UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TESE DE DOUTORADO

KÁTIA JANAÍNA ZANINI

DINÂMICA DE FLORESTAS SUBTROPICAIS:

ABORDAGENS POPULACIONAIS E DE COMUNIDADES VIA ATRIBUTOS FUNCIONAIS DE PLANTAS E INFORMAÇÃO FILOGENÉTICA.

PORTO ALEGRE, JULHO DE 2016

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TESE DE DOUTORADO APRESENTADA AO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, DO INSTITUTO DE BIOCIÊNCIAS DA UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL, COMO PARTE DOS REQUISITOS PARA OBTENÇÃO DO TÍTULO DE DOUTORA EM ECOLOGIA.

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Resumo

Mais de metade das florestas do mundo são florestas secundárias e a sucessão determinística prevê que muitos aspectos das florestas originais serão recuperados. Por outro lado, os remanescentes florestais encontram-se em paisagens fragmentadas nas quais às alterações microclimáticas induzidas por efeitos de bordas podem levar a uma sucessão retrogressiva, denominada "secundarização". Assim, as comunidades florestais atuais tendem a convergir em termos de estrutura e funções que desempenham no ecossistema, e a compreensão da dinâmica de espécies e de comunidades tornou-se uma preocupação fundamental dos estudos florestais. A heterogeneidade do habitat, juntamente com diferenças ecofisiológicas entre espécies, leva à segregação destas ao longo de gradientes espaciais ou temporais. Aqui, avaliamos a estrutura filogenética e a variação da composição filogenética das comunidades arbóreas florestais buscando evidenciar padrões de segregação ao longo do gradiente sucessional. No segundo capítulo, avaliamos o poder preditivo das características funcionais sobre as mudanças demográficas de curto prazo (intervalo de cinco anos) de 20 espécies arbóreas subtropicais. No terceiro, comparamos a dinâmica de curto prazo de comunidades florestais secundárias e remanescentes no fragmentado bioma da Mata Atlântica. Nossos resultados mostraram que as linhagens principais segregam ao longo do gradiente sucessional devido a requerimentos conservados de nichos de clados basais, revelando sua associação funcional a florestas mais antigas, enquanto Eudicots podem ocorrer ao longo do gradiente. No nível das espécies, atributos foliares foram preditivos de mudanças demográficas de curto prazo e, no nível de comunidade, atributos foliares e massa das sementes captaram melhor as mudanças na composição funcional de curto prazo. Constatou-se o aumento de atributos conservativos em florestas secundárias e a perda de biomassa, devido à queda de grandes árvores, nas florestas remanescentes, expressando a perda de uma importante característica estrutural dessas florestas.

Palavras chave: NRI, filobetadiversidade, composição funcional, florestas secundárias e remanescentes, mudanças temporais

Abstract

More than half of the natural world's forest is secondary forest and deterministic succession predicts that many features of pre-disturbed forests will be recovered. On the other hand, remnant old-growth forests are mostly within fragmented landscapes and edge-induced microclimatic conditions may lead to a retrogressive succession, named 'secondarization'. Thereby current forests tend to converge in terms of community structure and ecosystem function and the understanding of species and community dynamics became a main concern of forest studies. Habitat heterogeneity together with ecophysiological differences between species would carry to species segregation along spatial or temporal gradients. Here we evaluated the phylogenetic structure of communities and phylogenetic composition variation to evidence patterns of segregation along the succession of tree species. In the second chapter, we evaluated the predictive power of the functional traits on short-term demographic changes (five years interval) of 20 subtropical tree species. In the third, we compared the short-term dynamics of secondary and old-growth forest communities in the fragmented Atlantic forest biome. Our results showed that the main lineages segregate along the successional gradient due to conserved niche requirements of the early-divergent clades reveling their functional association to older successional forests, whereas Eudicots can occur over the gradient. At species level, leaf functional traits were predictive of the short-term demographic changes and, at the community level, leaf traits and seed mass better captured the short-term functional composition changes of the communities. We found the rise of conservative traits at secondary forests and biomass loss, due to fall of big trees, at the old-growth communities expressing the loss of an important structural feature of these forests.

Key words: NRI, phylobetadiversity, functional composition, secondary and old-

growth forests, temporal changes

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Introdução Geral

Introdução Geral

A Floresta Atlântica é uma das regiões floristicamente mais ricas e mais ameaçadas do mundo, possuindo um número excepcional de endemismos (Myers et al. 2000; Metzger 2009; Forzza et al. 2012). Porém, ao longo de 500 anos de ocupação pelo homem branco, cerca de 90% do bioma foi efetivamente desmatado (Ribeiro et al. 2009). Hoje, a floresta está restrita a fragmentos em geral pequenos (<100 ha; Ranta et al. 1998) e sob a pressão dos efeitos de borda associados à fragmentação (Laurance 2008; Tabarelli et al. 2012), resultando na perda de características funcionais ligadas ao interior da floresta (Nascimento et al. 2006; Girão et al. 2007; Michalski et al. 2007; Santos et al. 2008; Lopes et al. 2009). Apesar de inúmeras medidas protetivas legais, o Bioma segue perdendo área florestal para dar espaço a atividades econômicas (p. ex. agrícolas, pastoris, assentamentos urbanos).

Neste contexto, as florestas secundárias passam a ter uma grande importância na manutenção de espécies, na conectividade entre fragmentos florestais e no desempenho de diversos serviços ecossistêmicos, importância esta que excede em muito os limites da floresta Atlântica, pois as florestas secundárias representam cerca de 50% da cobertura florestal natural no mundo (Wright 2005; FAO 2015). Apesar de sua importância, as florestas secundárias não retornam ao estado pré-distúrbio (Chazdon 2003) e organismos que evoluíram em profunda dependência da floresta podem não encontrar refúgio em florestas sucessionais resultando em lacunas na recuperação da biodiversidade e dos serviços ambientais prestados pela floresta. Acresce-se ainda o fato de que florestas secundárias e remanescentes estão sujeitas a efeitos de mudanças ambientais locais decorrentes da fragmentação e das mudanças climáticas em escala global, as quais vêm alterando padrões de sobrevivência, crescimento e abundância de espécies (Laurance et al. 2006; Lewis et al. 2009).

A sucessão vegetal é caracterizada pela substituição de espécies, as quais segregam no espaço e no tempo de acordo com a variação na disponibilidade de recursos. As espécies arbóreas se distribuem ao longo de um *continuum* de distintas histórias de vida (Wright et al. 2010) possibilitando sua coexistência através da partição dos recursos no espaço e no tempo e resultando na substituição destas plantas ao longo de gradientes ambientais. Diferenças nas histórias de vida das espécies podem ser descritas pelos seus atributos funcionais, que são características morfológicos-fisiológicas-fenológicas que influenciam a sobrevivência, o crescimento e a reprodução das plantas (Violle et al. 2007). Num dos estremos deste *continuum* encontramos espécies com características funcionais aquisitivas que possibilitam a rápida conversão de nutrientes em tecidos resultando em um rápido crescimento e maturação reprodutiva. No outro extremo estão as espécies conservativas que produzem tecidos resistentes e duradouros, exigindo maior investimento da planta e um crescimento mais lento. Assim, diferentes estados de um mesmo atributo (diferenciando a história de vida das espécies) irão contribuir de forma diferencial para a performance dos indivíduos nas comunidades, e diferentes atributos irão capturar distintos aspectos das estratégias das plantas (Wright et al. 2007; Laughlin 2014). Desta forma, a segregação de espécies ao longo de gradientes ambientais associado ao uso de características funcionais pode evidenciar a maneira como as plantas respondem às mudanças ambientais, tornando-se uma ferramenta preditiva para o estudo da dinâmica florestal (McGill et al. 2006).

O objetivo geral deste estudo foi avaliar as mudanças estruturais, funcionais e filogenéticas entre estágios sucessionais, visando elucidar respostas funcionais e adaptativas das plantas às diferentes condições ambientais que estes estágios oferecem. No primeiro capítulo, relacionamos a história evolutiva das espécies arbóreas florestais e suas características funcionais ao gradiente sucessional. Utilizando a substituição do espaço pelo tempo (cronossequências) avaliamos florestas sucessionais com sítios entre 6 e 50 anos desde o abandono agrícola e florestas remanescentes (que nunca sofreram corte raso), buscando evidenciar a associação de diferentes linhagens/espécies e suas características adaptativas a partes deste gradiente. O segundo capítulo teve por objetivo avaliar a estrutura populacional e a dinâmica de espécies comuns em florestas secundárias e/ou em remanescentes florestais considerando a variação nas suas abundâncias e suas áreas basais e o poder preditivo de suas características funcionais na dinâmica de curta duração destas espécies (intervalo de cinco anos). No terceiro capítulo, objetivamos compreender como as comunidades estão mudando no tempo, para tanto, comparamos as mudanças funcionais e estruturais (abundância e área basal) na dinâmica de curta duração de comunidades florestais em estágio sucessional avançado (cerca de 50 anos) e em remanescentes florestais. Estes dois estágios da floresta apresentam características estruturais e ambientais semelhantes, porém distinta composição florística (Zanini et al. 2014) então buscamos responder as seguintes perguntas: Há diferenças na dinâmica funcional e estrutural entre estas florestas? Se a dinâmica é distinta, são direcionais estas mudanças? É esperado que florestas sucessionais adquiram características mais conservativas ao longo do tempo e que tenham ganho em área basal decorrente do crescimento dos indivíduos. Por outro lado a perda de área basal e de características conservativas (ou o aumento de atributos aquisitivos) pode indicar a abertura de clareiras ou a ‘secundarização’- um processo descrito como uma sucessão retrogressiva, no qual a floresta tardia perde indivíduos sensíveis a mudanças ambientais decorrentes da fragmentação florestal. Ao longo destes três capítulos abordamos dinâmica de comunidades e espécies sob a perspectiva histórica, populacional e de comunidades.

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Capítulo 1

Phylogenetic structure and niche conservatism in the succession of a subtropical forest

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Chapter 1: Phylogenetic structure and niche conservatism in the succession of a subtropical forest

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Abstract

The tropical Atlantic rainforest was fully developed at the Holocene and wetter and warmer environmental conditions made possible the migration of this forest to higher southern latitudes (30' S), already in the subtropical region. Here we used the space-for-time substitution to analyze phylogenetic structure of communities and phylogenetic composition variation to evidence patterns of species and lineages segregation along the succession for three ontogenetic stages of tree species. In addition, we correlated the phylogenetic composition variation with the community functional trait composition variation, searching for associations with functional and evolutionary history. We expected that lineages would segregate along the successional gradient reflecting clear patterns of phylogenetic structure and composition through the time, if lineages have conserved their niche requirements. However, if recent diversification had lead to convergence and divergence of traits in distinct lineages, enabling them to occur in different phases of the successional gradient, we should find neither segregations nor clear phylogenetic structure patterns. Our results showed that the main lineages segregate along the successional gradient due to conserved niche requirements of the early-divergent clades – Magnoliids and Monocots - reveling their association to older successional forests, whereas Eudicots were principally associated to early successional stages, but can occur over the gradient and their co-occurrence with the early divergent nodes in older successional stages lead to a higher phylogenetic dispersion in such communities. Moreover Magnoliids segregate along the three forest strata and is associated to functional features that enhance its performance in the dense forest. Further, the phylogenetic relationships of the terminal nodes suggest that more recent historical forces had shaped distinct ecological strategies enabling closely and distantly related species to coexist in the advanced succession.

Key words: NRI, clades, phylobetadiversity, functional composition

Introduction

Atlantic forest is regarded as the oldest forest formation in Brazil (Rizzini 1997) and one of the most diverse regions floristically in the world (Forzza et al. 2012). Historical events as remote as the Gondwana separation that had conformed South America geomorphology and more recent historical events associated to the last glaciation and interglacial period had shaped dispersal opportunities and barriers through time (Hughes et al. 2013). Along the quaternary, forest have expanded and retracted east and southwards creating great opportunities of speciation and shaping the phytophysiognomies that can be seen today: Atlantic rainforest on the coast line, seasonal forest towards west, and Araucaria forest in the highlands (Behling 1998, Carnaval and Moritz 2008, Ledru et al. 2015). The tropical Atlantic rainforest was fully developed at the Holocene and wetter and warmer environmental conditions made possible the migration of this forest through the coastal lowlands and Atlantic slopes to higher southern latitudes (30’ S), already in the subtropical region (Rambo 1956, Behling and Negrelle 2001).

Considering that plants will establish and regenerate in environments to which they are well adapted (Ackerly 2003), habitat heterogeneity along this latitudinal gradient together with ecophysiological differences between species would carry to a species segregation along spatial or temporal gradients (forest development). Under the evolutionary perspective, it is assumed that close related species tend to be more similar in term of traits, conserving characteristics along its evolutionary history, which is named phylogenetic conservatism of traits (Ackerly 2003, Losos 2008, Wiens et al. 2010). The retention of traits in a lineage is associated to the environmental condition in which the lineage evolved and can reveal environmental preferences or restrictions to the lineages (Ackerly 2003, Duarte 2011). The migration towards south with implicit lower temperatures and away from speciation centers (Carnaval and Moritz 2008, Murray-Smith et al. 2009) overpasses filters, but the number of species able to reach the southern subtropical Atlantic rainforest is reduced. This richness pattern is predicted by the tropical niche conservatism hypothesis (Wiens and Donoghue 2004), which expects higher richness in warm and rainy environments because this conditions match with the ancestral niche of many extant clades. Nevertheless, species may establish in suboptimal environments “challenging the held idea that species in communities are perfectly adapted to their current habitat” (Valiente-Banuet and Verdú 2013). The great speciation through drier and temperate environmental conditions along the Quaternary had lead more recently evolved clades to adapt to harsh conditions (Valiente-Banuet et al. 2006). The migration of tropical species may be though facilitated by such clades (Valiente-Banuet et al. 2006, Behling 2007) that can establish in harsh environments and ameliorate the conditions under their canopies for lineages with conserved ancient niche requirement (Valiente-Banuet and Verdú 2007, 2013).

In the ecological scale, coexistence of species in high diverse forests is the expression of evolutionary processes that distribute the tree species along a *continuum* of life-history characteristics (Wright et al. 2010), enabling them to partition the resources through space and time (Cavender-Bares et al. 2009, Götzenberger et al. 2012). Forest succession offers an opportunity to explore how species from a regional pool segregate from initial to mature forests expressing distinct life-histories and may shedding light in historical adaptations of different lineages to distinct environmental conditions provided along the succession. As considered earlier, species or lineages adaptations will be reflected in trait differences that may be or not phylogenetically conserved. Traits are phenotypic attributes (morphological, physiological, phenological) considered functional if they influence the ability of a plant to grow, survive and reproduce (Violle *et al*. 2007). They may be further considered adaptive if they occur in a particular environment enhancing the species (or individual) performance in that environment (Ackerly 2003).

Phylogenetic community studies commonly use phylogenetic structure as a proxy of functional structure, but this approach has been recently criticized (Gerhold et al. 2015). It is assumed that environmental harshness (as for example in the beginning of the succession) leads to an assembly of more similar species in traits and more closely related than expected by chance (phylogenetic clustering) and, with the improve of abiotic conditions (as in advanced succession), the similarity of traits between coexistent species may probably reduce under the limited resources, leading to communities with functionally distinct and phylogenetic distant species composition (phylogenetic overdispersion) (Cavender-Bares et al. 2009, Pausas and Verdú 2010). Tropical forest succession studies often find older communities displaying phylogenetic overdispersed patterns, but phylogenetic clustering has been less often found (Letcher 2009, Norden et al. 2012, Muscarella et al. 2016) and very little is known about the role of different lineages along the succession (Letcher et al. 2015).

Here we expect that lineages would segregate along the successional gradient reflecting clear patterns of phylogenetic structure and composition through the time, if lineages have conserved their niche requirements. However, if recent diversification had lead to convergence and divergence of traits in distinct lineages, enabling them to occur in different phases of the successional gradient, we should find neither segregations nor clear phylogenetic structure patterns. We used the space-for-time substitution (Pickett 1989) to analyze phylogenetic structure of communities (alpha diversity) and phylogenetic composition variation to evidence patterns of species and lineages segregation along the succession (beta diversity and phylobetadiversity) for three ontogenetic stages of tree species (seedlings, saplings and adult trees). In addition, we correlated the phylogenetic composition variation with the community functional trait composition variation, searching for associations with the functional and the evolutionary history.

