreme of the functional spectrum, TFTs 3 and 4 represent species with strategies for resource conservation, showing short leaves, sometimes evergreen or semi-deciduous species (particularly understory trees of TFT 3), with low growth rates and high wood density. In addition, we found that the most shade tolerant species show these functional traits related to resource conservation. Many understory tree species of TFT 3 (e.g. *P. tucumanum*, *Sebastiania brasiliensis*, *Trichilia clausenii*, *Eugenia uniflora*) are in the extreme of the shade-tolerance gradient, showing highest sapling abundance under adult trees. In agreement with Reich et al. (2003), a whole-plant shade tolerance strategy involves maintenance of captured resources rather than high resource gain, so traits that promote resource conservation should be selected.

Regeneration strategy, generally simplified in two groups as light demanding and shade tolerant species (Swaine and Whitmore, 1988), may also be more complex due to changes in species response at different developmental stages (Dalling et al., 2001; Méndez-Dewar et al., 2014). In this study, we found that, in general, tree saplings survive inside the forest at intermediate light

conditions and change their strategy by increasing their growth rates when a clearance occurs (e.g. tree-fall gaps, selective logging). Species responses to temporal light gradients reflect a trade-off between survival and growth with low and high light availability, respectively (Reich, 2014). In tropical forests, Wright et al. (2003) found that few species occurred in the extremes (low, high) of the shade-tolerance gradient and, in general, species exhibited intermediate light requirements and changed their strategies when this resource increased. We found that canopy premontane trees (TFTs 2 and 4) had saplings inside the forest, which may shift to a faster resource acquisition strategy in response to a canopy opening. Canopy species (mainly TFT 2) with high longevity may colonize early successional stages through high growth rates, and represent about 60% of aerial biomass in late-successional stages (e.g. *Anadenanthera colubrina*, *Myroxylon peruiferum*, *Cupania vernalis*). Poorter (2009) suggests that correlations between functional traits and light conditions during regeneration stages are weak in seasonal forests due to the opening of the canopy during the dry season. At the premontane forests of northwestern Argentina, intermediate light conditions occur during a long period in the year (6–7 months) when trees lose their leaves during the dry season, allowing more light penetration to the understory.

4.2. Distribution of functional traits across environmental and forest use gradients

Relationships among economic functional traits (e.g. SLA, leaf life span, leaf [N]) and temperature or precipitation gradients have been identified, but explained little variance (Wright et al., 2004; ter Steege et al., 2006). Climate explains a small fraction of variation in functional traits measured at the organ level because species with a variety of economic strategies are distributed in communities and ecosystems reflecting high diversity of microenvironments (Reich, 2014). Furthermore, demographic and morphological traits, measured at the individual level, reflect the physiological response to different environmental factors (Condit et al., 1996; Easdale et al., 2007b), and many studies have documented their variation across climatic gradients (e.g. Phillips et al., 2004; Condit et al., 2004; Poorter, 2009).

We found association between large-scale climatic variation and the distribution of demographic and morphological traits in subtropical premontane tree species. Although coefficients of correlation are low, its significance shows systematic variation between precipitation and temperature with respect to demographic and morphological traits. Sites with higher annual rainfall located in the northeastern side of the study area (with about 175 mm more annual rainfall than the southwestern side) are associated to higher turnover rates. In addition, the combination of heavy rains and steep topography promote more landslides in this portion of premontane forests (Cristóbal et al., 2009). Higher tree turnover in the northeastern side and the morphological traits associated to higher rainfall (i.e. lower maximum height and lower wood density) reflect higher natural disturbance regimes in this sector of the study area.

Furthermore, higher mean annual temperature, which characterizes the southwestern side of the study area, is associated to higher maximum tree height and, marginally, to higher wood density ($P < 0.06$). Species traits related to resource acquisition, distribution and conservation, influence forest productivity at the ecosystem level (Green et al., 2003; Reich, 2012). We explored biomass accumulation patterns and found that it varies according to high wood-density species abundance occurring at the large scale. For example, considering only those permanent plots established in older secondary forests (20–30 years without logging), plots in the southwestern side showed higher biomass than plots in

the northeastern side of the study area (425 vs. 289 ton C ha⁻¹ on average, in the southwestern and northeastern plots, respectively). Species with higher wood density, and consequently with higher carbon storage capacity, are more abundant in the southwestern side.

