



Natureza & Conservação

Brazilian Journal of Nature Conservation

Supported by Boticário Group Foundation for Nature Protection

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Research Letters

Assembly patterns and functional diversity of tree species in a successional gradient of Araucaria forest in Southern Brazil

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ARTICLE INFO

Article history:

Received 13 January 2015

Accepted 30 September 2016

Available online xxx

Keywords:

Plant functional traits

Divergence

Convergence

Forest strata

Functional diversity

ABSTRACT

Functional analysis of secondary succession may allow identifying and predicting processes of community assembly, which can be simultaneously driven by factors related to ecological filters and neutral forces. This study evaluated trait-convergence assembly patterns and trait-divergence assembly patterns in successional areas of Araucaria forest. Plant species were sampled in both the upper and lower strata and were described by 15 functional traits. Data analyses were based on multiplication and Procrustes adjustment of matrices, which permit to discriminate trait-convergence assembly patterns and trait-divergence assembly patterns along the forest succession (our environmental variable), and the influence of phylogeny on these patterns. Initial and late forests were highly different in species composition, but the regenerating stratum was already more similar especially in functional terms. Traits related to the acquisitive-conservative trade-off (wood density, leaf nitrogen content, leaf area, leaf dry matter content) revealed strong convergent patterns of successional changes. Moreover divergence was maximized by specific leaf area, seed mass, deciduousness, and dispersal mode, showing a higher functional diversity in late Araucaria forests.

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Introduction

The analysis of secondary succession may enable the identification and prediction of fundamental processes involved in community assembly (Lebrija-Trejos et al., 2010). The assembly of communities is defined by the colonization and

interaction of species coming from a regional pool to form local communities and can be simultaneously driven by factors related to ecological filters (abiotic and biotic environment) and neutral forces (dispersal limitation, ecological drift) (HilleRisLambers et al., 2012; Rosindell et al., 2011), but their proportional importance can vary along the successional time. Meiners et al. (2015) recently presented a conceptual

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<http://dx.doi.org/10.1016/j.ncon.2016.09.006>

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framework of successional drivers that simultaneously accounts for geographic and evolutionary contexts with filter models associated to local dynamics. The framework highlights how each level constrains lower levels (for example, how site conditions constrain species availability) and potential feedbacks among levels (for example, how species performance alters site conditions), considering a broad review of succession studies (Meiners et al., 2015).

Ecological filters in community assembly may result in patterns of both convergence (underdispersion) and divergence (overdispersion) in species traits (Pillar et al., 2009). Trait-convergence is related to a species ability to transpose abiotic filters, driving the assembly to be similar for particular functional traits. Such filters may act at the regional scale (defining the species pool), and then at the local habitat scale, selecting species that are able to get established under the prevailing environmental conditions (Meiners et al., 2015). During the process of succession, early species may change the local environmental conditions (e.g. improving shading) and interact with other species, facilitating or hindering the colonization of new species (Lebrija-Trejos et al., 2010; Schöb et al., 2013).

Pioneer species may facilitate colonization by species that have different traits or strategies, such as shade-tolerant species, influencing, thus, the community assembly of the next successional phase (Verdú et al., 2009). In this case, we can expect a trait divergence pattern between the species that are colonizing and those already established and also among the new recruits, since the species pool of secondary/late forests is larger than the pioneers, increasing the probability of trait-divergence. On the other hand, pioneer species can also delay the colonization of secondary species by, for example, a positive feedback in the recruitment mechanism ('persistent-monodominance'), hindering the successional process and keeping the community at an alternative state (Norden et al., 2011). This mechanism would maintain a convergence pattern. However, as local environmental conditions change over the time through the increase in vertical structure and canopy, abiotic filters of each successional phase may still lead to patterns of trait convergence within the communities. Secondary and late successional forest trees have evolved to the commonest environmental conditions – shaded habitats – causing species to converge on similar traits (Hubbell, 2005), at least in terms of those associated with light demand.

Considering the above, we would expect patterns of trait convergence along the forest succession process. However, at the scale where the coexisting species are competing for resources, having different strategies to obtain them may be more effective (Silvertown, 2004), leading to patterns of trait divergence. Processes of limiting similarity enhance species diversity through a finer niche partitioning, therefore increasing functional alpha diversity, here measured by the trait dissimilarity between local species (De Bello et al., 2009). As both trait convergence and divergence can be found over forest succession, simple conclusions about patterns of functional diversity and functional composition in forest succession have not yet been consistent (Böhnke et al., 2014). Whereas functional diversity measure the value, range and relative abundance of functional traits in a community, the functional composition can be represented by the community weighted mean value of traits (i.e. CWM) (Díaz et al., 2007). The number

and the nature of selected traits strongly influence such functional patterns, and the environmental gradient must be part of this choice (Pillar et al., 2009).

In this study we evaluated patterns of convergence and divergence of plant traits, investigating tree species in a successional chronosequence of Araucaria forest plots in southern Brazil, to answer the following questions: (1) How early successional stages differ from late ones in terms of species composition, considering both upper and lower strata? (2) Which functional traits are optimal for revealing patterns of trait-divergence and trait-convergence related to forest development? (3) What patterns of functional composition and functional diversity of both upper and lower strata become evident along forest succession?

Material and methods

Study site

The study site was in the Center for Research and Conservation of Nature Pro-Mata (CPCN Pró-Mata; 29°26'27" S and 50°08' to 50°14' W, 800 to 950 m a.s.l.), southern Brazil. The climate is temperate mesothermic super humid (Cfb climate, according to the Köppen classification), with average temperature of the warmest month not exceeding 22 °C and the annual isotherm below 18 °C.

The site has Araucaria forest in different regeneration stages after early logging activities, from initial to old-growth areas. After the establishment of the conservation area (in 1994), natural regeneration processes started. Late forests (with no signs of clearcutting) and initial successional forests were chosen for this study. Initial forests were under natural regeneration since at least 20 years and are situated very close (nearby) to old-growth forests.

Data collection

Three sites of late forest stage and four sites of initial stage forest were chosen for the vegetation survey. In each of the late forest sites, an area of 1 ha was delimited within which 12 random circular plots of 100 m² each were marked, three plots in each ¼ ha. These plots were used for sampling the upper stratum, including all individuals with at least 10 cm of diameter at breast height (DBH ≥ 10 cm). Within each 100 m²-plot, four subunits of 1 m² were used to sample the lower stratum (individuals of shrubs and trees with at least 10 cm height and <1 cm of DBH), systematically placed within each cardinal direction and considering a regular distance (2.8 m) from the center of the plot. For the initial stage forests, the sampled area was 0.50 ha to preserve the structural homogeneity of early successional stages, with six 100 m²-plots. As a result, we had 36 100 m²-plots for late forests and 24 for initial forests and for the lower strata we had 144 1 m²-plots for late and 96 for early forests.

Based on all sampled species, we selected a subset of the most frequent species (present in at least 10% of the 100 m²-plots) to be characterized by plant functional traits. This choice considers the biomass ratio hypothesis (Grime, 1998), that the most frequent and abundant species are

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