Methods

Study Area

We studied tree species communities in permanent plots (*Sistema de Parcelas Permanentes do Corredor Mata Atlântica Sul no Nordeste do Rio Grande do Sul*) installed in the southernmost part (29°42'S, 50°11'W - Maquiné county) of the Brazilian Atlantic Forest. Climate is humid subtropical, type Cfa according to Köppen's classification, with mean annual temperature above 18°C, absence of a dry period, and an annual mean rainfall of 1400 to 1800 mm (Hasenack and Ferraro 1989, Nimer 1990). Studied forests are located in the lower-montane forest zone, in plots that ranged from 259 to 456 m a.s.l., minimizing floristic variation related to altitude (Teixeira et al. 1986). Natural vegetation consists of subtropical moist broadleaf forest and corresponds to the subtropical portion of the Atlantic Forest *sensu stricto* (Oliveira-Filho 2009). Soils are derived from basalt, and are classified as shallow litic leptsols with occasional rocky outcrops and luvic phaeozem (Streck et al. 2008). Landscape was highly fragmented in the past centuries, but many crops production have moved recently (around 40 years) to more flat areas leaving extensive areas to natural recovery. Today the landscape is a highly connected system of secondary forests with distinct ages of natural regeneration and old-growth forest remnants.

Sampling design and species data collection

Four chronosequences were evaluated in three valleys of the Maquiné River Basin, each one containing a set of successional forests differing in time since abandonment, ranging between 6 to 45 years old, associated to old-growth stands without register of clearcuting. Successional forests were selected based on semi-structured interviews with local informants gauging land use-history and time elapsed since abandonment. Aerial photographs from 1964 and satellite images Landsat 5 TM and 7ETM (base year: 2002) were used to cross check information from informants. We delimited an area of 0.25 ha for each forest sampling, a common size for slash-and-burn fields in the region (the main subsistence agricultural practice in the past), within which vegetation data was sampled. Nested design was used to the survey of three forest strata. Each 0.25 ha forest area had three circular plots of 100 m^2, randomly located, for the sample of tree individuals with diameter at breast height (DBH) $\geq$ 10 cm. Within these plots, 40 m^2 was used for the sample of individuals between 1 and 9.9 cm DBH and 4 m^2 for seedlings (individuals taller than 0.30 cm and with less than 1 cm DBH). These size classes are hereafter referring as 'trees', 'juveniles' and 'seedlings'. All sub-samples were integrated within each forest area (0.25 ha), comprising then a total of 29 sampling units for each stratum. We obtained a matrix of species abundances in the communities (29 sampling units) that described the species composition along the chronosequence for each stratum. Arborescent ferns (two species) were excluded from the analysis due their strong phylogenetic and functional distinctiveness. Angiosperm trees were identified to species and grouped into families following APG IV (2016).

Traits and community functional composition (CWM)

The species had their leaf traits measured from field samples following standard protocols (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). Three to 15 individuals per species were measured and the average value was used to represent each species in the analysis. Leaf traits here considered are specific leaf area (SLA, $mm^2.mg^{-1}$), leaf surface area (LA, cm^2), leaf dry matter content (LDMC, $mg.g^{-1}$), leaf nitrogenous and phosphorus concentration (LNC and LPC, percent of N and P mass per total mass, %). Further traits were wood density (WD, $g.cm^{-3}$) and seed mass (SM, g), which were compiled from the literature. Average of the genus for WD was used for six species with just one occurrence following Chave et al. (2009). The traits WD and SM still had some missing data, but only for species with very few occurrences. Palms were maintained in the functional analysis, but without value for WD. Functional composition of communities was obtained scaling up species trait values to the community level considering species abundance per forest community (community-weighted means - CWM; FD package, Laliberté et al. 2014), for each forest stratum (seedlings, juveniles, and trees).

Phylogeny construction

The 150 species sampled in the three strata were integrated in the phylogenetic tree, which was built with molecular sequences of nuclear (ITS1, ITS2, and ETS) and chloroplastidial markers (rbcL, matK, trnL-trnF spacer, trnL, psbA-trnH spacer and ndhF), known to resolve species relationships at higher and lower taxonomic levels. Molecular data was accessed in the GenBank (December 2015, Benson et al. 2013); sequences were obtained for 81 species and congeneric were used for 39 species. The remaining 30 species were manually merged in the resulting phylogeny, splitting them halfway along their congener branch with sequence data. Sequences alignment were made using MAFFT v.7.266 (Katoh and Standley 2013), SATé v.2.2.7 (Liu et al. 2012) and AliView (Larsson 2014) programs and the phylogeny was reconstructed using a maximum-likelihood approach (ML) with estimated bootstrap support values for each node through the RAxML v.8.2.4 software (Stamatakis 2014). Branch lengths were adjusted to the rate of evolution of the used markers and transformed to become proportional to divergence time through rate smoothing. Molecular dating was calculated at the package "ape" v.3.2, chronopl function (Paradis et al. 2004), in the R Statistical Environment (R Core Team 2016). Further details of phylogeny construction can be seeing in the supplement material (Appendix 1, S1).

Phylogenetic community structure and composition

The net relatedness index (NRI) is a measure of community phylogenetic structure, which expresses alpha phylogenetic diversity and was calculated for each forest stratum. NRI measures the mean pairwise phylogenetic distance of the taxa in a sample relative to the species poll, and though accounting for deeper phylogenetic relationships (Webb et al. 2002). The index was abundance-weighted and tested for significance against 'phylogeny.pool' null model using the package ''picante'' (Kembel et al. 2010) in the R statistical software (R Core Team 2016). The values of the standardized effect sizes (ses.mpd and ses.mntd) were multiply by -1 to be equivalent to the Webb' indices. Positive NRI values indicate clustering and negative values indicate overdispersion.

Phylogenetic community composition was accessed performing phylogenetic fuzzy-weighting method (Pillar and Duarte 2010, Duarte et al. 2016), which uses the phylogenetic similarities between taxa to scale up the species phylogenetic relationships to the community level, accounting for species abundances. Analysis was run in the package SYNCSA (Debastiani and Pillar 2012) and the obtained phylogenetic matrix (matrix **P**) incorporates species pairwise phylogenetic distances and phylogenetic unbalance of clade distribution across communities, thus assessing phylogenetic beta diversity among communities (Duarte et al. 2016). We computed a **P** matrix for each forest stratum.

Data analysis

Successional stages were categorized for analyzes purpose according time of recovery: stage 1 (S1) comprised forests between 6 and 10 years of recovery (n= 5); stage 2 (S2) included those between 11 and 25 years (n= 7); stage 3 (S3) between 26 and 45 years (n= 8); and finally stage 4 (S4) comprised old-growth forests (n= 9). A vector with the successional stages was used to represent the successional gradient.

NRI was tested against the successional gradient by linear regression analysis. Phylogenetic composition variation was analyzed by Principal Coordinates of Phylogenetic Structure analysis (PCPS, Duarte 2011), which are vectors of a principal coordinates analysis (PCoA) of the **P** matrix that express the phylogenetic variation across communities (Pillar and Duarte 2010, Duarte et al. 2016). PCPS vectors enable to explored clade distribution and its association to environmental conditions (our successional gradient). The PCPS axes with higher eigenvalues describe phylogenetic patterns related to more basal nodes of the phylogeny and, as eigenvalues decrease, the corresponding PCPS tend to describe phylogenetic patterns related to more terminal nodes (Duarte et al. 2012). To test if the phylogenetic composition is associated to the successional gradient and if this variation is dependent on the relatedness of species, PCPS vectors with more than 5% of explanation were submitted to two distinct null models (site and taxa shuffles) tested by generalized linear models (GLM). *Site shuffle* is a permutation procedure that assumes the independence between communities and the environmental gradient, permuting communities across the gradient; if the null model is rejected we conclude that successional gradient affect species distribution across communities. *Taxa shuffle* permute terminal tips (species) across the phylogenetic tree to generate random phylogenetic relationships and test again the association with the environmental gradient; if null model is rejected, we concluded that the segregation of species along the succession is dependent on the phylogenetic relatedness among them. We also evaluated phylogenetic composition differences between successional stages by ANOVA and a further 'TukeyHSD' procedure to better visualize which stages were distinct, with the package 'stats' (R Core Team 2016).

Finally, PCPS vectors (phylogenetic composition) selected by GLM analyzes were tested for significant correlation with CWM values (functional composition) with randomization test performed with the software MULTIV (Pillar 2001)

Results

The studied successional gradient presented 150 species distributed in 46 families. Among the major lineages 56.6% of the species are representatives of the Superrosids, 26% of the Superasterids, 13.3% of the Magnoliids, 2.6% of the Monocots (Arecaceae family) and 1.3% of the Proteales (Proteaceae and Sabiaceae). The most represented families were Myrtaceae (14 species), Euphorbiaceae (10), Lauraceae (12), Fabaceae (9) and Meliaceae (8).

Phylogenetic structure described by NRI showed a clear increase in the phylogenetic overdispersion along the successional gradient for trees and juveniles (Fig. 1). Positive NRI values were found in younger successional forests (S1) moving towards more negative values as forests become older ($P < 0.001$), however most of the communities presented values between significance thresholds and can be considered as random structured. Old-growth forests (S4) displayed significant overdispersed communities (4 for trees and 5 for juveniles), but some clustered communities were also found (1 for trees and 2 for juveniles). Communities described by seedlings had a wide variation of NRI values along the successional gradient (i.e. regression model not significant), but some significant phylogenetic overdispersion values were found in all successional stages (Fig. 1).

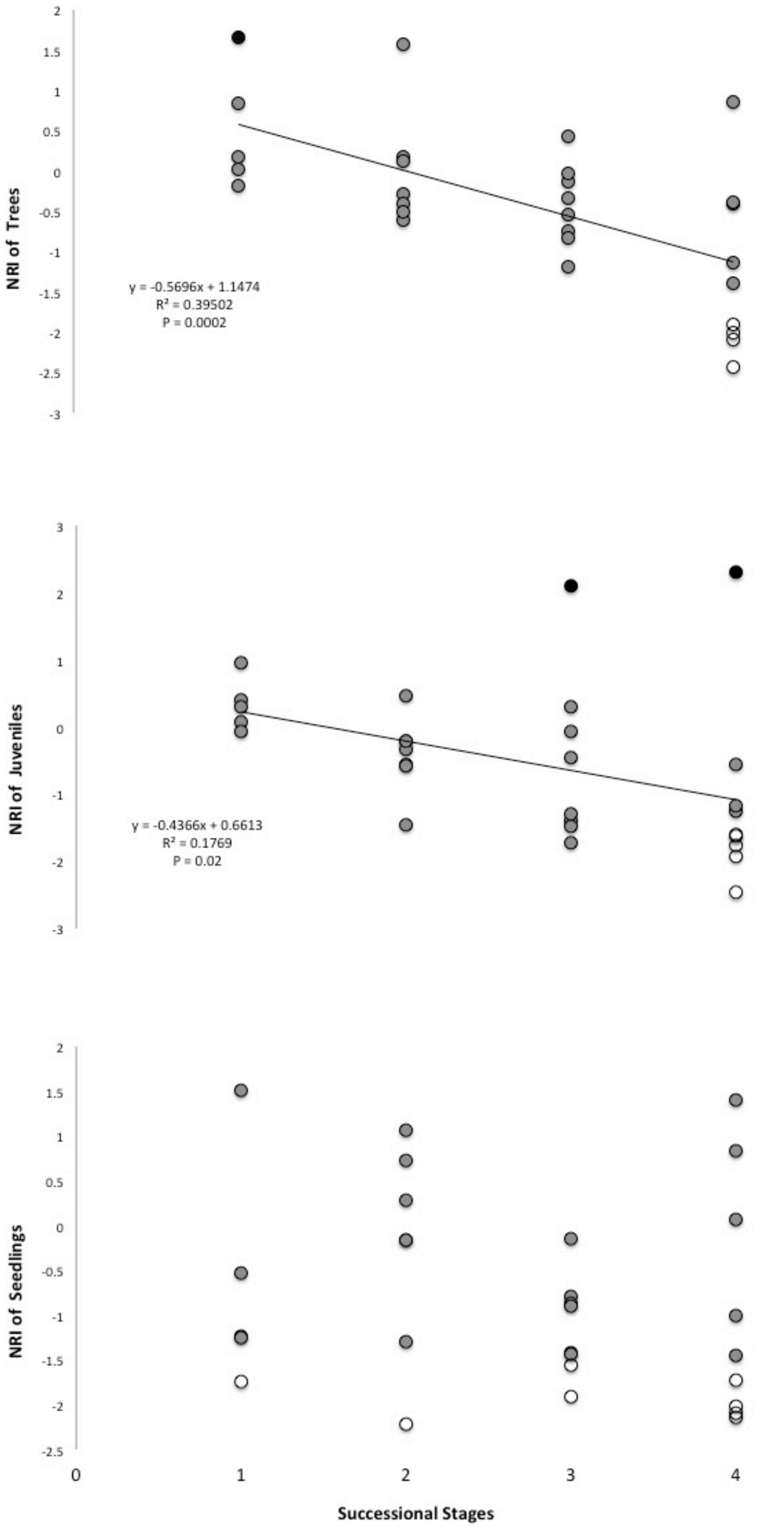

Figure 1: Phylogenetic structure of tree, juvenile and seedling communities along a successional gradient measured by Net Relatedness Index (NRI). Successional stages 1 to 3 represent intervals in years of natural regeneration since abandonment (S1: 6 to 10; S2: 10 to 24; S3: 25 to 45) and stage 4 (S4) are old-growth forests. White circles represent significant phylogenetic overdispersion and black circles represent phylogenetic clustering ($P < 0.05$).

The phylogenetic composition of forest communities had significant patterns along the successional gradient for all strata. Tree communities showed significant differences in species composition (P= 0.001 *site shuffle*) and lineages composition (P= 0.05 *taxa shuffle*) along the successional gradient (Tab. 1, Fig. 2). The first PCPS explained 24% of the tree phylogenetic variation (phylobetadiversity) and expressed the segregation of the major angiosperms lineages. Early divergent lineages related to more basal nodes of the phylogeny, i.e. Monocots (Arecaceae) and Magnoliids (Lauraceae, Monimiaceae, Annonaceae and Myristicaceae), were associated to older forests (S3 and S4). Variation in the main lineages expressed by PCPS 1 was strongly correlated with variation in functional composition of forests along the successional gradient (Tab. 2). Younger forests were associated to Eudicots (Superasterids, Superosids and Proteaceae) and to lower CWM values of LA, LDMC, LPC, SM and WD. Sabiaceae was recently included in the Proteales (APG IV 2016), but here it segregated from Proteaceae. Sabiaceae stayed with older communities (S3, S4) and Proteaceae clustered with the younger communities (S1, S2).

Table1: Significant principal coordinates of phylogenetic structure (PCPS, phylogenetic composition) tested against null models (*taxa shuffle* and *site shuffle*) along the successional gradient for three forest strata: trees, juveniles and seedlings. GLM results (R^2 and P) are given. Distinct letters among successional stages (see legend in Fig. 1) indicate significant contrasts (P<0.007), given the variation of the respective PCPS.

Stratum	**PCPS axes**	R^2	**P**	**Differences**	**Successional stages**			
Trees	PCPS.1 (24%)	0.49	< 0.001	*site and taxa*	$S1^{a}$	$S2^{ab}$	$S3^{bc}$	$S4^{c}$
Juveniles	PCPS.1 (29%)	0.55	< 0.001	*site*	$S1^{a}$	$S2^{a}$	$S3^{a}$	$S4^{b}$
	PCPS.2 (15%)	0.55	< 0.001	*site*	$S1^{a}$	$S2^{a}$	$S3^{b}$	$S4^{a}$
Seedlings	PCPS.1 (31%)	0.32	< 0.001	*site*	$S1^{ac}$	$S2^{ac}$	$S3^{ab}$	$S4^{c}$
	PCPS.4 (5%)	0.19	0.03	*site*	$S1^{a}$	$S2^{a}$	$S3^{ab}$	$S4^{b}$

Table 2: Pearson correlation between functional composition (CWM, community weighted means of traits) and phylogenetic composition (PCPS, principal components of phylogenetic structure that displayed significant patterns with the successional gradient, Tab. 1) for three forest strata (trees, juveniles and seedlings) (* P< 0.05; ** P< 0.005).