Forest use history, estimated as years without logging, is also associated to demographic and morphological traits, as shown in the second RLQ axis, although with less relative importance. Plots established in older secondary forests, frequently in hilly areas, are dominated by species with high maximum height, wind-dispersal, high wood density and low recruitment and growth rates. Forest use history allows understanding vegetation response along anthropic disturbance gradients, especially changes in species abundance and in the emerging functional traits within plant communities (Lienin and Kleyer, 2011; Raavel et al., 2012). The correlation between years without logging and the mean slope across the 20 1-ha plots ($r = 0.39$, $P = 0.081$) might suggest a pattern of lower pressure of forest use in hilly areas where selective logging involves the use of a more developed infrastructure. However, older secondary forest plots in flat areas (e.g. SM, Yu in Fig. 3 b) also harbored many species with high maximum height, wind-dispersal, high wood density, and low recruitment and growth rates.

5. Conclusion

Studies at the community scale analyzing distribution of functional traits (e.g. Lienin and Kleyer, 2011; Cavender-Bares and Reich, 2012), indicate the role of multiple processes and the signature of spatial scale on those processes. We found that environmental and forest use gradients operate hierarchically over subtropical premontane tree species influencing the distribution of demographic and morphological traits. The interaction between climate and topographic variation influence the distribution of functional traits at the regional scale. In addition, the history of forest use seems to operate at the landscape scale and explains the distribution of species traits along a functional differentiation axis, which reflects a trade-off between resource acquisition and conservation strategies in secondary forests after selective logging. Our study provides evidence that climate, topography and forest use are associated to shifts in the distribution of functional traits and determine community composition and forest dynamics. The functional traits-environment approach is promising to achieve a better understanding on how climatic change will affect the distribution of tree species in seasonal forests, and how selective logging will affect community composition and productivity in secondary forests.

Author contributions

CB, LM and MGE conceived the idea, CB and LM conducted fieldwork, CB analyzed the data and wrote the manuscript, MGE and LM provided editorial advice.

Acknowledgments

We thank C. Aguirre, A. Piggot, D. Delgado, E. Cuyckens, and S. Lorenzatti for fieldwork on the permanent plots and for soil sampling. S. Nanni and S. Lomascolo provided language help. We acknowledge funding from CONICET, Rufford Small Grant, ECOSUR and Fundación ProYungas for field work and travel. We thank many private owners for allowing us to work on their properties.

Appendix A

Table A.1

Demographic, morphological and regeneration niche characteristics of 54 subtropical tree species of premontane forest in northwestern Argentina. M = mortality rate, R = recruitment rate, TT = tree turnover rate, G = growth rate, H = maximum height, WD = wood density, D = dispersion mode (1: anemochory; 2: zoochory; 3: autochory), L = leaf length, ASF = affinity to soil fertility, ST = shade tolerance (frequency of sapling, frequency of adult-tree⁻¹). Nomenclature: The Plant List (<http://www.theplantlist.org/>; accessed on 1 Feb 2015).

