



Phylogenetic patterns of Atlantic forest restoration communities are mainly driven by stochastic, dispersal related factors



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ABSTRACT

Phylogenetic ecology complements trait-based analysis on community assembly by considering that species are not independent units but are related to each other by their evolutionary history. Phylogenetic patterns clustered when there are more close relatives than expected by chance or overdispersed with less close relatives than expected. Patterns among species in a community indicate underlying biotic and abiotic processes acting on species functional traits. However, phylogenetic ecology has seldom been applied to forest restoration. We used floristic and abundance data from six forest restoration sites of different ages and four old-growth reference forests in the Brazilian Atlantic forest to evaluate similarities in phylogenetic patterns between restoration and reference forests as a measure of restoration success. The presence of an initial tree canopy in restoration forests conducted by planting species increases seed dispersal. Nevertheless, we expected random phylogenetic patterns early in restoration due to dispersal limitation in a highly fragmented landscape. As time since planting increases and in reference forests, we expected less of an effect of dispersal on community composition and more of an effect of negative biotic interactions among close relatives to lead to overdispersed patterns. We did not find a clear trajectory showing that restoration sites would resemble the phylogenetic patterns of reference sites with age since planting. We found significant clustering patterns in two sites, the oldest restoration site and one reference forest. The other reference forests showed, non-significant yet clustering tendencies. The functional traits studied were less conserved than expected by chance, therefore, we cannot relate clustering to be solely the result of environmental filters leading to the presence of close relatives with similar habitat requirements. The presence of closely related species in the Meliaceae family in reference forests and in the oldest restoration site, which was next to a forest remnant, points toward dispersal as the main factor driving phylogenetic patterns in the sites studied. Despite the use of a high number of planted species, differences in the composition of planted species among sites also affected the observed phylogenetic structure. We believe that phylogenetic ecology complements floristic studies by providing information on trait conservatism and shedding light on community assembly processes that affect the successional trajectory of restoration forest.

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1. Introduction

Human-derived degradation of forest landscapes can take these ecosystems over a threshold after which the passive recovery of forest cover is no longer possible or may take several hundred years (Melo et al., 2013). Under this scenario, active forest restoration becomes necessary (Holl and Aide, 2011). One objective of

active forest restoration is to establish a canopy that would facilitate recruitment of other forest species by ameliorating site conditions and attracting seed dispersers. With time the restoration forest will resemble an old-growth forest (reference site) in some of its ecosystem functions, structure and species composition (Young et al., 2001; Chazdon, 2008; Bullock et al., 2011).

An understanding of communities assembly during succession after restoration is key to evaluate the degree to which restoration sites will resemble reference sites in time (Matthews and Spyreas, 2010). A recent synthesis on communities assembly states the importance of both niche and neutral processes acting on communities taxonomic and functional trait composition (Weiher et al.,

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2011). Niche-based processes include abiotic or fundamental niche filters, such as light and soil conditions, and biotic or realized filters, such as competitive species interactions. Both filters act upon species functional traits so that, from a regional species pool, only those species with the traits to overcome a given set of filters will be present in a community. Neutral processes are related to dispersal, ecological drift and historical inertia, which add a stochastic component to community taxonomic composition (Chave, 2004).

Studies have found that forests undergoing restoration recover structure, species richness and density attributes of reference, old-growth forests (Catterall et al., 2012; Suganuma and Durigan, 2015). These are important parameters to evaluate restoration success (Ruiz-Jaen and Aide, 2005), however, inclusion of recovery in phylogenetic structure complements floristic and trait composition studies by considering that species are not independent units but are related to one another by their evolutionary history. Phylogenetic ecology adds information on the degree of trait conservatism among species in a community and allows inferring about niche-based and neutral processes affecting species community composition and thus restoration success (Weiher et al., 2011).

Species present in a restoration site may be more or less evolutionary related than expected by chance, thus showing significant phylogenetic patterns. There are two possible phylogenetic patterns: clustering and overdispersion. In a clustered community species are more closely related than expected by chance, while in an overdispersed community there is a higher presence of far relatives (Webb et al., 2002). The classic interpretation of phylogenetic patterns is based on the presence of a phylogenetic signal in trait evolution (trait conservatism), by which close relatives share similar trait values and thus similar habitat use (Blomberg and Garland, 2002; Wiens et al., 2010; Burns and Strauss, 2011). Studies have found several functional traits, including reproductive, morphological, and physiological, to be conserved in the phylogeny of various taxa (Prinzing et al., 2001; Blomberg et al., 2003; Gomez et al., 2010; Liu et al., 2012).