	Trees	**Juveniles**		**Seedlings**	
CWM of traits	**PCPS.1**	**PCPS.1**	**PCPS.2**	**PCPS.1**	**PCPS.4**
SLA	-0.30	-0.36	-0.13	0.10	-0.03
LA	0.42*	0.71**	0.18	-0.13	0.18
LDMC	0.55**	0.31	0.51**	-0.13	-0.59
LNC	0.05	-0.65**	-0.02	0.31	-0.38
LPC	0.47*	0.07	0.34	-0.12	-0.19
SM	0.78**	0.89**	-0.02	0.03	0.01
WD	0.50**	-0.19	0.35	-0.02	-0.51

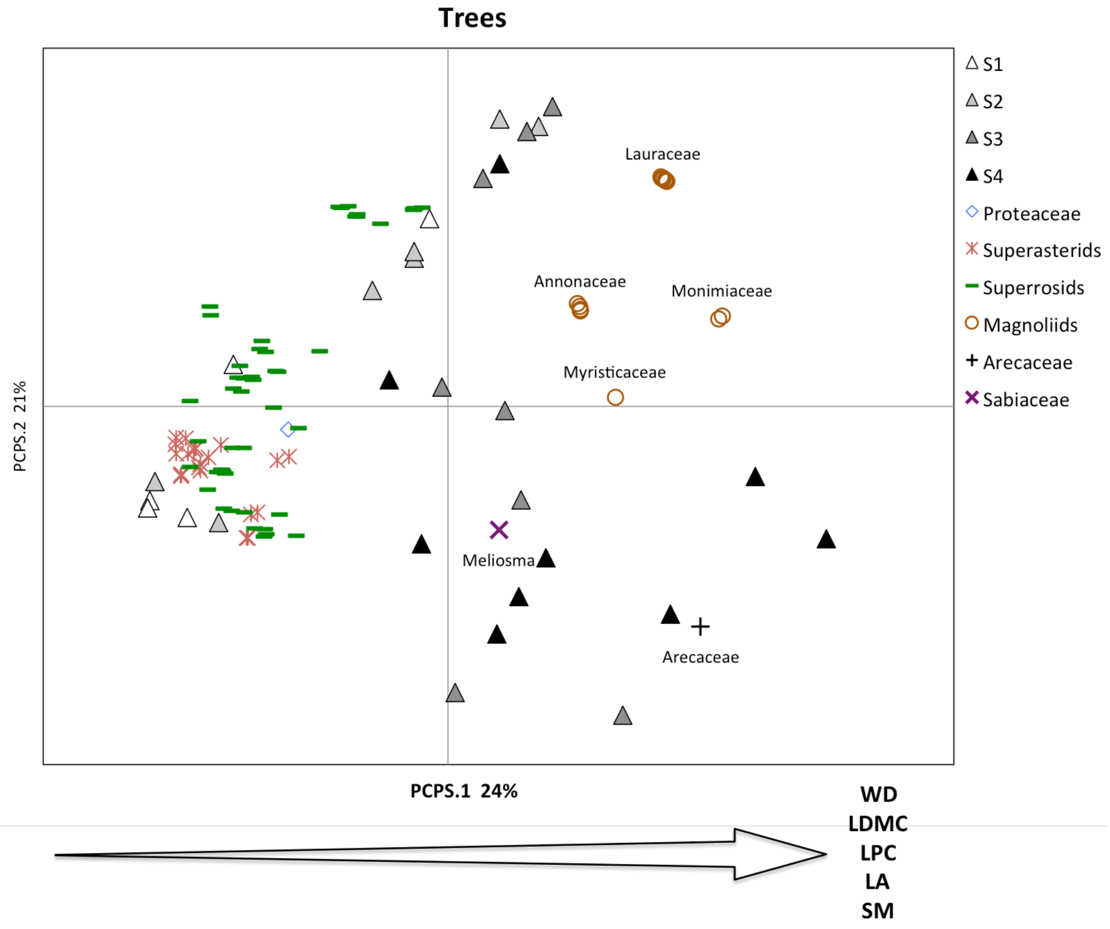

Figure 2: Ordination diagram of the first two PCPS vectors representing the phylogenetic composition of tree communities. Successional communities (S1 to S4, see legend in Fig. 1) are represented by triangles: white=S1, pale gray=S2, dark gray=S3 and black=old growth. Distinct shapes represented the main angiosperm lineages, and representative families can be seen on the scatter diagram. Significant correlations between functional composition and the PCPS.1 can be seen following the direction of the arrow (WD: wood density, LDMC: leaf dry matter content, LPC: leaf phosphorous concentration, LA: leaf area, SM: seed mass).

Considering the juveniles and seedlings, we also saw differences in the phylogenetic composition along the successional stages (*site shuffle*; P=0.001 for juveniles and P=0.007 for seedlings), but the patterns were not dependent on the phylogenetic relatedness among species (*taxa shuffle*). Juveniles of old-growth forests (S4) differed from all other forest stages (PCPS 1, 29% explanation), showing straight relations with Arecaceae (*Euterpe edulis, Bactris setosa, Geonoma gamiova*) and the species *Virola bicuhyba*, the only representative of Myristicaceae. The variation in the phylogenetic composition was also correlated with the functional composition (Tab. 2). Old-growth juvenile communities displayed bigger leaves (LA), heavier seeds (SM) and lower leaf nitrogen content (LNC). The second PCPS (15% explanation) indicated juvenile communities of S3 differing from all other successional stages, due to its relation with three Magnoliid families: Lauraceae (mainly represented by *Endlicheria paniculata* and *Nectandra oppositifolia*, but with 5 other species), Magnoliaceae (*Magnolia ovata*) and Monimiaceae (*Mollinedia schottiana*). Phylogenetic composition of S3 communities (positive values of PCPS.2) is correlated to lower CWM values of LDMC (Fig. 3; Tab. 1 and 2).

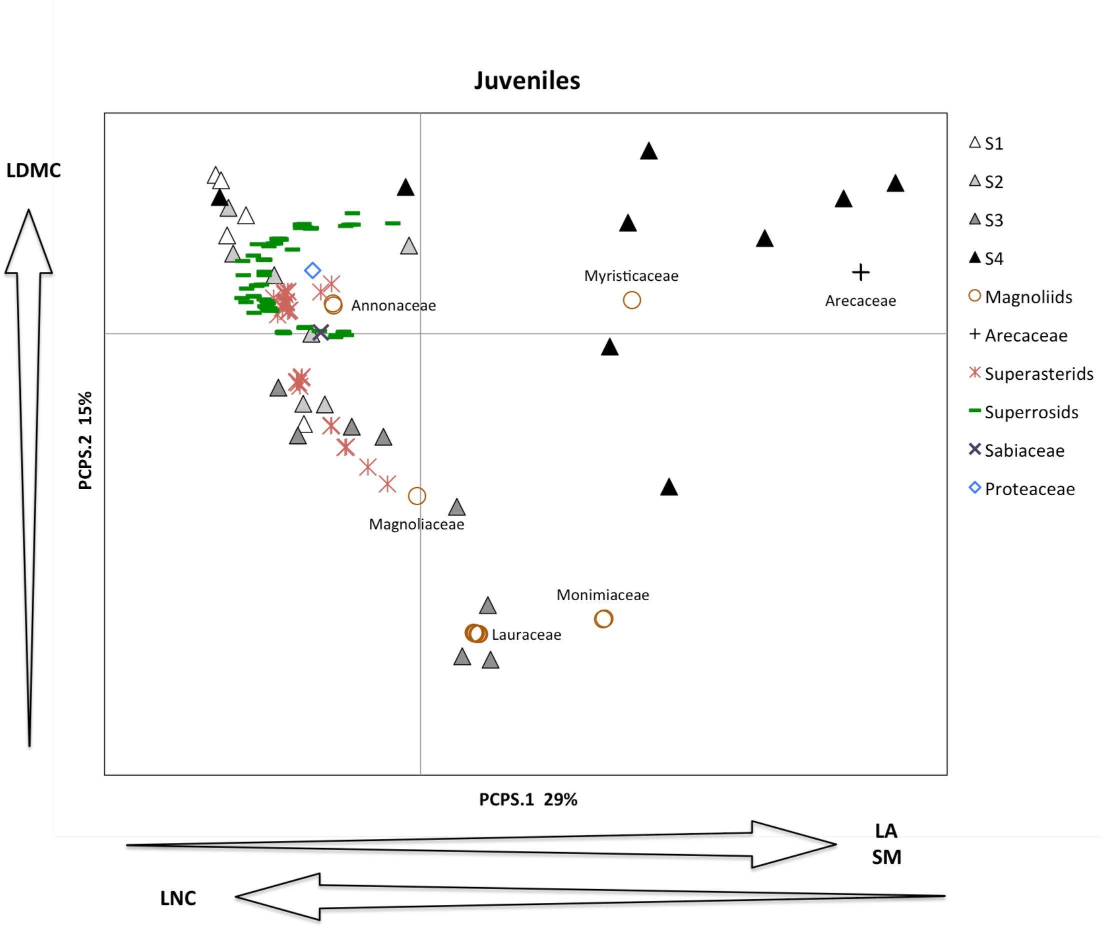

Figure 3: Ordination diagram of the juvenile phylogenetic community composition described by the first two PCPS vectors. Successional communities are represented by triangles: white=S1, pale gray=S2, dark gray=S3 and black=old growth. Distinct shapes represented the main angiosperm lineages, and representative families can be seen on the scatter diagram. Correlation and the direction of the relationship between community functional composition and the PCPS.1, related to LA, SM and LNCA and PCPS.2 considering leaf dry matter content are indicated by the arrows.

Two PCPS (PCPS.1 and PCPS.4) showed significant differences for seedling species composition along the succession (Tab. 1 and Fig. 4). The first PCPS (31% of explanation) reveals differences between the two older stages (S3 and S4): a strong participation of species from Magnoliids in S3 (Lauraceae, Monimiaceae, Magnoliaceae, Annonaceae and Myristicaceae) and species from distinct lineages sharing importance in S4. Beyond the great importance of *E. edulis* in the old-growth seedling communities, six species from Myrtaceae and three of Meliaceae, among other families, increased their importance in S4 forests. The PCPS.4 explained only

5% of the phylogenetic composition variation and indicate significant differences between S4 and S1 and S2 (Tab.1). Seedlings of S4 were associated manly to Superasterids. No correlation between functional and phylogenetic composition was found for seedlings communities (Tab. 2).

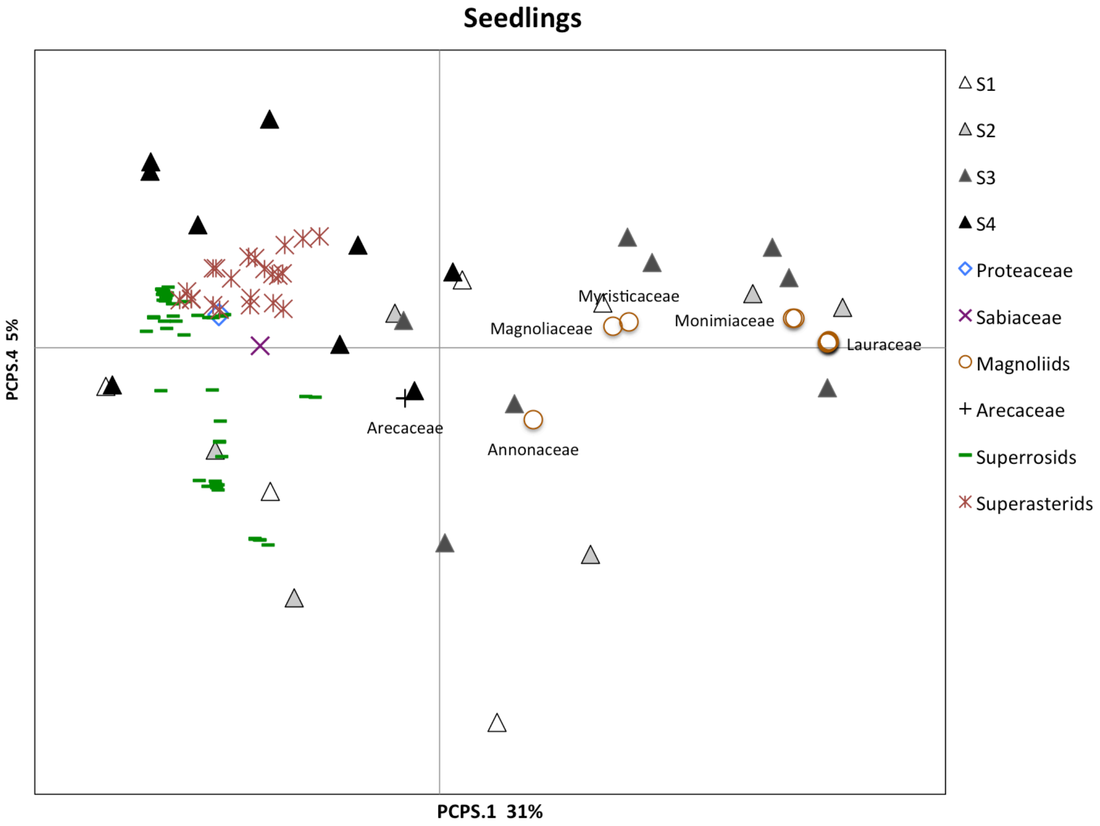

Figure 4: Ordination diagram of the phylogenetic community composition of seedlings described by the first and the fourth PCPS vectors. Successional communities are represented by triangles: white=S1, pale gray=S2, dark gray=S3 and black=old growth. Distinct shapes represented the main angiosperm lineages, and representative families can be seen on the scatter diagram.

Discussion

We found that phylogenetic structure and composition respond to forest succession, generally increasing the phylogenetic dispersion and the participation of early-divergent nodes as forest became older. The increasing phylogenetic dispersion indicated by the NRI values of trees along the successional gradient expresses deeper clade relationship, as the co-occurrence of Monocots (Arecaceae), Magnoliids and Eudicots in older forests (S3, S4), in contrast with the predominance of Eudicots (Superrosids, Superasterids and Proteaceae) in younger stages (S1, S2). Besides, this PCPS.1 reinforce the clade segregation along the gradient, also revealed by species substitution (Zanini et al. 2014), which demonstrate phylobetadiversity pattern given the time of forest succession.

Early-divergent nodes (e.g. Arecaceae and Magnoliids) were associated to dense forest environmental conditions. This may be explained by drought intolerance and high moisture dependence of the early angiosperms (Feild and Arens 2007, Feild et al. 2009), supporting the niche conservatism idea for these lineages (Wiens and Donoghue 2004, Wiens et al. 2010). The Magnolliids association to shady and wet environments is attributed to conserved traits that limit the photosynthetic performance to a narrow range of water availability (Feild et al. 2009). The segregation of Magnolliids to certain environmental conditions has been found in local gradient scale (Duarte 2011) and macroecological (Carlucci et al. 2016) studies. Arecaceae is a pantropical distributed clade, being among the oldest monocots (Janssen and Bremer 2004). Because of its association to warm and humid climates it has been used as a paleoindicator (Walther et al. 2007) and its actual distribution is constrained by low temperatures (Gatti et al. 2008) reveling temperature-related niche conservatism (Eiserhardt et al. 2011, Kissling et al. 2012). Therefore distribution and physiological requirements of those lineages support the hypothesis that lineages track environment to which they are already adapted (Donoghue 2008), evidenced here by their segregation along the successional gradient, supporting phylogenetic niche conservatism (Ackerly 2003) and phylogenetic habitat filtering (Duarte 2011).

CWM of traits correlated with the PCPS.1 of trees evidence the adaptation of these lineages (Magnoliids and Arecaceae) to the shaded forest and follow the predicted differences in life-history strategies accordingly to older forest stages (Poorter et al. 2008, Wright et al. 2010). Such strategies characterize slow-growth shade-tolerant species as conservative species that invest in long-leaved tissues (high leaf dry matter content, leaf area, wood density) and heavy seeds. Moreover, high leaf phosphorus concentration enhances the photosynthetic capacity (Reich et al. 2009) and may confer an adaptive advantage of these lineages to deep shade environments.

NRI values of juvenile communities had a similar phylogenetic structure of trees. However segregation of species was not dependent on the relatedness indicating that species from distinct clades can occupy different positions along the successional gradient. The association of Arecaceae and *Virola bicuhyba* (PCPS.1) to heavy seeds and bigger leaves in this stratum also express adaptive strategies to shade (Givnish et al. 2005), optimizing light interception (LA) (Reich et al. 2003) and shade tolerance during the establishment (SM) (Muller-Landau 2010, Lebrija-Trejos et al. 2016). On the other end of this axis we found the association of (mainly) Eudicots species with communities functionally described by higher leaf nitrogen concentration, which is a trait of fast-growth species (Wright et al. 2004, Reich 2014), often important at initial successional stages. Further the PCPS.1 of trees and juveniles evidenced the role of the Eudicots in the colonization of open environments facilitating the establishment of early-divergent lineages (Valiente-Banuet et al. 2006). Among Eudicots, Superasterids seedlings were also related to old-growth forests (PCPS.4), indicating the participation of small statured gap-dependent and understory species. The PCPS.2 of juveniles reveals the association of Magnoliids species to S3 (about 40-50 years of succession), which appears again in the seedling communities (PCPS.1 of seedlings). This association reinforce the clade segregation found at the tree stratum, which may not be evidenced by the PCPS analysis for juveniles due to the ameliorated conditions offered by the already established canopy (tree stratum) making possible the recruitment of this lineage in younger successional stages. The association of functional composition of juveniles and the phylogenetic composition indicates lower values of LDMC in S3 than in initial (S1, S2) and older (S4) stages. Thinner leaves promote better CO_2 diffusion due to lower number of cells and less thickness of mesophyll layers and is an adaptation to shade environments that lead to lower LDMC values (Pérez-Harguindeguy et al. 2013) and reinforce the affinity of Magnoliid species to such conditions. The higher LDMC values associated to initial and final successional stages are expected due to adaptations to avoid desiccation under high insolation (as in the initial successional stages), but also due the need of long-lived resistant leaves able to persist in the resources poor environment of older successional stages (Cornelissen et al. 2003).