Species	Code	Demography			
		M	R	TT	G
		%	%	%	mm yr ⁻¹
<i>Achatocarpus praecox</i>	Acpr	4.44	0.73	2.58	1.0
<i>Agonandra excelsa</i>	Agex	1.61	0.31	0.96	1.5
<i>Allophylus edulis</i>	Aled	3.21	1.70	2.46	1.3
<i>Anadenanthera colubrina</i>	Anco	1.89	1.30	1.59	4.8
<i>Aralia soratensis</i>	Arso	2.63	0.00	1.32	1.2
<i>Astronium urundeuva</i>	Asur	1.13	0.36	0.75	3.1
<i>Blepharocalix salicifolia</i>	Blsa	0.58	1.66	1.12	2.2
<i>Bounganvillea stipitata</i>	Bost	8.91	0.00	4.45	1.1
<i>Calycophyllum multiflorum</i>	Camu	1.26	1.00	1.13	1.9
<i>Caesalpinia paraguayensis</i>	Capa	1.92	0.00	0.96	0.6
<i>Capparis prisca</i>	Capr	1.17	1.11	1.14	1.1
<i>Cedrela balansae</i>	Ceba	1.95	2.02	1.98	5.5
<i>Chrysophyllum gonocarpum</i>	Chgo	1.01	0.84	0.93	2.0
<i>Chrysophyllum marginatum</i>	Chma	1.98	0.62	1.30	1.8
<i>Cinnamomum porphyrium</i>	Cipo	2.58	0.79	1.68	4.4
<i>Cnicothamnus vitifolia</i>	Cnvi	13.97	0.71	7.34	1.7
<i>Coutarea hexandra</i>	Cohc	3.11	2.05	2.58	1.6
<i>Cordia americana</i>	Coam	1.10	0.38	0.74	2.3
<i>Cordia trichotoma</i>	Cotr	2.35	0.90	1.63	3.4
<i>Cordia saccelia</i>	Cosa	1.60	0.57	1.08	1.5
<i>Coccoloba tiliacea</i>	Coti	0.98	0.00	0.49	4.4
<i>Croton piluliferus</i>	Crpi	7.25	1.47	4.36	6.7
<i>Cupania vernalis</i>	Cuve	2.57	4.56	3.56	3.9
<i>Diatenopteryx sorbifolia</i>	Diso	1.74	0.46	1.10	2.6
<i>Erythroxylon argentinum</i>	Erar	8.91	0.71	4.81	1.6
<i>Eugenia uniflora</i>	Euun	2.96	1.59	2.28	0.9
<i>Gleditsia amorphoides</i>	Glam	1.21	1.83	1.52	2.3
<i>Handroanthus impetiginosus</i>	Haim	2.12	0.50	1.31	1.5
<i>Handroanthus lapacho</i>	Hala	2.12	0.00	1.06	2.0
<i>Handroanthus ochracea</i>	Haoc	0.00	1.92	0.96	1.5
<i>Jacaranda mimosifolia</i>	Jami	1.75	0.00	0.88	2.6
<i>Lonchocarpus lilloi</i>	Loli	2.64	1.37	2.00	4.8
<i>Maclura tinctoria</i>	Mati	1.75	1.61	1.68	0.4
<i>Myroxylon peruiferum</i>	Mype	0.60	1.15	0.88	2.7
<i>Myrcianthes pungens</i>	Mypu	2.52	0.49	1.51	1.1
<i>Myriocarpa stipitata</i>	Myst	6.93	2.25	4.59	3.3
<i>Ocotea puberula</i>	Ocpu	3.55	3.95	3.75	5.7
<i>Parapiptadenia excelsa</i>	Paex	3.50	1.29	2.40	2.6
<i>Phyllostylon rhamnoides</i>	Phrh	0.74	1.19	0.97	1.2
<i>Pisonia zapallo</i>	Piza	2.02	2.90	2.46	3.6
<i>Piper tucumanum</i>	Pitu	4.08	3.39	3.74	1.7
<i>Pogonopus tubulosus</i>	Potu	4.26	1.39	2.83	1.0
<i>Pseudobombax argentinum</i>	Psar	1.44	0.68	1.06	2.9
<i>Ruprechtia apetala</i>	Ruap	3.99	1.52	2.76	1.2
<i>Ruprechtia laxiflora</i>	Rula	2.07	1.88	1.97	2.3
<i>Sebastiania brasiliensis</i>	Sebr	7.26	0.00	3.63	0.8
<i>Solanum umbellatum</i>	Soum	11.85	2.12	6.99	4.8
<i>Terminalia triflora</i>	Tetr	0.50	1.88	1.19	1.4
<i>Trichilia clausenii</i>	Trcl	3.48	1.99	2.73	1.2
<i>Urera baccifera</i>	Urba	8.94	2.44	5.69	2.4
<i>Urera caracasana</i>	Urca	11.44	3.43	7.44	4.2
<i>Vassobia breviflora</i>	Vabr	8.17	0.00	4.09	1.9
<i>Xylosma longipetiolata</i>	Xylo	0.98	0.94	0.96	2.2
<i>Zanthoxylum petiolare</i>	Zape	4.24	0.34	2.29	2.4