Based on the trait conservatism assumption, phylogenetic clustering is due to strong habitat filters leading to the presence of closely related species that share traits to overcome the filter (e.g. nitrogen fixing among legume trees). Overdispersion is related to negative biotic interactions among close relatives, such as competition or the sharing pests and pathogens (Tilman, 1994; Weiher et al., 1998; Cavender-Bares et al., 2006; Merwin et al., 2012). In order to validate conclusions from observed phylogenetic patterns, the hypothesis of trait conservatism needs to be tested, since trait convergence or divergence may also lead to non-random phylogenetic patterns as a consequence of abiotic or biotic processes (Losos, 2008; Swenson and Enquist, 2009; Vamosi et al., 2009; Ding et al., 2012). For example, if far relatives share the trait to withstand seasonal drought, they will be able to recruit in a site if they disperse to that site, or in the case of restoration, if they were planted at the site. The final phylogenetic structure could then be random, overdispersed or clustered depending on the identity of the planted and immigrant species.

To date, phylogenetic ecology has seldom been employed in the field of restoration ecology (but see Schweizer et al., 2013), despite calls that stress the importance of recovering species evolutionary relationships (Verdu et al., 2012). Tests of phylogenetic ecology on restoration sites are usually difficult due to the lack of restoration sites of different ages and the long-term nature of forest succession (Chazdon, 2014). However, in the Brazilian Atlantic forest, species-rich restoration plantations (at least of 70 native tree species) have been implemented since 1861 (Rodrigues et al., 2009), and constitute a unique opportunity to examine the use of phylogenetic tools in restoration.

We assessed the phylogenetic structure of six restoration communities, of different ages, and compared it to four old-growth reference forests in the semideciduous Brazilian Atlantic forest biome. Under the assumption of trait conservatism, we expected random to clustered phylogenetic patterns early in restoration as the result of dispersal limitation in a highly fragmented landscape and/or of environmental filters remaining after tree planting, such as soil compaction, as the sites were under intense agriculture for over 100 years (Brancalion, *pers. comm.*). We expected an overdispersed structure with age since planting in restoration sites and in old-growth, reference forests reflecting the importance of negative biotic interactions among close relatives as has been observed in old-growth and successional tropical forests elsewhere (Webb et al., 2006; Letcher, 2010; Letcher et al., 2012). In addition to age, we looked at the effects of distance to a forest remnant and density of initially planted individuals on the phylogenetic structure of restoration sites. We expected an increase in the significance of the phylogenetic index with proximity to a forest remnant as dispersal limitation is expected to diminish. We did not expect initial density of planted individuals to have a strong effect given that in most sites over a quarter of the planted species have gone locally extinct.

We assessed the phylogenetic conservatism of three functional traits related to forest succession: wood density, specific leaf area (SLA), and seed mass (Westoby et al., 2002; Chazdon, 2014). Wood density is related to species growth rate and resistance to drought. Denser wood has been found on drought-tolerant deciduous species and also on late-successional, slow-growing tree species (Preston et al., 2006; Chazdon, 2014). In the tropics, wood density is negatively related to tree mortality as short-lived species tend to have smaller values of wood density than long-lived species (Chazdon, 2014). SLA represents a plants biomass allocated to light interception. Plants with high SLA have thinner leaf tissue, tend to have a shorter life span, but are more productive than those with low SLA (Ackerly and Cornwell, 2007). Species with high SLA tend to be present in resource rich environments (Wilson et al., 1999). Seed size relates to the dispersal syndrome of the species, plant stature and seedling establishment needs (Ackerly and Cornwell, 2007). Marked differences in SLA and seed size have been found among species during forest succession as pioneer species tend to have higher specific leaf areas and smaller seed sizes than shade-tolerant species (Bonal et al., 2007; Chazdon, 2014).

2. Material and methods

2.1. Study sites

Our sites consisted of six restoration and four reference sites (Table 1), which are a subset of sites from the research project “Study of the successional trajectories and possible factors influencing riparian forest restoration success” (National Council for Scientific and Technological Development – CNPq #302939/2009-1). This project analyzed the sites under different perspectives: common attributes among reference forests (Suganuma et al., 2013), and models of changes in structure, floristic composition and functional attributes of the restored forests over time toward the reference ecosystems (Suganuma and Durigan, 2015).

The sites employed in the present study are located in the State of São Paulo, southeastern Brazil. The sites belong to the Brazilian Atlantic forest biome, semideciduous tropical forest sub-type. The predominant climate is humid subtropical (Cfa, Cwa, according to Köppen’s classification), with the rainy season occurring in the hot summer months and the dry season in the cool winter months. Mean annual precipitation is around 1000 mm/year and mean temperature is around 21 and 24 °C (Sentelhas et al., 2003).

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