Conclusions

We found that the main lineages segregate along the successional gradient due to conserved niche requirements of the early-divergent clades. Early-divergent clades establish under the developed canopy reveling their association to dense forests (older successional forests) and to phylogenetic habitat filtering, whereas Eudicots were principally associated to early successional stages. Eudicots can, however, also occur over the gradient and their co-occurrence with the early divergent nodes in older successional stages lead to a higher phylogenetic dispersion in such communities. Moreover phylogenetic relationships of the terminal nodes suggest that more recent historical forces had shaped distinct ecological strategies enabling closely and distantly related species to coexist in the advanced succession.

Further the association of phylogenetic and functional perspectives of the communities along the succession shed light in the evolutionary history that had shaped life-history strategies and adaptive features of species and clades current found along the successional gradient.

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Supplementary material. Chapter 1

Appendix 1: Phylogenetic tree in Newick format and the molecular phylogeny reconstruction workflow.

Molecular phylogeny reconstruction

To reconstruct the phylogenetic tree containing the species sampled at the tree, juvenile, and seedling stages, we used molecular sequences available at GenBank (accessed in December 2015; Benson et al. 2013). We used sequences of nuclear (ITS1, ITS2, and ETS) and chloroplastidial markers (rbcL, matK, trnL-trnF spacer, trnL, psbA-trnH spacer and ndhF), known to resolve species relationships at higher and lower taxonomic levels. When searching for sequences at GenBank, we checked for species synonyms and found sequences for 81 species of 150 sampled species. The remaining 69 species without sequence data were represented by 39 genera of which we used sequences of congeneric relatives, always looking for species that occur geographically close to the sampled area and/or presenting most of the used markers. For genera with more than one species within these 39 genera, we used only one species. Remaining species (30 spp.) were manually merged in the resulting phylogeny, splitting them halfway along their congener branch with sequence data. There was only one genus (*Myrrhinium* Schott), which did not present any sequence at GenBank, and it was merged at the root of Myrtaceae family.

The sequences were aligned using the MAFFT v.7.266 software (Katoh & Standley 2013), choosing the X-INS-i alignment strategy (Katoh & Toh 2008) for the markers ITS1, ITS2, ETS, trnL-trnF spacer and trnL intron, which takes into account a secondary structure information of RNA. For rbcL, matK and ndhF we used the E-INS-i alignment strategy. The sequences aligned using MAFFT v.7.266 software were employed via the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). For the psbA-trnH spacer we used the software SATé v.2.2.7 (Liu et al. 2012), aligning subgroups through MAFFT, merging sub-alignments through MUSCLE (Edgar 2004) and using a start tree reconstructed through the Phylocom/Phylomatic software (Webb & Donoghue 2005; Webb et al. 2008) according to the phylogenetic hypothesis of Magallón et al. (2015). Using the AliView software (Larsson 2014), we manually trimmed the alignment tips. Finally, the alignments were concatenated in a supermatrix using the software FASconCAT (Kück & Meusemann 2010).

The phylogenetic tree was reconstructed using a maximum-likelihood approach (ML) through the RAxML v.8.2.4 software (Stamatakis 2014) via the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). The chosen model was the GTR+GAMMA+I, setting partitions for each marker. The ML searches were defined to 1,000 times and a bootstrap support value was estimated for each node. We chose *Amborella trichopoda* Baill. (Amborellaceae) and *Nymphaea alba* L. (Nymphaeaceae), early-divergent angiosperm species, as the outgroup and used a backbone constraint tree reconstructed using the Phylocom/Phylomatic software (Webb & Donoghue 2005; Webb et al. 2008) based on the APG4 phylogenetic hypothesis (APG 2016) with a resolution to the order level. The constraint tree was used to limit the software searches to trees compatible with its topology, reducing the artifact of patchy dataset (Roquet et al. 2013). Moreover, the order resolution level of the constraint tree let free the ML inference to determine the relationships between families within each order.

The resulting phylogeny had their branch lengths representing the rate of evolution of the used markers, and we transformed it to be proportional to divergence time through rate smoothing. For this we used the non-parametric rate smoothing technique (Sanderson 1997), setting the smoothing parameter (lambda) to one. The molecular dating was calculated through the function chronopl using the correlated model at the package ape v.3.2, (Paradis et al. 2004), in the R Statistical Environment (R Core Team 2016).

Phylogenetic tree

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Capítulo 2

What short-term demographic changes and patterns of stem size distribution can tell us about subtropical tree dynamics?

Kátia J. Zanini

Cristiane F. Jurinitz

Sandra C. Müller

This manuscript will be submitted to Journal of Plant Ecology.

Chapter 2: What short-term demographic changes and patterns of stem size distribution can tell us about subtropical tree dynamics?

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Running title: Demographic patterns and subtropical trees dynamics

Abstract

Aims Secondary forests represent about 50% of current natural forest cover and the understanding of its dynamic for species conservation became extremely important. Meanwhile remaining old-growth forests face human disturbances at global and local scales that affect species performance in short and long-term. The response of trees to the environment is mediated by functional traits that influence the ability of a plant to grow, survive and reproduce, shaping individual fitness and leading to a differential demographic performance. Stem size distribution (SSD) of trees is assumed to predict population changes, since long-lived organisms lack adequate demographic data. Forest conservation state, global, and local environmental changes are likely to influence both, fitness and demography. Here we evaluated the predictive power of SSD, summarized by the coefficient of skewness (*g1*), and functional traits on short-term demographic changes of 20 subtropical trees, considering two ontogenetic stages. We also compared the SSD of four common species between secondary and old-growth forests.

Methods Tree species data are from permanent plots installed in the southernmost part (29°42'S, 50°11'W) of the Atlantic Forest in Brazil. Most abundant tree species in secondary and old-growth forest had their patterns of SSD evaluated and significance of skewness (*g1*) tested for normality by Shapiro-Wilk normality-test with Bonferroni correction ($p \leq 0.0025$). Short-term demographic changes corresponded to the variations in abundance (ΔA) and basal area (ΔBA) within five years of monitoring, while the functional traits comprised four plant dimensions: leaf traits, height at maturity, wood density, and seed mass. The influence of these functional dimensions and of stem size distribution (*g1*) on species demographic changes (ΔA and ΔBA) of trees (dbh $\geq$ 5cm) and juveniles ($\geq$1cm dbh <5cm) was tested with multiple linear regression models and model selection with Akaike Information Criterion.

Important findings Short-term demographic changes were better captured by leaf traits and the *g1* revealing that (i) common secondary species with high positive *g1* values are predicted to have greater basal area gain due to growth and recruitment of new individuals at adult stages, (ii) species characterized by acquisitive leaf traits and displaying a negative *g1* are predicted to lose juvenile and adult individuals, and (iii) species with conservative leaf traits (old-growth species) are predicted to lose adult individuals, irrespective of positive or negative *g1* values, but basal area loss due to mortality is partially recovered by growth and recruitment of juveniles with conservative leaf strategies. Regarding the four species analyzed in both forest conservation statuses, we observed a greater proportion of saplings in secondary forests, indicating a higher fitness in disturbed environments. The combination of *g1* and leaf traits to understand local scale subtropical trees dynamics has shown to be a useful tool, even in a short-term demographic study.

Key words: secondary and old-growth forests, functional traits, temporal changes, species abundance, growth-mortality trade-off

Introduction

Tree species are distributed along a continuum of the growth-mortality trade-off, in which species that grow fast are more susceptible to early death and the slow-growing are able to compete and survive longer within poor resource conditions (Tilman 1994; Rees 2001). Differences in the species life histories are determined by functional traits that are morphological-physiological-phenological attributes that influence the ability of a plant to grow, survive and reproduce (Violle *et al.* 2007), shaping individuals fitness, and leading to a differential demographic performance of the species (Poorter *et al.* 2008; Wright *et al.* 2010). Therefore in one extreme of the growth-mortality trade-off are the fast-growing species usually associated to resource-rich environments, such as forest gaps and disturbed sites. These species are characterized by high-acquisitive traits, as for example high leaf nitrogen and phosphorous concentration, high specific leaf area and low wood density, enabling them to reach the canopy quickly (Wright *et al.* 2010; Reich 2014) or to fade at juvenile stage if environmental conditions become unfavorable (Coomes *et al.* 2003; Uriarte *et al.* 2012). In the other side long-lived and thicker leaves, with high leaf dry matter content, and hard woods characterize slow-growing species. These species can tolerate stresses such as shaded environments for long, until the access to light become available (Kobe *et al.* 1995), enabling then the small plants to grow to larger sizes. Hence, the fitness of an individual is also related to its maturity, leading to differential species growth and survival rates (Kraft *et al.* 2010). Such differences may be further associated to the relative importance of distinct traits on the plant fitness among ontogenetic stages (Visser *et al.* 2016), contributing to shape the species population structure.

The species life history is reflected in its stem size distribution (SSD), which can be seen as a picture of the population structure in a certain time. Slow-growing species usually have many small plants waiting for an opportunity to get larger, while fast-growing species invest in overtop its neighbors passing quick to larger size classes and leaving few youngers behind (Condit *et al.* 1998; Wright *et al.* 2003). So, in the population perspective, a SSD right skewed usually characterize slow-growing species, while a SSD left skewed characterize the fast-growing ones (Wright et al. 2003). It is also often assumed that species with SSD skewed to many young individuals (right skewed) would suggest population maintenance or increase, while species with more adult trees in relation to the young (left skewed) would indicate population decline (Condit *et al.* 1998; Feeley *et al.* 2007). Further, temporal and spatial resource-partition within forest habitats support species coexistence, in which plant abilities to explore distinct resources are associated to species life history and functional traits (Kobe *et al.* 1995; Pacala and Rees 1998), likely influencing individuals fitness and SSD of the species. Gap-dependent species, for example, can persist due to resource-rich ‘windows’ in the time and space and their left skew distribution is a consequence of these processes.

Worldwide forests are facing global and local environmental changes that affect species differentially, leading to changes in species abundance and growth patterns (Laurance *et al.* 2006; Lewis *et al.* 2009) and even causing species die-offs (Allen *et al.* 2010). The response of trees to the environmental changes is mediated by plants functional traits. Changes in the environmental conditions (local human-induced and climate driven changes) thus alter individual fitness and change species demographic performances (Pacala and Rees 1998; Coomes and Allen 2007; Uriarte *et al.* 2012). Besides, the forecast of the incapability of tropical forest species to respond to climate changes through acclimation, adaptation or migration (Feeley *et al.* 2012) makes urgent the need of understanding how species populations respond to environmental changes: which traits are the most affected (response traits) and what sort of consequences can be expected in the species demography? These are questions that deserve to be assigned.

Here we first evaluate the SSD of 20 subtropical tree species to have a picture of their population structure. We predicted the SSD of species as being associated to the growth-mortality trade-off, with fast-growing species having a left skewed SSD and slow-growing a right skewed. Considering that environmental conditions can alter the fitness of individuals, we selected four common species that occur in both secondary and old-growth forests and compared their SSD in relation to the conservation status of the forest, aiming to understand intraspecific shifts in demography.

Second, we evaluated the predictive power of the coefficient of skewness (*g1*), which summarizes the symmetry of species SSD (Bendel *et al.* 1989), and of four functional dimensions of plant strategies (Wright *et al.* 2007; Laughlin 2014) on short-term changes (5 years) in abundance and basal area of juveniles and adults of tree species (hereafter referred as 'juveniles' *versus* 'trees') with pooled data from both forest status. Functional dimensions were represented by traits expressing (1) competition for light (height at maturity - H), (2) plant growth ability (wood density - WD) (Poorter *et al.* 2008), (3) stress tolerance and fecundity (seed mass - SM) (Muller-Landau 2010; Terborgh *et al.* 2014), and (4) plant investments in light interception and water economy (leaf surface area), metabolic rates (specific leaf area, leaf nitrogen and phosphorous concentration, N:P ratio), resistance to hazards and leaf-life-span (leaf thickness, leaf dry matter content, leaf deciduousness) (Reich *et al.*

1997; Wright *et al*. 2004). We expected species with a left-skewed SSD (negative *g1*) and acquisitive plant strategies (fast-growing species) to loose individuals and gain basal area, strongly affecting the juvenile stage. Acquisitive traits lead to fast individual growth (basal area gain), but as these species are often gap-associated, under shaded conditions, they either may move quickly to higher size classes or fade. On the other side, we predicted right-skewed species distributions (positive *g1*) and conservative plant strategies (*e.g.* high WD, SM, H, and leaf dry matter content – slow-growing species) having lower demographic changes or just an increase in abundance due to the recruitment of individuals, that consequently contribute to the maintenance or increase of the total basal area of the species.

Methods

Study Area

Tree species data are from permanent plots (*Sistema de Parcelas Permanentes do Corredor Mata Atlântica Sul no Nordeste do Rio Grande do Sul*) installed in the southernmost part (29°42'S, 50°11'W- Maquiné county) of the Atlantic Forest in Brazil. Climate is subtropical humid, type Cfa according to Köppen's classification, with mean annual temperature above 18°C, absence of a dry period, and an annual mean rainfall of 1400 to 1800 mm (Hasenack and Ferraro 1989; Nimer 1990). Forest are located in the lower-montane forest zone (Teixeira *et al.* 1986) of the Maquiné River Hydrographic Basin, in sites that ranged from 50 to 456 m a.s.l.. Natural vegetation consists of subtropical moist broadleaf forest and corresponds to the subtropical portion of the Atlantic Forest *sensu stricto* (Oliveira-Filho 2009). Study forests comprise two successional categories, secondary (6 to 50 years since abandonment) and old-growth forests (remnants without register of clearcuting), characterizing two distinct conservation statuses. Notwithstanding, forests in distinct successional stages are currently the predominant vegetation cover of the region, characterizing a highly connected system (Zanini *et al.* 2014). Soils are derived from basalt, and are classified as shallow litic leptsols with occasional rocky outcrops and luvic phaeozem (Streck *et al.* 2008).

Species data

We disposed randomly 39 circular sampling units (100 m^2) in old-growth forests and 72 in secondary forests to sample trees ≥ 10 cm of diameter at breast height (dbh), obtaining 0.39 ha and 0.72 ha of sampling area respectively. Within the 100 m^2 sampling units we situated subplots of 40 m^2 for the survey of individuals between 1-10 cm dbh, obtaining a sample of 0.156 and 0.288 ha for the juveniles in old-growth and secondary forests, respectively. Demographic parameters (see *Demographic changes*) were obtained from older secondary forest (fifty-year secondary forests – 24 sampling units) and old-growth forests (24 sampling units) pooled, which were surveyed in 2009 (t_1) and again in 2014 (t_2).

Stem size distributions (SSD)

Twenty most abundant tree species (from 19 to 350 individuals each) had their patterns of SSD evaluated. For that purpose, we calculated the coefficient of skewness (*g1*), which summarizes the evenness or symmetry of truncated lognormal distributions (Bendel *et al.* 1989) and is defined by

$$g1 = \frac{n\ \sum_i (x_i - \bar{x})^3}{(n-1)(n-2)S^3}$$

where n, x_i, $\bar{x}$ and s represent the number of individuals, the logarithm of dbh for individual i, the mean of x_i, and the standard deviation of the x_i, respectively. $g1<0$

expresses SSD with relatively few small and many large stems (left-skewed); *g1*>0 expresses SSD with few large and many smaller stems (right-skewed) (Bendel *et al.* 1989). Trees with multiple stems had an averaged stem diameter value calculated.

The *g1* of four species that were sufficiently common was analyzed separately for each forest status (secondary and old-growth) and also together, just to have a general SSD in comparison to all other species. These four species were: *Mollinedia* schottiana (Spreng.) Perkins, *Actinostemon concolor* (Spreng.) Müll. Arg, *Psychotria suterella* Müll. Arg, and *Euterpe edulis* Mart..