Table A.1 (continued)

Species	Code	Morphology				Regeneration	
		H	WD	D	L	ASF	ST
		m	g cm ⁻³		cm	PCA 1	
<i>Achatocarpus praecox</i>	Acpr	11.5	0.87	3	5	0.56	1.60
<i>Agonandra excelsa</i>	Agex	17.5	0.82	2	6	0.66	0.22
<i>Allophylus edulis</i>	Aled	12	0.54	2	5.5	0.84	1.82
<i>Anadenanthera colubrina</i>	Anco	29	1.02	1	12.5	-0.58	0.24
<i>Aralia soratensis</i>	Arso	22	0.42	1	47.5	-1.69	0.18
<i>Astronium urundeuva</i>	Asur	28	1.18	1	20	-2.70	0.10
<i>Blepharocalix salicifolia</i>	Blsa	22	0.60	2	5	0.55	1.13
<i>Bounganvillea stipitata</i>	Bost	12	0.56	1	5.75	-4.95	0.17
<i>Calycophyllum multiflorum</i>	Camu	29.5	0.85	1	6	1.47	0.71
<i>Caesalpinia paraguayensis</i>	Capa	20	1.15	1	3.5	-6.20	0.25
<i>Capparis prisca</i>	Capr	12	0.66	2	6	2.38	0.89
<i>Cedrela balansae</i>	Ceba	25	0.44	1	23	-2.03	0.48
<i>Chrysophyllum gonocarpum</i>	Chgo	16	0.67	2	13.5	1.57	0.68
<i>Chrysophyllum marginatum</i>	Chma	11.5	0.79	2	5	1.84	0.38
<i>Cinnamomum porphyrium</i>	Cipo	21	0.42	2	12.5	2.85	0.17
<i>Cnicothamnus vitifolia</i>	Cnvi	9	0.44	3	15.5	-1.01	0.50
<i>Coutarea hexandra</i>	Cohc	13.5	0.60	1	5	0.92	1.17
<i>Cordia americana</i>	Coam	23.5	0.78	1	7	0.33	0.46
<i>Cordia trichotoma</i>	Cotr	21.5	0.60	1	10.5	0.61	0.39
<i>Cordia saccelia</i>	Cosa	19	0.80	1	8.5	0.81	0.14
<i>Coccoloba tiliacea</i>	Coti	13.5	0.69	3	18	0.98	1.00
<i>Croton piluliferus</i>	Crpi	20	0.33	3	13.5	0.61	0.57
<i>Cupania vernalis</i>	Cuve	21	0.85	2	25	1.50	1.50
<i>Diatenopteryx sorbifolia</i>	Diso	16	0.96	1	11.5	1.47	0.62
<i>Erythroxylon argentinum</i>	Erar	15.5	0.76	3	6.5	-2.26	1.00
<i>Eugenia uniflora</i>	Euun	13.5	0.99	2	3.75	1.18	2.34
<i>Gleditsia amorphoides</i>	Glam	20	0.87	2	13	0.47	0.65
<i>Handroanthus impetiginosus</i>	Haim	28	0.96	1	8	1.59	0.40
<i>Handroanthus lapacho</i>	Hala	21.5	0.54	1	12	2.67	0.29
<i>Handroanthus ochracea</i>	Haoc	22	0.87	1	9	0.81	0.22
<i>Jacaranda mimosifolia</i>	Jami	22.5	0.58	1	45	-4.05	0.20
<i>Lonchocarpus lilloi</i>	Loli	25	0.75	1	8.5	1.19	0.78
<i>Maclura tinctoria</i>	Mati	21	0.87	2	5	-5.54	0.50
<i>Myroxylon peruiferum</i>	Mype	26.5	0.97	1	15	1.44	1.86
<i>Myrcianthes pungens</i>	Mypu	15.5	0.85	2	5	1.23	0.51
<i>Myriocarpa stipitata</i>	Myst	11	0.27	3	17.5	0.07	0.33
<i>Ocotea puberula</i>	Ocpu	15	0.47	2	13.5	1.10	0.82
<i>Parapiptadenia excelsa</i>	Paex	25.5	0.61	1	7.5	-2.23	0.44
<i>Phyllostylon rhamnoides</i>	Phrh	24.5	0.90	1	3.25	-1.14	0.97
<i>Pisonia zapallo</i>	Piza	16	0.41	1	10	-0.91	0.60
<i>Piper tucumanum</i>	Pitu	10	0.46	2	9.5	1.50	4.06
<i>Pogonopus tubulosus</i>	Potu	13	0.67	3	10.5	1.20	0.81
<i>Pseudobombax argentinum</i>	Psar	18	0.39	1	25	-4.95	0.20
<i>Ruprechtia apetala</i>	Ruap	17.5	0.66	1	7	0.63	0.77
<i>Ruprechtia laxiflora</i>	Rula	16	0.75	1	5	1.66	0.73
<i>Sebastiania brasiliensis</i>	Sebr	11.5	0.63	2	5.5	1.27	3.60
<i>Solanum umbellatum</i>	Soum	14.5	0.49	2	15	0.05	0.29
<i>Terminalia triflora</i>	Tetr	22.5	0.66	1	3.5	-0.85	0.30
<i>Trichilia clausenii</i>	Trcl	15	0.77	2	8	0.03	2.52
<i>Urera baccifera</i>	Urba	12.5	0.17	2	22.5	-0.13	1.21
<i>Urera caracasana</i>	Urca	12.5	0.17	2	21	0.56	0.59
<i>Vassobia breviflora</i>	Vabr	8.5	0.50	2	8	0.07	0.80
<i>Xylosma longipetiolata</i>	Xylo	10	0.62	3	10	-0.86	0.67
<i>Zanthoxylum petiolare</i>	Zape	14	0.78	3	10	3.43	0.20

