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Dinâmica da biomassa em uma floresta subtropical: efeito de componentes bióticos e abióticos

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Dedicatória

À minha família,

a qual me mostrou o significado do amor.

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Resumo

As florestas subtropicais têm um papel importante nos serviços ecossistêmicos, embora pouco se conheça sobre a sua dinâmica e funcionamento, especialmente na porção sul da Mata Atlântica. A dinâmica florestal é frequentemente avaliada pela variação líquida da biomassa de árvores. Essa dinâmica de biomassa é influenciada por processos demográficos nas comunidades, os quais correspondem ao crescimento (de sobreviventes), recrutamento e mortalidade de indivíduos. Avaliamos a influência de fatores bióticos (atributos funcionais de plantas e a estrutura inicial da floresta) e fatores abióticos (variáveis do solo) sobre a dinâmica de biomassa de uma floresta subtropical, em um intervalo de 18 anos. Também avaliamos o efeito dos processos demográficos sobre a mudança de biomassa líquida da floresta. O estudo foi realizado no sul do Brasil, em uma área de transição entre a Floresta com Araucária e a Floresta Estacional, sem registro de distúrbio há pelo menos 60 anos, mas com histórico anterior de corte seletivo de madeira. Os levantamentos foram realizados em 1999 e em 2017, em 24 parcelas permanentes de 500 m^2 cada, mensurando todos os indivíduos com CAP $\geq$ 30 cm. Atributos funcionais foliares, de densidade de madeira e altura potencial foram obtidos para todas as espécies. Modelos lineares foram utilizados para avaliar o efeito de atributos funcionais (considerando valores médios da comunidade inicial (CWM= ‘*community-weighted mean*’) e a diversidade funcional (FD)), da estrutura inicial (área basal no tempo inicial) e de variáveis do solo sobre as variáveis resposta (taxa anual de crescimento, recrutamento e mortalidade). Modelos lineares também foram utilizados para avaliar o efeito dos processes demográficos (taxa de crescimento, recrutamento e mortalidade) e incremento em biomassa (biomassa de sobreviventes + recrutas) sobre a variação líquida de biomassa na comunidade. Observamos um efeito positivo do CWM da altura máxima sobre o crescimento de sobreviventes, e um efeito negativo do CWM do conteúdo de fósforo foliar, do FD de conteúdo de matéria seca foliar (LDMC) e da FD da altura máxima. A biomassa de recrutados teve um efeito positivo do pH e negativo do K do solo, enquanto a mortalidade foi positivamente associada à estrutura inicial da comunidade. Observamos ainda que a mudança líquida de biomassa desta floresta teve influência significativa da mortalidade e do incremento total (biomassa de sobreviventes + recrutados). Comunidades com indivíduos mais altos e com atributos relacionados à conservação de recursos em média crescem mais, enquanto que o menor crescimento teve relação com comunidades funcionalmente mais diversas em termos de LDMC e altura, potencialmente associado a espécies de sub-bosque. Solos menos ácidos permitiram o maior recrutamento, enquanto que a alta concentração de K limitou o recrutamento. Comunidades com maior cobertura inicial apresentaram maior mortalidade de espécies no período. Este trabalho traz importantes resultados sobre a dinâmica de florestas subtropicais, demonstrando que as características iniciais da comunidade, tanto bióticas quanto abióticas, tiveram influência no incremento e/ou perda em biomassa deste ecossistema num período de quase duas décadas.

Palavras-chave: Taxas de crescimento, recrutamento e mortalidade; Processos demográficos em comunidades; Atributos funcionais de plantas.