Species Traits

Leaf traits were measured in the field following standard protocols (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). Traits from 3 to 15 individuals per species were measured and the average value was used to represent each species in the analysis. Leaf traits here considered are specific leaf area (SLA, $mm^2.mg^{-1}$), leaf surface area (LA, cm^2), leaf dry matter content (LDMC, $mg.g^{-1}$), leaf nitrogenous and phosphorus concentration (LNC and LNP, percent N and P mass per total mass, %), leaf N:P ratio (NP, unitless) and leaf thickness (LT, mm). Leaf thickness was estimated following Vile *et al.* (2005) ($LT= 1/SLA*LDMC$). Together with these leaf traits we used leaf deciduousness (LD, 1= deciduous and semi-deciduous; 0= evergreen), height at maturity (H, m), wood density (WD, $g.cm^{-3}$), and seed mass (SM, g), with data compiled from the literature.

Demographic changes

We estimated the species abundance variation ($\Delta A_i = ln(N_{t1}) - ln(N_{t2})/t$; where N is the number of individuals of species *i*, t_1 and t_2 are, respectively, the first and the second survey, and t is the time interval in years) and the species basal area variation

($\Delta BA_i = ln(Ba_{t2}) - ln(Ba_{t1})/t$; where Ba (m^2) is the sum of stem basal area of species *i* in t_1 and t_2 respectively). According to this, "ΔA > 0" represents loss of individuals and "ΔBA > 0" represents gain in stem biomass. We are referring to these rates as 'demographic changes' throughout the text and they were calculated with pooled data for forests, but separately for trees (dbh≥5cm) and juveniles (≥1cm dbh <5cm). As we considered species with at least six individuals in the first survey, from the 20 species evaluated for the adult stage (trees), we remained with 12 species for the juvenile stage analysis.

Data analysis

The significance of skewness at the stem size distribution (*g1*) was tested for normality by Shapiro-Wilk normality-test with Bonferroni correction ($p \leq 0.0025$). Non-significant skewed distribution indicates that SSD do not differ from a normal distribution.

We tested the influence of four functional plant dimensions (leaf, wood density, height at maturity and seed mass) and stem size distribution (*g1*) on species demographic changes (ΔA and ΔBA) of trees and juveniles with multiple linear regression models. Leaf thickness was log-transformed to meet normality. To reduce the number of leaf variables, we first submit them to Relative Variable Importance analysis (MiMIn Package, Barton 2015), which sums Akaike weights of all models including each explanatory variable, considering all combinations of models. So we just included in the tested regression models leaf variables with higher importance values (Supplement 1), which were: LNC and LPC for abundance variation (ΔA) and LNC, LPC and N:P for basal area variation (ΔBA) of juveniles; LA, LNC, LPC, LD, N:P for ΔA and LD, LA, LT for ΔBA of trees. The explanatory variables of the models were then composed by these respective leaf traits, wood density, seed mass, height at maturity, and the *g1*, while species demographic changes (ΔA, ΔBA) of trees and juveniles were employed as response variables. Principal Component Analysis (PCA) was performed to visualize traits relationships among the species and, afterwards, demographic changes (ΔA, ΔBA) and size distributions (*g1*) were correlated with the axes and added on the diagram.

The best models for species demographic changes were selected using Akaike Information Criterion (Burnham and Anderson 2002), with correction for small samples (AICc) (Hurvich and Tsai 1998). A rank of the models according to their support of the data was generated, where the differences between the lowest AICc and the other AICc values (delta AICc) were used to visualize distinctions in model support. Differences greater than 2 in the delta AICc were considered as a threshold for model support (Burnham and Anderson 2002) ('bbmle' package, Bolker 2015).

Models were tested with and without *Euterpe edulis* Mart. (Arecaceae), as palms lack secondary growth, but as results did not change with its inclusion we are maintaining it.

Results

Stem size distribution (SSD)

A total of 1,610 individuals were measured in the first survey, 922 in secondary forest sites and 688 in old-growth forest sites. Irrespectively of the site occurrence, most of the values of the coefficient of skewness (*g1*) of the 20 species were around zero (Fig. 1a), showing few extreme values, and the huge majority of individuals were in the lowest dbh category (Fig. 1b). Four species have significant negative *g1* values, indicating the concentration of SSD towards larger stem sizes, and 10 species have significant positive *g1* values, that express a greater abundance of small stems compared to larger ones (Tab. 1). Five species with negative *g1* and one with positive *g1* were not significant different from normal distributions, suggesting an even distribution (P≤0.0025) (Tab. 1).

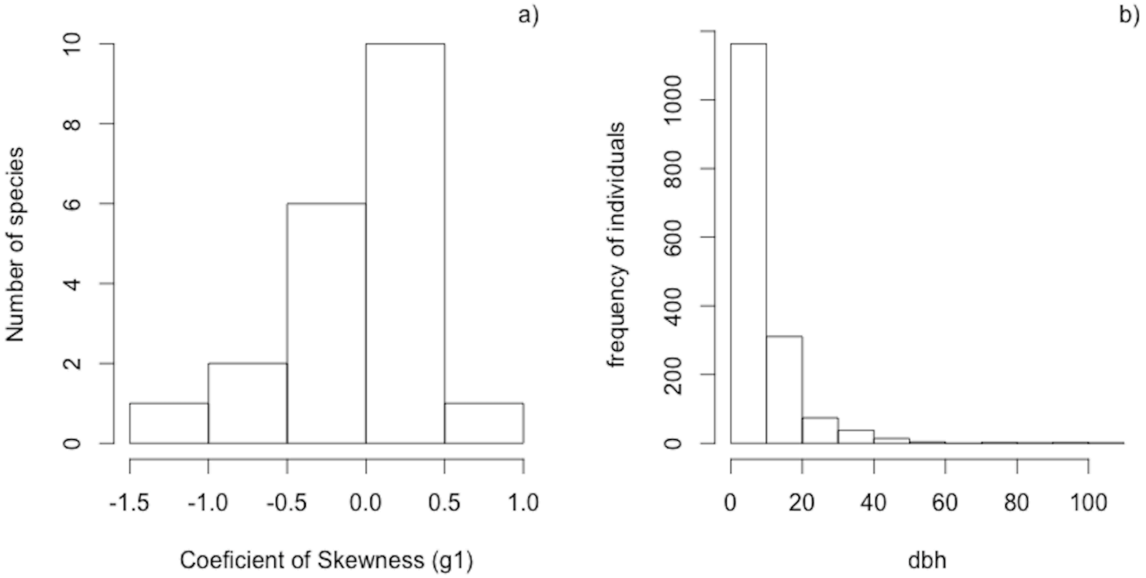

Figure 1: Stem size distribution patterns of 20 tree species from southern Atlantic forest. (a) Distribution histogram of the coefficient of skewness values (*g1*) of all 20 species, and the (b) histogram of the dbh distribution of all individuals.

By considering all individuals sampled either in secondary or in old-growth forests, we have positives SSD for both forest types (*g1*= 0.44 and 0.26, respectively; Supplement 2), as most individuals have dbh smaller or equal to 20 cm. Small differences can be observed between size classes, but the main difference was among the proportion of individuals within the first classe (1-10 cm dbh): secondary forest had 57% of individuals between 1-5 cm dbh and 15% between 5-10 cm dbh, while in old-growth forests these classes represented 43% and 27%, respectively.

Table 1: Number of individuals (n) according to the sampled species in old-growth and secondary forests, and their respective general coefficient of skewness (*g1*), that is, irrespective of site occurrence. '*' indicates significant skewed values. Species are also identified by its successional group, following Grings and Brack (2009):

pio=pioneer, ise= initial secondary, lse=late secondary. Species are ordered according the *g1* value.

Species	Old-growth (n)	Secondary (n)	*g1*	Successiona group
Meliosma sellowii (Spreng.) Perkins	21	2	-1.09	lse
Alchornea triplinervia (Spreng.) Müll. Arg.	6	24	-0.87	ise
Chrysophyllum inornatum Mart.	22	-	-0.66	lse
Sapium glandulosum (L.) Morong	1	24	-0.41	pio
Tetrorchidium rubrivenium Poepp.	9	36	-0.40*	lse
Cabralea canjerana (Vell.) Mart.	16	155	-0.29*	ise
Actinostemon concolor (Spreng.) Müll. Arg.	106	18	-0.06*	lse
Casearia sylvestris Sw.	7	70	-0.05*	ise
Ficus adhatodifolia Schott ex Spreng.	4	20	-0.01	lse
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima	1	41	0.003*	ise
Mollinedia triflora (Spreng.) Tul.	8	24	0.09*	lse
Sorocea bonplandii (Baill.) W.C. Burger, Lanjouw & Boer	69	6	0.23*	lse
Euterpe edulis Mart.	230	120	0.23*	lse
Mollinedia schottiana (Spreng.) Perkins	59	97	0.27*	lse
Garcinia gardneriana (Planch. & Triana) Zappi	19	-	0.29	lse
Psychotria suterella Müll.Arg	34	159	0.36*	lse
Luehea divaricata Mart.	1	19	0.36*	ise
Inga marginata Wild.	8	90	0.41*	ise
Trichilia claussenii C. DC.	40	5	0.43*	lse
Guapira opposita (Vell.) Reitz	27	12	0.64*	ise

Differences in the proportional abundance of species (Tab. 1) can indicate the predominance of the species either in old-growth or secondary sites, but we find species with positive and negative *g1* for each forest type. Concerning the four species that were analyzed for SSD in both forest conservation statuses (*M. schottiana*, *A. concolor*, *P. suterella*, and *E. edulis*), we can evidence some influences on the SSD of these species, being the *g1* values smaller in old-growth sites. *M. schottiana* and *A. concolor* changed significantly from left skewed negative *g1* values in old-growth forests (-0.18 and -0.18, respectively) to positive right-skewed distributions in secondary forests (0.26 and 1.22, respectively). *P. suterella* displayed a positive *g1* in secondary forests (0.49) and a normal distribution in the old-growth, which expresses a proportional number between juveniles and trees. *E. edulis* had positive right-skewed values in both forests types (0.20 and 0.29, respectively in secondary and old-growth forests).

Demographic changes

PCA diagrams show the association between species functional traits and their correlation with demographic changes of each stage (juvenile and trees) and SSD (*g1*) (Fig. 2). The diagram with axes PC1 and PC2 displays a gradient from acquisitive light-demanding species (on the upper right) to acquisitive shade-tolerant, on the upper left side, ending with conservative shade-tolerant species in the lower part. More specifically, axis 1 separates light-demanding trees with higher LPC and LNC, large and deciduous leaves (LA, LD), and taller at maturity (H) (right side) from shade-tolerant species (left side). Axis 2 splits shade-tolerant conservative species with thicker and resistant leaves (LT, LDMC), dense woods (WD) and heavy seeds (SM) (bottom) from acquisitive species with higher metabolic rates (higher SLA, LNC), which may are light-demanding (on the right) or shade-tolerant species (on the left). Axis 3 splits light-demanding species (bottom), with higher N:P ratio, deciduous (LD) and taller, from those with large and perennial leaves, higher LPC, dense wood and heavy seeds.

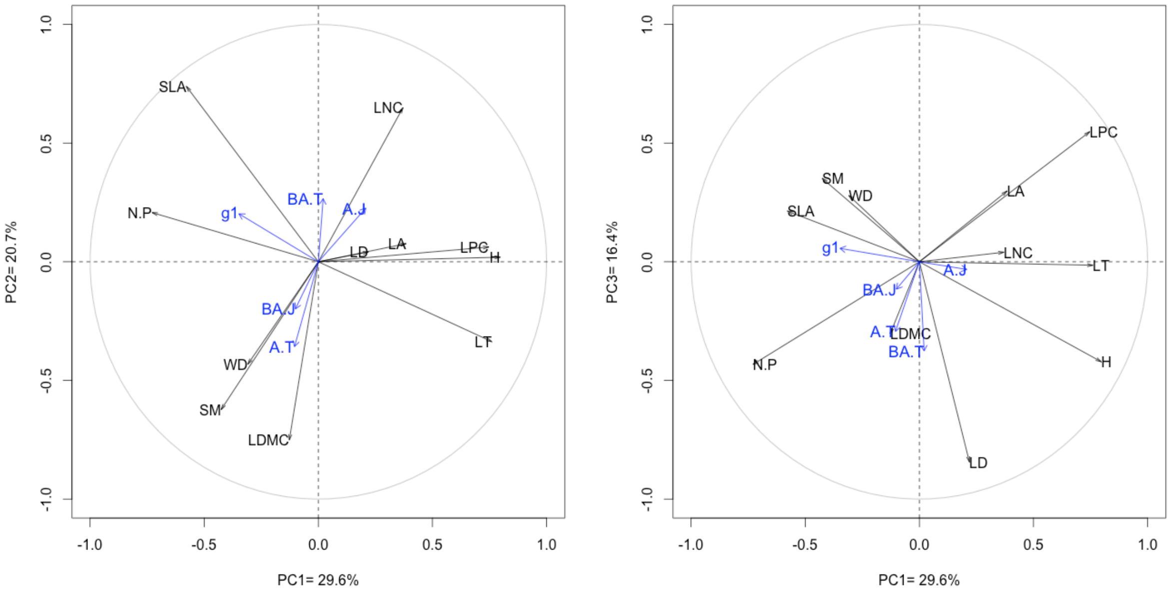

Figure 2: PCA ordination diagrams of 20 tree species described by their functional traits (SLA, specific leaf area; LA, leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorous content; N.P, N:P ratio; LD, leaf deciduousness, LDMC, leaf dry matter content, LT, leaf thickness; WD, wood density; H, height at maturity; SM, seed mass). Coefficient of skewness (g1) and species demographic changes, regarding variation in basal area (BA) and abundance (A) for trees (T) and juveniles (J), were correlated with PCA axis afterwards. Diagrams comprise the variation of axes 1 and 2 (left plot) and axes 1 and 3 (right plot).

The selected regression models (Tab. 2) indicated trees with small leaves (-LA), lower leaf nitrogen concentration (-LNC), taller at maturity (+ H) and deciduous (+LD) to be more prone to lose individuals (models ΔA_{T1} and $_{T2}$; see also ‘A.T’ at the Fig. 2). These models predicted loss of individuals of species with conservative traits (small leaves, lower LNC), and deciduous, tall pioneer/initial secondary species. Some representative species of the conservative strategy are *Actinostemon concolor, Garcinia gardneriana, Sorocea bonplandii*, whereas pioneer/initial secondary species are *Sapium glandulosum*, *Luehea divaricata*, *Lonchocarpus cultratus* and *Achornea triplinervia*.

Table 2: Best models for the variation in abundance (ΔA, number of individuals) and variation in basal area (ΔBA) of tree species in adult stage (n=20) and in the juvenile

stage (n=12), regressed four traits strategy dimensions and the population structure descriptor (g1). Only the selected variables for the models are shown: LA, leaf area; LNC and LPC, leaf nitrogen and phosphorous concentration; N:P, nitrogen and phosphorous ratio; LD, leaf deciduousness; LDMC, leaf dry matter content; LT, leaf thickness; H, height at maturity. Akaike information criterion (AICc), models weight and Delta AICc are given.

	Models	**LA**	**LNC**	**LPC**	**N:P**	**LD**	**LT**	**H**	**g1**	**ΔAICc**	**df**	**weight**	**AICc**
Trees	ΔA_{T1}	-0.001	-0.06	-	-	-	-	0.004	-	0	5	0.23	-71.13
	ΔA_{T2}	-0.001	-0.04	-	-	0.03	-	-	-	1.7	6	0.10	-69.40
	ΔBA_{T1}	0.002	-	-	-	0.11	-0.07	-	0.05	0	6	0.36	-63.55
	ΔBA_{T2}	0.001	-	-	-	0.10	-	-	0.06	2.0	5	0.13	-61.51
Juvenile	ΔA_{J1}	-	0.03	0.05	-		-	0.004	-	0	5	0.26	-45.88
	ΔA_{J2}	-	0.04	0.05	-		-	-	-	1.1	4	0.15	-44.76
	ΔA_{J3}	-	0.05	-	-		-	-	-	1.4	3	0.13	-44.47
	ΔA_{J4}	-	0.04	-	-		-	0.004	-	1.7	4	0.11	-44.15
	ΔA_{J5}	-	-	0.07	-		-	0.005	-	1.8	4	0.11	-44.10
	ΔBA_{J1}	-	-	-0.22	-		-	-	-	0	3	0.23	-24.26
	ΔBA_{J2}	-	-0.07	-0.18	-		-	-	-	0.2	4	0.21	-24.05
	ΔBA_{J3}	-	-0.11	-	0.01		-	-	-	1.4	4	0.11	-22.81

Basal area increase was predicted for trees with large, deciduous and thinner leaves (+LA, +LD, -LT) and positive *g1*. Axis 3, in the diagram shows the association of basal area increment of trees (BA.T) with LD of those fast-growing pioneer and secondary species. Axis 2 shed light on the participation of the shade-tolerant species manly recruiting new individuals (lower A.T, upper part of the diagram). These species display a high number of established juveniles (high *g1*), high SLA and thinner leaves and they are the late secondary dominants, such as *Guapira opposita*, *Mollinedia schottiana*, *M. triflora* and *P. suterella*.