References

- Bianchi, A.R., Yáñez, C., 1992. Las Precipitaciones del Noroeste Argentino. INTA.
 Bianchi, A.R., et al., 2008. SIG climático del NOA. INTA.
 Brown, A.D., et al., 2001. Argentina. In: Kappelle, M., Brown, A.D. (Eds.), Bosques nublados del Neotrópico. INBio, pp. 623–659.
 Cavender-Bares, J., Reich, P.B., 2012. Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology* 93, S52–S69.
 Chase, J.M., 2005. Toward a really unified theory for metacommunities. *Funct. Ecol.* 19, 182–186.
 Chave, J., et al., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.* 159, 1–23.

- Condit, R., et al., 1996. Assessing the response of plant functional types to climatic change in tropical forests. *J. Veg. Sci.* 7, 405–416.
- Condit, R., et al., 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.* 20, 51–72.
- Cristóbal, L., et al., 2009. Dinámica de deslizamientos en la selva pedemontana del departamento San Martín. In: Brown, A.D., et al. (Eds.), *Selva Pedemontana de las Yungas: historia natural, ecología y manejo de un ecosistema en peligro*, Ediciones del Subtrópico, pp. 333–343.
- Dalling, J.W., et al., 2001. The unusual life history of *Alseis blackiana*: a shade tolerant pioneer tree? *Ecology* 82, 933–945.
- Díaz, S., et al., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.* 38, 497–508.
- Digilio, A., Legname, P., 1966. Los árboles indígenas de la Provincia de Tucumán. *Opera Lilloana* 15, 1–107.
- Dolédec, S., et al., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166.
- Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412.
- Easdale, T., et al., 2007a. Tree morphology in seasonally dry montane forest in Argentina: relationships with shade tolerance and nutrient shortage. *J. Veg. Sci.* 18, 313–326.
- Easdale, T., et al., 2007b. Tree life histories in a montane subtropical forest: species differ independently by shade-tolerance, turnover rate and substrate preference. *J. Ecol.* 95, 1234–1249.
- Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* 75, 1–34.
- Giannini, N.P., 1999. La interacción de aves-murciélagos-plantas en el sistema de frugivoría y dispersión de semillas en San Javier. *Univ. Nac. Tuc. Tucumán, Argentina*.
- Gourlet-Fleury, S., et al., 2005. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. *Ann. For. Sci.* 62, 785–796.
- Gower, J.C., 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27, 857–874.
- Green, D.S., et al., 2003. Foliar morphology and canopy nitrogen as predictors of light-use efficiency in terrestrial vegetation. *Agric. For. Meteorol.* 115, 163–171.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.* 17, 255–260.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- Killen, T.J., et al., 1993. Guía de árboles de Bolivia. *Herbario Nacional de Bolivia*. Missouri Botanical Garden, La Paz.
- Kraft, N.J.B., et al., 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322, 580–582.
- Laurance, W.F., et al., 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *For. Ecol. Manage.* 190, 131–143.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits - revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Legendre, P., et al., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562.
