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

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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.

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 McPeek, 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

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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 km^2 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 m^2 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