Juvenile demographic changes were well explained by traits associated to the second axis (PC2) of the Fig. 2. Given the juvenile stage, species with higher values of leaf nitrogen (+LNC) and phosphorous concentration (+LPC), and taller at maturity were predicted to have a higher loss of individuals (models ΔA_{J1} to $_{J5}$; see ‘A.J’ at the Fig. 2). Within this stage, we could not analyze pioneers (too few individuals) and examples of more acquisitive species are *Casearia sylvestris, Guapira opposita* and *Cabralea canjerana*. Furthermore, juveniles of species with lower nitrogen (-LNC) and phosphorous concentration (-LPC) and higher N:P ratio are predicted to have higher biomass gain (models ΔBA_{J1} to $_{J3}$; see ‘BA.J’ at the Fig. 2). These are species with conservative leaf traits (low LPC and LNC) that are frequent in old-growth forests, such as *S. bonplandii*, *G. gardneriana, A. concolor* and *E. edulis*.

Discussion

Some insights were found for the species dynamics through their population structure (SSD) and their short-term demographic variation. The first is that although species life histories are prevalent to determine SSD, habitat conditions influenced the fitness of individuals of some species, changing the population structure and the coefficient of skewness under forests with distinct conservation statuses (old-growth *vs.* secondary). The second is that two functional dimensions, leaf traits and the whole plant (here, height at maturity), predicted changes in the short-term species demography, with slight differences among which leaf traits have explained the dynamic of adults or juveniles.

Demographic structure and dynamics in changing environments

SSD is often considered a weak predictor of population changes (Condit *et al.* 1998). Nevertheless Feeley and collaborators (2007) found among distinct indices of SSD that the coefficient of skewness was the only one that captured population changes over the subsequent 10-15 years more often than a random expectation. At local scale, as in our study, populations with many saplings tended to increase abundance and those with few saplings tend to decline or increase slowly, but *g1* would not be informative across broader spatial scales. Also, intraspecific differences in sapling abundances characterized by the coefficient of skewness as those found here between forest conservation statuses are considered useful tools to predict trends in population changes (Feeley *et al.* 2007).

The four species that were compared according to their demography in each forest status are trees that established mainly after canopy closure (about 20 years after abandonment, Zanini *et al*. 2014). These species had higher *g1* values in secondary forests, suggesting a higher fitness of the juveniles in this resource-rich-environment (Uriarte *et al*. 2012). In the old-growth forests three of these species displayed a higher proportion of adults, suggesting an earlier establishment of such individuals likely associated to local disturbance events, such as forest gaps. Lower resource availability and competition (Tilman 1994; Rees 2001; Reich 2014) in old-growth forests may reduce the establishment of new individuals of these species and influence the fitness of those already established, affecting the proportion of small stems in some populations (Coomes *et al*. 2003). So, the positive *g1* value found for these three species irrespectively to forest conservation state expresses the high number of small stems of these species at the secondary forests. *E. edulis* did not change its SSD significantly between the forest conservation statuses here analyzed, but by looking in the database we can see that the establishment starts in older secondary forests (the species is absent in young secondary forests), which may indicate some requirements of mature forest conditions to a successful establishment (Givnish et al. 2005). Although the wide niche germination breath of *E. edulis* (Braz *et al*. 2012) saplings establishment is limited by frost (Gatti et al. 2008) and high sun exposure due to photoinhibition and the lack of hydraulic adjustments to high evaporative demand conditions (Gatti et al. 2014) limiting its success in open areas.

The higher *g1* values in the secondary forest indicate a general higher proportion of small stems in species populations and describe the ‘immaturity’ of these forests. Differences in the occurrence and/or the abundance of the species between secondary and old-growth forest reveal a striking different florist composition between forests. In our study we found an association between negative *g1* values and species classified as initial secondary species (ise). This and their abundance pattern (higher in the secondary forests) are expressions of species life history. They are acquisitive species, with individuals growing fast to higher size classes and associated to disturbed environments. Although this pattern of negative *g1* can indicate a population “decline” of a species, when associated to fast-growing species, it can be seen as a temporal and spatial resource partition strategy, in which the species will disperse from one period or local site to another place with favorable conditions (Denslow 1980; Pacala 1996). Among the species with negative *g1*, *Tetrorchidium rubrivenium* was originally classified as late secondary species (Grings and Brack 2009). However, given its leaf traits and the abundance in secondary forests, it should be better consider this species as an initial secondary tree in further studies (Aidar *et al*. 2003).

Relations between demographic changes, functional traits and population structure

Species with acquisitive strategies were predicted to increase in basal area of adults and to lose juveniles and adults. These findings are consonant with the growth mortality trade-off (Poorter *et al*. 2008; Wright *et al*. 2010). As pointed out by Reich *et al* (1997), photosynthesis, dark respiration, and leaf nitrogen concentration decline with increasing leaf life span, a gradient described here by the first and second axes of the PCA and captured by the models. The predicted mortality of acquisitive species in the juvenile stage elucidated the bottleneck commonly observed in species with this life history. Further, the predicted basal area gain of adults as a response of higher *g1* values may thus be an expression of the growth and recruitment of shade-tolerant species. Some of the species with positive *g1* are uncommon in old-growth forests but abundant in secondary forests. These are manly understory secondary species with acquisitive leaf strategies (high SLA and low LT). The potential greater photosynthetic rates, due to their higher LNC (light demanding and deciduous species) and higher SLA (light demanding and understory/shade-tolerant acquisitive species) (Reich *et al.* 1997; Cornelissen *et al.* 2003), allow these two groups of acquisitive species to grow fast to the maturity, providing seeds to the system more quickly (Pacala and Rees 1998; Moles and Westoby 2006). Secondary shade-tolerant species are likely maintaining their populations and dominance in secondary forests due to the favorable environmental conditions and their high number of juveniles.

On the other hand, some low-abundant species quite exclusive from old-growth forest (e.g. *G. gardneriana*, *M. sellowii* and *C. inornatum*) presented size distributions that did not differ from a normal distribution. These are slow-growing species that are expected to have positive *g1* with many small stems waiting for an opportunity to grow. Nevertheless, the lower proportion of juveniles of such conservative species may be related to a dispersal limitation, as they have large fruits and seeds dispersed by large animals such as monkeys (Galetti *et al.* 2011). The defaunation of large-bodied seed dispersers is indicated as a driver of the loss of large-seeded trees (Cramer *et al.* 2007; Bello *et al.* 2015). Thus given the functional strategy of such late successional species, the SSD found here suggest they can be under a shift in their population structure in the near future as, contrarily to the initial expectation, these species did not present many seedlings and saplings in comparison to their adult proportion.

The loss of adult trees was also predicted for species with small leaves and low leaf nitrogen concentration, which expresses the mortality of old-growth species with low metabolic rates mainly limited by nitrogen (Reich *et al.* 2009; Wu *et al.* 2012). Moreover, given the juvenile stage models, we can see a new generation of species with conservative leaf strategies recruiting and growing in the forests. The basal area gain of juveniles with conservative leaf strategies (low LNC e LPC) is expressing the growth of survivors and new recruiters of late successional species (Finegan *et al.* 2015), which agree with a higher potential survival of conservative species, predicted by the growth mortality trade-off. However, our results also predicted higher mortality for conservative species in the adult stage. That is, such species are losing adult individuals and some of them were characterized by SSD not strongly positive skewed or yet negative skewed. So the maintenance of some old-growing species in the studied forests may be under concern because they do not meet the parameters of population grow suggested by Condit *et al.* (1998) and Feeley *et al.* (2007), which should meet high survival rates, growth of juveniles, and right skewed distribution.

Conservation implications

Secondary forests worldwide represent about 50% of the remaining natural forest cover (Wright 2005) and the understandings of its dynamic and role in the conservation of species have became extremely important. Meanwhile remaining old-growth forest face human disturbance at global and local scales (Lewis *et al.* 2004; Lewis *et al.* 2009), despite its undeniable importance for biodiversity, that affects species performance in short and long-term. In our study we found (i) abundant secondary species with high *g1* values having higher basal area gain in the short-term dynamic, suggesting they still can keep high abundance in this forest, (ii) some old-growth species were absent or in very low abundance in the secondary forests shedding light on the requirement of mature forests conditions for the establishment and survival of some species (Laurance 2008; Gardner *et al.* 2009), and (iii) adult trees limited by leaf nitrogen are predicted to have a higher loss of individuals in the short-term dynamics, which was not expected by the growth-mortality trade-off (Poorter *et al*. 2008; Wright *et al*. 2010).

The 20 species here analyzed are considered common in the southern Atlantic Forest, widely distributed and able to occupy various forest habitats, with abundant local populations (Caiafa and Martins 2010). Although, some of these 20 species were better associated to mature forests, being found only in old-growth forests with relative low frequency and abundance, whereas some species with very few individuals could not be included in the analyses and others were found only as seedlings with slightly or no changes along the studied period. Despite we recognize the natural presence of many rare species in tropical and subtropical forest communities (Hubbell 1979), defaunation, selective logging in the past, and reduced fecundity (Hobbs *et al.* 2003) are possible causes of their low frequency and abundance. These factors, together with stochastic hazards they may be exposed during the time elapsed from seedlings to the reproductive maturity (Moles and Westoby 2006), give us a picture of the challenges those species face to not perish under current conditions of remaining forests.

Considering our results and making a parallel with studies in highly fragmented forests we suggest that mid-successional disturbance-adapted species are likely to dominate for decades due to their greater abundance and elevated seed rain and they can be favored by the increasing frequency and intensity of disturbances associated to extreme climatic events (like El Niño Southern Oscillations) (Wright and Calderon 2006). The maintenance of early successional species by self-replacement is being suggested for the highly fragmented Atlantic forest (Tabarelli *et al*. 2012). In our study, forests are not isolated fragments but are within a matrix of different successional stages. Early successional species fade after canopy closure. However composition of the older secondary forests (40- 50 years) is still more similar to younger sites than to the old-growth forests (Zanini *et al*. 2014) and our results evidenced the loose of conservative old-growth species, the maintenance of abundant secondary species, and the challenge faced by old-growth species in maintain their populations.

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Supplementary material. Chapter 2

Supplement 1. Importance values of the leaf traits on basal area variation and abundance variation (ΔBA and ΔA) found for adult stature ‘Trees’ (dbh≥5cm) and for ‘Juvenile’ trees (1cm≤dbh ≤5cm); bold indicates the selected variables used in further analysis.

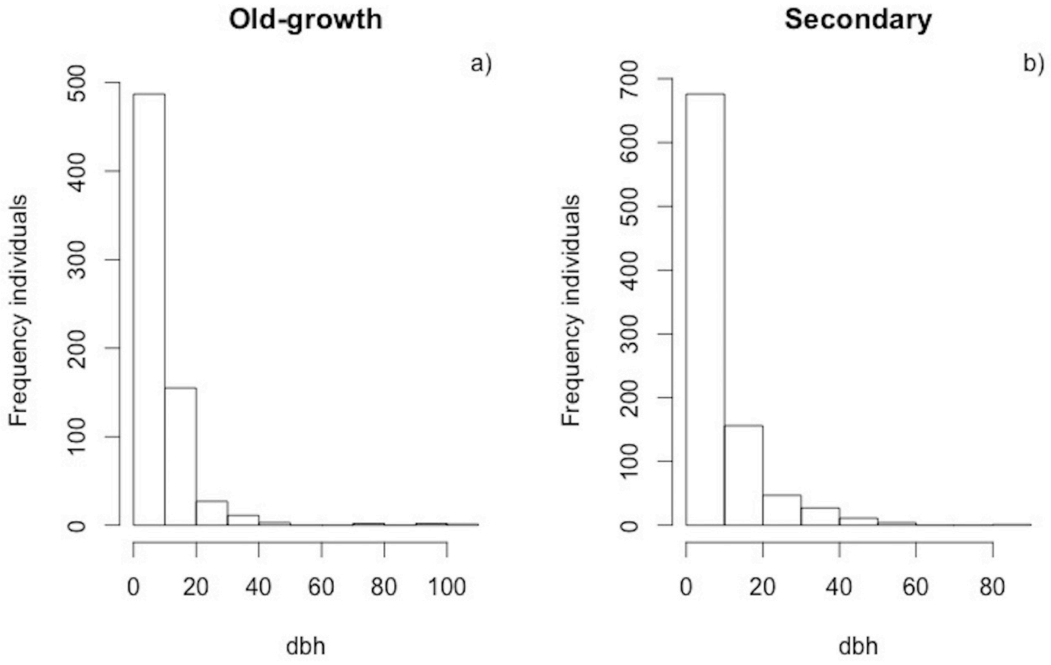
Trees (128 models)

ΔBA	**LD**	**LA**	**LT**	SLA	N.P	LNC	LDMC	LPC
Importance:	0.97	0.96	0.78	0.17	0.17	0.16	0.13	0.12
ΔA	**LA**	**LNC**	**LPC**	**LD**	**N.P**	LT	LDM	SLA
Importance:	0.52	0.51	0.29	0.28	0.28	0.16	0.15	0.15

Juveniles (64 models)

ΔBA	**LPC**	**LNC**	**N:P**	LT	SLA	LDMC	SLA
Importance:	0.76	0.49	0.23	0.12	0.09	0.8	0.7
ΔA	**LNC**	**LPC**	LDMC	N:P	SLA	LA	LT
Importance:	0.93	0.38	0.2	0.19	0.11	0.06	0.06

Supplement 2. Histogram of stem size distribution (SSD) of all individuals sampled in old-growth (a) and secondary (b) forests. Considering this SSD, *g1* for (a) is 0.26 and for (b) is 0.44.



Supplement 3. Description of species traits (LDMC: leaf dry matter content; SLA: specific leaf area; LA: leaf area; LNC and LPC: leaf nitrogen and phosphorous concentration; N:P, nitrogen and phosphorus ratio; LD: leaf deciduousness; LT: leaf thickness; WD: wood density; H: height at maturity; SM: seed mass) and demographic changes (ΔA= variation in individuals abundance; ΔBA=variation in basal area) for adult stature trees and juveniles.

	Trees		Juveniles		Traits										
Specie	**ΔA**	**ΔBA**	**ΔA**	**ΔBA**	**LDMC**	**SLA**	**LA**	**LNC**	**LPC**	**N:P**	**LD**	**LT**	**WD**	**H**	**SM**
Actinostemon concolor	0.026	-0.056	-0.033	0.022	366.13	8.77	29.38	1.14	0.07	16.21	0	0.31	0.66	20	0.380
Alchornea triplinervia	0.019	0.021	NA	NA	430.56	8.04	26.50	1.82	0.13	14.00	1	0.29	0.467	28	0.021
Cabralea canjerana	0.000	0.015	0.017	-0.087	313.78	16.64	33.97	2.11	0.15	14.07	0	0.19	0.54	25	0.833
Casearia sylvestris	0.000	-0.047	0.081	-0.248	366.89	11.17	14.97	2.28	1.21	1.89	0	0.24	0.71	22	0.012
Chrysophyllum inornatum	0	-0.05	NA	NA	389.77	9.63	13.59	1.56	0.83	1.88	0	0.27	0.78	17	1.900
Euterpe edulis	-0.067	0.142	-0.007	0.031	419.74	13.00	96.58	1.42	0.11	12.91	0	0.18	0.39	20	0.50
Ficus adhatodifolia	-0.024	0.051	NA	NA	281.07	9.58	90.88	2.12	1.14	1.86	0	0.37	0.58	30	0.0002
Garcinia gardneriana	0.027	0.008	-0.031	0.054	449.65	8.13	22.96	1.01	0.07	14.43	0	0.27	0.87	16	3.000
Guapira opposita	-0.071	0.033	0.024	0.027	229.15	15.15	25.36	2.78	0.14	19.86	0	0.29	0.83	21	0.143
Inga marginata	0.024	-0.007	0.081	-0.193	427.48	11.93	15.43	2.62	0.15	17.47	0	0.20	0.58	26	1.000
Lonchocarpus cultratus	0.015	0.123	0.033	-0.009	337.04	17.75	10.33	2.09	0.11	19.00	1	0.17	0.77	25	0.164
Luehea divaricata	0.027	0.137	NA	NA	365.38	12.59	19.55	1.68	0.23	7.30	1	0.22	0.563	26	0.004

Meliosma sellowii	0.062	-0.025	NA	NA	290.40	15.89	42.56	1.23	0.10	12.30	0	0.22	0.62	24	2.000
Mollinedia schottiana	0.000	0.005	-0.014	-0.032	283.65	23.64	33.36	1.87	0.18	10.39	0	0.15	0.6	15	0.381
Mollinedia triflora	-0.102	0.103	NA	NA	295.65	20.53	24.07	1.90	0.09	21.11	0	0.16	0.494	11	0.381
Psychotria suterella	0.052	-0.044	-0.006	-0.038	221.94	25.65	16.43	1.75	0.09	19.44	0	0.18	0.56	15	0.800
Sapium glandulosum	0.031	0.022	NA	NA	290.08	8.99	21.10	1.96	0.15	13.08	1	0.38	0.44	31	0.059
Sorocea bonplandii	0.010	0.001	-0.006	0.029	430.99	9.59	22.67	1.23	0.10	12.30	0	0.24	0.615	24	0.313
Tetrorchidium rubrivenium	-0.067	0.017	NA	NA	226.13	13.05	46.82	2.61	1.41	1.85	0	0.34	0.46	29	0.025
Trichilia claussenii	-0.048	0.011	-0.040	-0.015	401.39	14.00	27.98	1.82	0.11	16.55	0	0.18	0.68	18	0.161

Capítulo 3

What short-term functional changes of tree communities can tell us about small-scale forest dynamic in subtropical moist forests?