- Legname, P., 1982. Árboles indígenas del noroeste argentino. *Opera Lilloana* 34, 1–226.
- Leibold, M.A., McPeck, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87, 1399–1410.
- Lienin, P., Kleyer, M., 2011. Plant leaf economics and reproductive investment are responsive to gradients of land use intensity. *Agric. Ecosyst. Environ.* 145, 67–76.
- Loehle, C., 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *Am. Nat.* 156, 14–33.
- McGill, B.J., et al., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185.
- McIntyre, S., et al., 1999. Plant functional types and disturbance dynamics: introduction. *J. Veg. Sci.* 10, 604–608.
- Méndez-Dewar, G., et al., 2014. Spatial Heterogeneity of Light and Tree Sapling Responses in the Understory of Disturbed Montane Forests. *IForest Biogeosc.* <http://dx.doi.org/10.3832/ifer1195-007>.
- Müller, S.C., et al., 2007. Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecol.* 189, 1–14.
- Paine, C.E.T., et al., 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120, 720–727.
- Phillips, O.L., et al., 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Phil. Trans. R. Soc. B* 359, 381–407.
- Poorter, L., 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytol.* 181, 890–900.
- Poorter, L., et al., 2006. Architecture of 54 moist-forest tree species: traits, trade-offs and functional groups. *Ecology* 87, 1289–1301.
- Raevel, V., et al., 2012. Mechanisms of ecological succession: insights from plant functional strategies. *Oikos* 121, 1761–1770.
- Reich, P.B., et al., 2003. The evolution of plant functional variation: traits, spectra and strategies. *Int. J. Plant Sci.* 164, 143–164.
- Reich, P.B., 2012. Key canopy traits drive forest productivity. *Proc. R. Soc. B* 79, 2128–2134.
- Reich, P.B., 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301.
- Ricklefs, R.E., 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7, 1–15.
- Saldaña-Acosta, A., et al., 2008. Variation of functional traits in trees from a biogeographically complex Mexican cloud forest. *Acta Oecol.* 34, 111–121.
- Silvertown, J., 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* 19, 605–611.
- Souza, A.F., et al., 2014. Detecting ecological groups from traits: a classification of subtropical tree species based on ecological strategies. *Braz. J. Bot.* 37, 441–442.
- Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. *Vegetation* 75, 81–86.
- ter Steege, H., et al., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443, 444–447.
- Turner, I.M., 2001. *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press.
- Vázquez, G.A., Givnish, T.J., 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manantlán. *J. Ecol.* 86, 999–1020.
- Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227.
- Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. *Trends Ecol. Evol.* 21, 261–268.
- Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanism of species coexistence. *Oecologia* 130, 1–14.
- Wright, S.J., et al., 2003. Gap-dependent recruitment, realized vital rates and size distributions of tropical trees. *Ecology* 84, 3174–3185.
- Wright, I.J., et al., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.