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Chapter 3: What short-term functional changes of tree communities can tell us about small-scale forest dynamic in subtropical moist forests?

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Running title: Short-term forest dynamics and functional changes

Abstract

Aims More than half of the natural world's forest is secondary forest and deterministic succession predicts that many features of pre-disturbed forests will be recovered. On the other hand, remnant old-growth forests are mostly within fragmented landscapes and edge-induced microclimatic conditions may lead to a retrogressive succession, named 'secondarization'. Thereby current forests tend to converge in terms of community structure and ecosystem function. Here we compared the short-term dynamics (five years interval) of secondary and old-growth forest communities in the highly fragmented Atlantic forest biome. Considering these two processes – succession and secondarization - we expected the rise of conservative plant traits and biomass for secondary forests and the reduction of such traits and biomass loss for remnant old-growth forests.

Methods Community data consist of permanent plots (100 m^2) installed in old-growth and secondary forests in the southernmost part (29°42'S, 50°11'W) of the Atlantic Forest in Brazil. We analyzed (i) 'community structure changes' - variation in community abundance and basal area per sampling unit - and 'functional composition changes' – percent of change in the community weighted mean of traits - of tree communities between two surveys (t_1 and t_2), and (ii) the predictive power of the functional composition of t_1 regarding four trait dimensions (leaf traits, seed mass, height at maturity, and wood density) on the community structure changes for juveniles (≥1cm dbh <5cm) and adult trees (dbh ≥ 5cm) tested by Linear Mixed Models and selected by Akaike Information Criterion.

Important findings Leaf traits and seed mass better captured the short-term functional composition changes. The advance of secondary forest towards conservative traits was confirmed for both strata. Old-growth communities lose biomass due to fall of big trees expressing the loss of an important structural feature of these forests. But functional composition changes did not evidence secondarization. Five-year interval might be a short period for the dynamic of long-lived organisms, such as trees, but with the association of structural and functional features of the communities it proved to be a useful time span to reveal interesting aspects of forest dynamics.

Key words: forest conservation, succession, functional traits, Atlantic forest, biomass changes

> “There is a pressing need for better process-level understanding of the dynamics of tree communities in the moist and wet tropics.”
>
> “Realistic forest dynamics models of these ecosystems will be needed for simulation of how these complex communities function and how they will respond to future environmental change. Empirical assessments of the growth patterns of representative tree species in these forests will be fundamental for the development of such models.”
>
> (Clark and Clark 2001)

Introduction

Worldwide changes of forest cover reflect both the opening of new agricultural lands and the regrowth of secondary forests after abandonment of croplands. In the tropics, the high loss of forest cover is being masked by the rapid re-growth of secondary forests (Letcher and Chazdon 2009; Metzger et al. 2009; Hansen et al. 2013), which comprehend about 65% of world’s natural forest cover (FAO 2015). If, on the one hand, ecological succession recovers biomass, diversity, and partially the structure of pre-disturbed forests (Chazdon 2003), on the other hand, remnants of old-growth forests may be negatively affected by environmental shifts associated with edge-effects (Laurance 2008). In this context the understanding of secondary and old-growth forest dynamics is a main concern of human-modified environments.

Deterministic processes predict that as succession progresses late successional species may outcompete early successional plants. Thus, fast-growth high-acquisitive species will gradually be replaced by more conservative ones (Rees 2001; Carreño-Rocabado et al. 2012; Whitfeld et al. 2012). But, in some cases, succession may lead to alternative stable states, in which early successional trees keep their dominance through cycles of self-replacement (Tabarelli et al. 2008). Such alternative state can be a consequence of land use history (Mesquita et al. 2001; Chazdon et al. 2007; Jakovac et al. 2016) and/or of edge-induced microclimatic conditions, which favor the performance of early successional species (Laurance et al. 2002; Laurance et al. 2006; Lôbo et al. 2011). If the succession progresses, a rapid recovery in biomass and structural features is expected, as shown by chronosequence studies, but not in species composition (Guariguata and Ostertag 2001; Chazdon 2003; Goosem et al. 2016; Poorter et al. 2016) and function (Carreño-Rocabado et al. 2012; Whitfeld et al. 2012; Lohbeck et al. 2014). Therefore, secondary forests have shown to be still distinct from old-growth forests (Piotto et al. 2009; Dent et al. 2013; Zanini et al. 2014), and the understanding of community dynamics and processes that underlie the recovery and the functions of these forests are still incomplete (Fridley 2013).

At the same time, landscape driven processes have been pointed as responsible for changes in fragmented old-growth forests. Most of the old-growth forests are remnants of the once continuous forest, immersed in fragmented landscapes (e.g. Ribeiro et al. 2009) and under the pressure of edge effects. These remnants experience changes in species composition and functional traits specially in their edges (≈100 m into the forest) (Laurance et al. 2006; Tabarelli et al. 2012). Some reported changes are the loss of large trees (due to physiological stress and wind turbulence) (Oliveira et al. 2008) and reproductive traits diversity (Girão et al. 2007; Santos et al. 2008; Lopes et al. 2009), and the increase of small-seeded softwood species (Laurance et al. 2006; Michalski et al. 2007). Further, it has been suggested that communities exposed to pervasive disturbances may experience an endogenous process of biotic homogenization, a retrogressive succession, called ‘secondarization’ (Tabarelli et al. 2008; Tabarelli et al. 2012). This process is characterized by predictable changes in the relative contribution of species sharing similar life history traits, as the proliferation of *r*-strategists species and the collapse of the shade-tolerant/old-growth flora in forest edges and small fragments (Oliveira et al. 2008; Santos et al. 2008; Lôbo et al. 2011; Tabarelli et al. 2012).

Facing these two processes, forest recovery (succession) and degeneration (secondarization), remnants and secondary forests tend to converge in terms of community structure and ecosystem function (Joly et al. 2014). In this study, we compare short-term dynamics of juvenile and adult tree forest communities (hereafter 'juveniles' and 'trees') of two successional stages – advanced secondary forests (with about 50 years of recovery since abandonment) and old-growth forest remnants. Dynamics are expressed by the variation in abundance (ΔA) and in basal area (ΔBA) of tree communities in five years interval, referred hereafter as 'community structure changes'. Considering that many ecosystem processes are determined by the dominant species (mass-effect theory; Grime 1998), we are also analyzing the community dynamics through changes in the community functional composition – i.e., the community-weighted mean of trait values (Carreño-Rocabado et al. 2012; Iida et al. 2014; Finegan et al. 2015), which describe de dominant trait value of communities by weighting species trait values by species abundance. For this purpose, we used four trait dimensions of plant strategies (leaf, wood density, seed mass, height at maturity) to express distinct functional facets, as suggested by Laughlin (2014). These trait dimensions can also tell us about the position of the trees along the successional spectrum (Wright et al. 2010; Reich 2014), in which early successional species are mainly described by acquisitive traits, such as high values of specific leaf area (SLA) and leaf nitrogen concentration (LNC), softwoods, high fecundity (many and small seeds) and dispersal capacity. Those characteristics enable the trees to growth fast, quickly achieving the canopy and the reproductive maturity. In the other extreme of the spectrum we find species with high conservative strategies (e.g., low SLA and LNC, hardwoods, big seeds) characterized by slow-growth and high survivorship under scarce resource conditions (Rees 2001; Poorter et al. 2008; Wright et al. 2010). Therefore, functional composition based on such traits would express the community position along the successional stages (from early to late successional communities).

We hypothesize that secondary forest dynamics progress towards more conservative communities, losing early successional species and increasing the participation of conservative ones in both strata, with a positive balance in biomass gain of adult trees. At the same time, old-growth remnant forests would be losing adult individuals and biomass due to the response of environmental changes, caused by fragmentation, leading to reduction in conservative traits. Thus, we first search for differences in community structure changes between secondary and remnant old-growth forests for both juveniles and trees. Then we test if the community functional composition from the first survey (t_1) could predict the community structure changes (ΔA and ΔBA) occurred in the juvenile and the tree strata within five years of interval. Finally, we compared the functional composition changes between the first survey (t_1) and the second survey (t_2) of juveniles and trees in secondary and in remnant forests.

Methods

Study Area

We studied tree communities in permanent plots (*Sistema de Parcelas Permanentes do Corredor Mata Atlântica Sul no Nordeste do Rio Grande do Sul*) installed in the southernmost part (29°42’S, 50°11’W- Maquiné county) of the Brazilian Atlantic Forest. Climate is subtropical humid, type Cfa according to Köppen’s classification, with mean annual temperature above 18°C, absence of a dry period, and an annual mean rainfall of 1400 to 1800 mm (Hasenack and Ferraro 1989; Nimer 1990). Study sites are located in the lower-montane forest zone, from 50 to 456 m a.s.l. (Teixeira et al. 1986). Natural vegetation consists of subtropical moist broadleaf forest and corresponds to the subtropical portion of the Atlantic Forest *sensu stricto* (Oliveira-Filho 2009). Soils are derived from basalt, and are classified as shallow litic leptsols and luvic phaeozem (Streck et al. 2008). Landscape was highly fragmented in the past centuries until the end of 1960’s, since then crops production moved to flatter areas leaving extensive areas to natural forest recovery. Today the landscape is a highly connected system of secondary forests and old-growth forest remnants (most remnants are no longer isolated).

Species and community data

Twenty-four random plots were installed in two distinct secondary forests, with about 50 years since abandonment, and twenty-four in two remnants of old-growth forests, without register of clearcuting. Sampling units are circular plots with an area of 100 m^2 established for the survey of trees ≥10 cm diameter at breast height (dbh). Within them we situated 4 systematic subplots of 10 m^2 for individuals with dbh between 1 and 10 cm dbh. Data of plants between 5 and 10 cm dbh were integrated with those of large trees (≥10 cm) to compose the adult tree stratum, also named ‘tree community’. Individuals between 1 and 4.99 cm dbh were considered juveniles, named ‘juvenile community’. Community plots were surveyed in 2009 (t_1) and again in 2014 (t_2). One hundred and fourteen tree species were registered in the surveys (92 of trees and 77 of juveniles), out of which, four palms and 1 arborescent fern were excluded from the analysis due to their distinct life form and ecological strategies. Therefore, plots with the dominance of the arborescent fern or palms were removed and we analyzed 24 communities of secondary forest, but 23 and 22 of remnants, respectively for trees and juveniles. Final tree community data presented 89 species and juvenile community 73 species.

Traits

The species had their leaf traits measured from field samples following standard protocols (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013) considering mature leaves of adult trees. Three to 15 individuals per species were measured and the average value was used to represent each species in the analysis. Leaf traits we considered were specific leaf area (SLA, $mm^2.mg^{-1}$), leaf surface area (LA, cm^2), leaf dry matter content (LDMC, $mg.g^{-1}$), leaf nitrogenous and phosphorus concentration (LNC and LNP, percent N and P mass per total mass, %) and leaf thickness (LT, mm). Leaf thickness was estimated following Vile et al. (2005) (LT= 1/SLA*LDMC). Further traits were leaf deciduousness (LD, 1= deciduous and semi-deciduous trees; 0= evergreen trees), height at maturity (H, m), wood density (WD, $g.cm^{-3}$), and seed mass (SM, g), all compiled from the literature. Average of the genus for WD was used for some species with just one occurrence following Chave et al. (2009).

Community functional composition

Functional composition of communities was obtained scaling up species trait values to the community level considering species abundance per community in the first (t_1) and in the second (t_2) survey (Community-weighted means - CWM; FD package, Laliberté et al. 2014). Each trait has a mean value per community per time (t_1 and t_2) and per forest stratum (trees and juveniles). Functional composition differences between surveys for each forest stratum and successional stage were calculated as percentage of changes between t_1 and t_2: $\Delta CWM= [(t_2 - t_1)/ t_1]*100$.

Community structure

Variation in abundance of individuals (ΔA) and variation in basal area (ΔBA) were calculated for each community to express forest dynamics. Here we consider all co-occurring individuals and calculate sampling unit (community) values not taking into account species identity. We estimated the abundance variation ($\Delta A = ln(N_{t1}) - ln(N_{t2})/t$; where N is the number of individuals, t_1 and t_2 are, respectively, the first and the second survey, and t is the time interval in years) and the basal area variation ($\Delta BA = ln(Ba_{t2}) - ln(Ba_{t1})/t$; where Ba is the stem basal area) calculated for juveniles and trees separately. According to this, "$\Delta A > 0$" represents loss of individuals and "$\Delta BA > 0$" represents gain in basal area (i.e. above ground biomass gain).

Data analysis

We tested the differences in ΔA and ΔBA for trees and juveniles between the forest successional stages (remnants and secondary communities) with variance analysis ('stats' package - R Core Team 2012).

The predictive power of functional composition based on four trait dimensions (leaf features, wood density, height at maturity and seed mass) on ΔA and ΔBA was analyzed with regression models. For this purpose community functional composition of t_1 (CWM t_1) was used as a predictor of ΔA and ΔBA for each forest strata and successional stage separately. Prior to this analysis we applied the Multi-Model inference ('MuMIn' Package, Barton 2015) to select the most important leaf trait to ΔA and ΔBA for each forest strata and successional stage. We included then only the variables with importance above 0.1 in the models (Supplementary material 1). Linear Mixed Models, with site as a random variable, were run with the selected leaf variables together with the others functional dimensions (i.e. wood density, height at maturity, seed mass) and tested against null models. The best models were selected using Akaike Information Criterion (Burnham and Anderson 2002) with correction for small samples (AICc) (Hurvich and Tsai 1998). A rank of the models according to their support of the data was generated, where the differences between the lowest AICc and the other AICc values (delta AICc) were used to visualize distinctions in model support. Differences greater than 2 in the delta AICc were considered as a threshold for model support (Burnham and Anderson 2002) (MuMIn Package, Barton 2015).

Differences in functional composition between t_1 and t_2 or functional changes in time were tested with MANOVA for juveniles and trees in each successional stage. These variance analyses were blocked within each community (sampling unit) and tested with permutation (1000 iterations) with the software MULTIV (Pillar 2012).

Results

Variance analysis indicated differences in the basal area gain and loss between secondary and remnant tree communities in the short-term dynamics (ΔBA, $P=0.002$; fig. 1). Remnants had lost more basal area than they had recovered in five-years time. Secondary communities had more gain then loss of basal area. Differences in the tree abundance (ΔA) were not significant between successional stages, although secondary forest showed higher rates of recruitment (negative values). Juvenile communities did not show significant differences neither for ΔBA nor for ΔA (Supplementary material 2), though recruitment tends to be higher (ΔA, P=0.07) at secondary forests than at remnants.

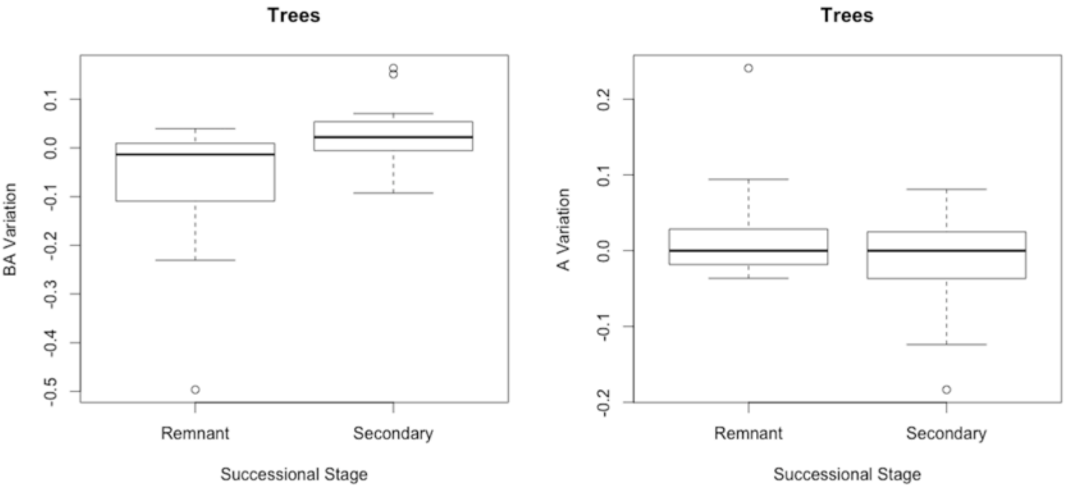

Figure 1: Boxplots between remnant and secondary forest communities considering basal area variation (ΔBA) and abundance variation (ΔA) for tree communities. Differences are significant only for ΔBA of trees (*P*= 0.002).

Community functional composition of the first survey predicted only the ΔBA of trees in remnants (tab. 1). Leaf thickness was negatively related with basal area gain and was the only variable selected in the model. Variation in basal area of trees in the secondary forests and variation in abundance of individuals (ΔA) of trees and juveniles from both successional stages did not differ from null models.

Table 1: Best model for community variation in basal area (ΔBA) of remnant forests predicted by the community functional composition (CWM) of four trait dimensions of plant strategies: selected leaf variables (LT, leaf thickness; LPC, leaf phosphorous concentration; LNC, leaf nitrogen concentration, LD, leaf deciduousness); WD, wood density; H, height at maturity; SM, seed mass. Akaike information criterion (AICc), delta and model weight are given.

Communities	effect value of CWM of traits							AICc	delta	weight
Models	LT	LPC	LNC	LD	WD	H	SM			
ΔBA Remnant	-2.02	-	-	-	-	-	-	-23.72	0	0.385

Functional composition changes between t_1 and t_2 were significant in secondary forests for juveniles (P=0.03) and trees (P=0.04). Percentages of changes from the first survey are expressed in the Figure 2. The greater changes in tree communities (fig. 2a) were the reduction of LA (-31.7%), SM (-14.1%), SLA (-5.6%) and LD (-2.8%), and the increase of LPC (5.2%), LT (3.5%), H (1.7%), LDMC (1.5%) and WD (0.18%). Juvenile communities (fig. 2b) had the biggest change in LD (-23%) and small changes in H, SM, WD and LA (-4%, -3.1%, -2.7%, 1.5% respectively). Remnant communities did not have significant functional composition changes in this five years interval.

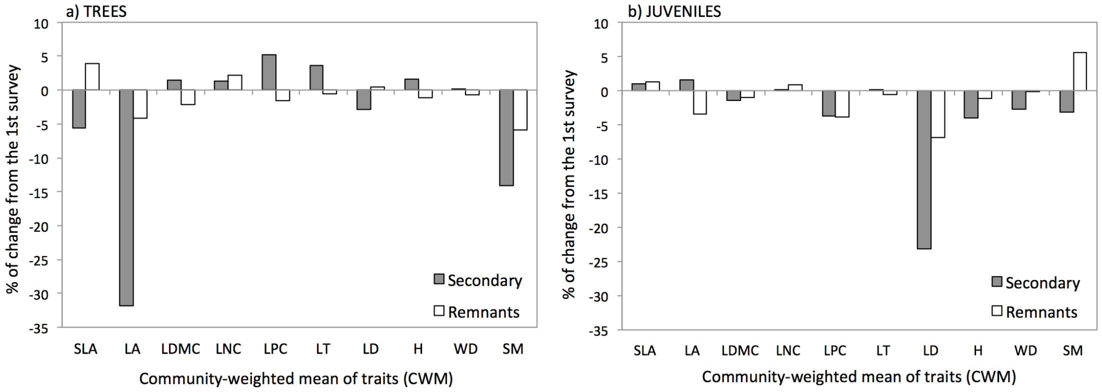

Figure 2: Percent of changes in the community functional composition in five years interval (t_1 and t_2) considering SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; LPC, leaf phosphorous concentration; LT, leaf thickness; LD, leaf deciduousness; H, height at maturity; WD, wood density and SM, seed mass.

Discussion

Secondary forests

In our short-term study we found secondary tree communities increasing their basal area (aboveground biomass) and having a great stem turnover (mortality and recruitment, data range of ΔA). The detected gain in basal area in the secondary communities indicates their higher productivity, and express the higher acquisitive functional composition of the established tree community (Finegan et al. 2015).

We expected higher mortality rates at secondary forests due to the high density of individuals (Zanini et al. 2014) and the *thinning process* predicted for secondary forests, as found, for example, in the study of Rozendaal and Chazdon (2014). Instead, we evidenced higher values of recruitment (negative ΔA) in secondary communities, which is indicating that juveniles achieved the tree layer (dbh ≥ 5 cm) along the last five years and suggests that gaps are still being filled in these successional forests with approximately 50 years of development.

Secondary forest structure changes (of both strata) were not predicted by initial functional composition (t_1), which can suggest that stochastic demographic events are prevailing over predictive directional changes in the short-term dynamics. Distinctly from early successional forests dominated by pioneers that certainly loose their dominance (dying) when the canopy closes, our secondary forests are advanced successional forests composed mainly by long lived secondary species (Zanini et al. 2014), but the mortality of these individuals is little predictable yet. The high turnover of stems and the lack of predictive power of the models suggest that these secondary forests are still extremely dynamic.

Nevertheless, the tree and juvenile strata of secondary forests showed significant functional composition changes in five years interval. The most prominent changes at the tree layer were the reduction of SLA, LA and LD and the increase in

LPC and LT. This set of functional changes are expected considering the advance of the succession (Lohbeck et al. 2015; Schönbeck et al. 2015) and indicates that functional composition of communities are becoming more conservative, with a predominance of smaller, thicker evergreen leaves. However, the reduction of SM for the tree stratum is contrary to the expected ongoing of the succession. Surrounding vegetation matrix is suggested to be an important driver of floristic changes in forest fragments (Nascimento et al. 2006) and is likely to influence composition through succession. The study region has been highly degraded in the past and today 57% of the respective river basin land is covered by initial (22%) and intermediate (35%) secondary forests (Becker et al. 2004). The reduction of SM may be due to the high abundance of small-seeded shade-tolerant species in the surrounding successional forests. Further, late successional species with large fruits and heavy seeds may experience limitations in their dispersion (Cramer et al. 2007; Bello et al. 2015), and if propagules arrive, the new individuals may take decades to reach the reproductive size (Moles and Westoby 2006). Considering juveniles, changes were subtle and some traits displayed the same direction and a similar range of variation found for juveniles of remnant communities (e.g. changes in SLA, LDMC, LPC). The stronger change for secondary juvenile communities was found in LD, which is a trait closely related with early successional light-demanding species and indicates that juvenile deciduous species did not thrive in this shaded and competitive environment. The reduction of plant height, seed mass and wood density at juvenile layer, although small, is possibly an effect of the "understory reinitiation" (Chazdon 2008) with the recruitment of shade-tolerant understory and subcanopy species. Further, juvenile communities did not differ in basal area variation between forest stages, suggesting that juvenile communities are performing a similar productivity in secondary and remnant forests.

This can be explained by the compensatory effects among photosynthetic capacity of shade-intolerant and assimilation rates of shade-tolerant juveniles growing under low light conditions (Niinemets 2006) resulting in similar productivity.

Remnant old-growth forests

Remnant tree communities are mainly loosing biomass, which differs from secondary forests that showed biomass gain. Considering that variation in abundance of individuals did not differ significantly between these two forest stages we can conclude that this loss is manly due to the falling of big trees, which store higher biomass in their stems. The resource availability hypothesis predicts the increase in above ground biomass and stem turnover through time in mature forests (Lewis et al. 2004; Lewis et al. 2009) due to the increment of atmospheric CO_2, but we found biomass loss instead. In a small-scale, as in our study, this result may express gap openings in which new recruits were not in sufficient numbers and/or did not grow fast enough to neutralize the loss of basal area during the studied time interval. In a 15-year long study that investigated the contribution of gap phase in the biomass variation of four distinct mature forests, Feeley et al. (2007) found increase, decrease and stable biomass, suggesting that local drivers may prevail over global drivers. Thus, local drivers, such as edge effects and defaunation, may play a more important role. Remnant communities in our study areas that had experienced fragmentation during decades are small sized (Ribeiro et al. 2009) and within a forest matrix with different successional stages. Biomass loss near forest edges (≈100 m of the edge) due to desiccation and wind turbulence has been evidenced in other fragmented systems (Nascimento and Laurance 2004; Laurance et al. 2006). Moreover, the decay in large bodied frugivorous lead to a decay in large-seeded animal dispersed trees, which have high carbon storage and positive correlation with maximum tree height and wood density (Bello et al. 2015).

Models predicted that tree communities with thicker leaves are prone to have the highest loss of basal area. This result expresses the predicted loss of late successional canopy species with thicker leaves, a conservative leaf strategy (Iida et al. 2014). Nevertheless, functional changes in the short time did not reveal directional shifts neither for trees nor for juveniles in remnant communities, thus not evidencing a clear ‘secondarization’ process. However, trees are affected by a past landscape structure showing a time-lag response to past events (Metzger 2009). Therefore, the fall of larger and older trees, which leaded to the biomass loss of conservative species, may be partially attributed to the strong fragmentation and defaunation experienced by these forests.

What short-term functional composition changes can tell us about forest dynamics?

To our knowledge this is the first study of forest dynamics focused on functional community traits in the subtropical portion of the Atlantic Forest, which is a hotspot of biodiversity and an extremely threatened forest (Myers et al. 2000; Metzger 2009). Leaf traits and seed mass better captured the short-term functional composition changes. Our study confirmed the hypothesis of the directional changes in functional composition of secondary forests towards more advanced successional communities (conservative traits). Secondary forests are getting more conservative leaves, but the recovery to heavier seed mass, which would be also expected, did not occurred. We also confirmed the loss of biomass and conservative traits in old-growth forests, which are associated to the fall of big trees that in turn express the loss of an important structural feature of these forests. Further changes in the remnant communities did not express directional changes that could evidence the 'secondarization' hypothesis. Nevertheless, to complete the understanding of the dynamics of remnant forest communities will be necessary further monitoring. Five-year interval can be considered a short period to analyze dynamics of long-lived organisms, such as trees. However, when the changes in community structure are associated with changes in functional composition, short-term dynamics proved to be a useful time spans to reveal interesting properties of community dynamic, especially considering forests under anthropic pressure (as fragmentation and hunting) and under recovery (as secondary forests).

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Supplementary material. Chapter 3

Appendix 1

Multi-model inference of the leaf functional composition, for tree and juvenile communities at remnant and secondary forest, considering variation in basal area (ΔBA) and number of individuals (ΔA). Selected variables are in bold.

Remnant tree communities							
ΔBA	**LT**	**LD**	**LNC**	LPC	SLA	LDMC	LA
Importance:	0.72	0.18	0.12	0.07	<0.01	<0.01	<0.01
ΔA	**LT**	**LPC**	LD	LNC	SLA	LDMC	LA
Importance:	0.36	0.1	0.07	0.05	<0.01	<0.01	<0.01
Secondary tree communities							
ΔBA	**LPC**	**LNC**	**LT**	LD	LDMC	SLA	LA
Importance:	0.51	0.25	0.17	0.03	0.02	0.01	<0.01
ΔA	**LNC**	**LT**	**LPC**	LD	LA	SLA	LDMC
Importance:	0.268	0.149	0.114	0.06	0.016	<0.01	<0.01

Remnant juvenile communities							
ΔBA	**LT**	**LD**	**LNC**	LPC	SLA	LA	LDMC
Importance:	0.291	0.162	0.129	0.045	0.025	<0.01	<0.01
ΔA	**LT**	**LD**	**LNC**	LPC	SLA	LA	LDMC
Importance:	0.214	0.164	0.13	0.027	<0.01	<0.01	<0.01
Secondary juvenile communities							
ΔBA	**LT**	**LNC**	**LPC**	LD	LA	SLA	LDMC
Importance:	0.278	0.162	0.131	0.084	0.061	<0.01	<0.01
ΔA	**LT**	**LNC**	LPC	LD	SLA	LA	LDMC
Importance:	0.217	0.132	0.083	0.052	<0.01	<0.01	<0.01

Conclusões

Neste estudo evidenciamos a segregação entre as principais linhagens das angiospermas – Magniliids, Monocots, Eudicots – ao longo do gradiente sucessional, identificando que Magnoliids e Monocts (Arecaceae), clados ancestrais, conservam requerimentos de nicho que remontam às condições ambientais nas quais tiveram suas origens. No ambiente atual, encontram-se ligados ao ambiente florestal avançado (estágios avançados de sucessão), e suas características funcionais elucidam estratégias adaptativas que otimizam sua performance no ambiente florestal. Além disso, evidenciamos filtros ambientais filogenéticos que limitam o estabelecimento destes clados em ambientes abertos (estágios iniciais da sucessão), nos quais reinam os Eudicots. A coexistência das principais linhagens de angiospermas nos estágios mais avançados da sucessão leva ao aumento da diversidade filogenética e evidencia a diferenciação dos Eudicots a uma ampla gama de condições ambientais. Os requerimentos de nicho evidenciados para Magnoliids e Arecaceae sugerem que, perante os cenários de fragmentação das florestas, a regeneração de muitas espécies destes grupos seja afetada.

Quando consideramos a estrutura populacional de 20 espécies abundantes na floresta, observamos que o ganho de área basal no estrato superior da floresta foi predito por dois grupos de espécies iniciais secundárias: aquelas normalmente ocupantes de clareiras e as tolerantes à sombra e com grande número de indivíduos jovens. Encontramos, ainda, que a perda de indivíduos foi prevista por estratégias conservativas, as quais são ligadas as espécies de crescimento lento associadas às florestas mais preservadas. Em um intervalo de cinco anos, espécies com estratégias aquisitivas ganharam biomassa, crescendo e/ou recrutando novos indivíduos no estrato superior. Estas espécies, normalmente ligadas a ambientes perturbados, quando estabelecidas atingem rapidamente o dossel potencializando sua capacidade de maturação e dispersão. Por outro lado, espécies mais conservativas perderam indivíduos neste estrato, sugerindo senescência ou morte decorrente de estresses gerados por alterações ambientais relacionadas à fragmentação. Quando consideramos os indivíduos juvenis, o resultado se inverte: aquisitivas perdem indivíduos e conservativas ganham área basal. Indicando que espécies aquisitivas ligadas a ambientes mais ensolarados recrutam mas não sobrevivem até a fase adulta no ambiente sombreado. Nossos resultados seguem padrões previstos pelo *trade-off* entre mortalidade-crescimento, relacionado as diferentes estratégias de vida das espécies; porém, a ocorrência da perda de indivíduos de espécies conservativas não pode ser explicada por este *trade-off*, visto que estas espécies geralmente possuem alta sobrevivência e longevidade. Observou-se, ainda, a ocorrência de altos valores do *coeficiente de skewness* – que reflete a estrutura das populações – associados às espécies iniciais secundárias tolerantes a sombra, indicando que estas seguem regenerando e que, provavelmente, seguirão mantendo suas altas abundâncias, especialmente nas florestas secundárias onde são dominantes.

Saindo do nível dos clados e das espécies e passando para o nível da comunidade, comparamos a dinâmica de florestas remanescentes e secundárias. Encontramos que as florestas remanescentes estão perdendo área basal (i.e. perdendo biomassa), a qual não é decorrente de uma maior perda de indivíduos, mas especificamente da perda de indivíduos grandes - detentores de grande área basal. Nossos modelos indicaram que indivíduos mais suscetíveis são aqueles possuidores de folhas espessas, uma característica foliar de conservação de nutrientes ligada a espécies de crescimento lento e tolerantes a sombra. No entanto, mudanças funcionais significativas nas comunidades no intervalo de cinco anos foram encontradas apenas para as florestas secundárias, indicando mudanças direcionais que expressam o amadurecimento destas florestas levando ao aumento de características conservativas nessas comunidades.

Com estes três estudos conseguimos elucidar os requerimentos de clados e espécies e suas associações a ambientes perturbados ou conservados, os quais levam à segregação destes no espaço e no tempo. Concluímos que a conservação de clados basais e espécies de características conservativas está ligada aos estágios mais avançados da floresta e que mudanças ambientais como aquelas decorrentes da fragmentação florestal podem afetar negativamente as populações destas e positivamente aquelas espécies dominantes de florestas secundárias. Mudanças nas abundâncias e na produtividade (ganho de área basal) foram preditas por características funcionais das espécies e comunidades. Desta forma, as características funcionais das espécies e a composição funcional são informações que podem auxiliar no monitoramento da dinâmica florestal, bem como na elaboração de projetos de restauração florestal e no desenvolvimento de modelos que incorporem cenários de mudanças climáticas.