Abstract

Subtropical forests play an important role on ecosystem services, but the drivers of biomass dynamics and ecosystem functioning specially at the southern portion of Mata Atlântica are poorly understood. The forest dynamics is often evaluated by tree net biomass change, which is underlied by the community demographic processes. These demographic processes correspond to the growth of survival trees, recruitment and mortality. Here we evaluated the influence of biotic factors (plant functional traits and the initial forest structure) and abiotic factors (soil variables) on biomass dynamics of a subtropical forest in an interval of 18 years. We also evaluated the effect of demographic processes on the net biomass change of the forest. This study was carried out in a subtropical forest in southern Brazil and the region is characterized by the Atlantic forest *s.l*, in a transitional area between Araucaria and Seasonal forest. The study area corresponds to a protected area (Chapecó National Forest) that did not suffer disturbance since at least 60 years but had some selective logging before. The forestry inventories were realized in 1999 and 2017, in 24 permanent plots with 500 m^2 each one. All the individuals with circumference at breast height $\geq$ 30 cm were measured, identified and tagged. Leaf functional traits, wood density and maximum height were obtained for all species. We performed linear models to evaluate the effect of functional traits (following the mean values of initial community, community-weighted mean (CWM) and functional trait diversity (FD)), initial forest structure (community basal area in initial time) and soil variables, on the response variables (annual rate of growth of survival, recruits and mortality). Linear models were also used to evaluate the effect of tree demographic processes (biomass growth of survival, recruits, mortality and biomass increment (growth of survival + recruits)) on the net biomass change. We observed a positive effect of CWM and FD of maximum height, FD of leaf dry matter content (LDMC) and a negative of CWM of leaf nitrogen content on the growth of survivors. The biomass of recruits had a negative effect of soil K content, and a positive effect of soil pH. Biomass mortality was positive related to the initial forest structure. The net biomass change was negatively influenced by the biomass mortality and positively related to the biomass increment. Communities with taller individuals in mean and traits related to resources conserving grew more. The lower growth was related to more diverse communities in terms of LDMC and maximum height, probably associated to understory species. Less acid soils allowed more recruitment, and high availability of soil K limited the recruitment. Communities with more initial tree cover had more mortality along the time. This work provided important results about the biomass dynamics in subtropical forests, showing that biotic and abiotic community initial characteristics influenced the gain or loss of biomass of this ecosystem in a period of almost two decades.

Key-words: Growth, recruitment and mortality rates; community demographic processes; Plant functional traits.

Sumário

Introdução geral

As comunidades de plantas são estruturadas por duas categorias de processos principais: estocásticos e determinísticos, mediados pelas histórias de vida das espécies que as compõem (Cavender-Bares et al. 2009). A estocasticidade está relacionada a processos neutros (por exemplo, limitação de dispersão) em detrimento de efeitos ambientais (Hubbel 2001). Já os processos determinísticos consideram a influência do ambiente na ocorrência e abundância de espécies e constituem a teoria baseada em nicho (Cornwell & Ackerly 2009; Violle & Jiang 2009; Xu et al. 2017).

As diferenças interespecíficas nas estratégias ecológicas promovem a diversidade e permitem a coexistência entre as espécies, que por sua vez estruturam as comunidades (McGill et al. 2006; Lasky et al. 2014). As espécies ocorrem em um ambiente se tiverem melhor desempenho (por exemplo, taxas de crescimento mais altas) ou melhores habilidades competitivas nas condições do ambiente (Mayfield & Levine 2010; Lasky et al. 2014). As características das espécies definem a habilidade competitiva ou a adaptação de uma espécie, e podem ser acessadas através da variação de características funcionais (Garnier et al. 2015; D'Ándrea & Ostling 2016; Cadotte 2017).

A avaliação dos efeitos de variáveis ambientais na composição da comunidade de árvores proporciona uma compreensão adicional sobre os mecanismos que estruturam essas comunidades (Lavorel & Garnier 2002, Poorter et al. 2008; Lebrija-Trejos et al. 2010; Pinho et al. 2018). Condições edáficas, por exemplo, representam condições abióticas importantes para o entendimento de mecanismos relacionados a filtros ambientais (Kraft et al. 2015). Além disso, tais avaliações contribuem para o entendimento acerca do efeito desses fatores sobre a produtividade em florestas, uma vez que a disponibilidade de nutrientes no solo está relacionada à produção de biomassa ao longo do tempo (van der Sande et al. 2017).

Por outro lado, condições bióticas também são importantes para promover a compreensão acerca da estruturação e dinâmica de comunidades florestais. Neste sentido, a ecologia funcional tem se estabelecido como uma ferramenta com bom poder de predição para o entendimento de processos ecológicos em comunidades. A utilização de atributos funcionais de espécies (*i.e.* características morfológicas, fisiológicas ou fenológicas que impactam o desempenho das espécies, Violle et al. 2007) permite a avaliação do estado funcional das comunidades, bem como a compreensão da estrutura e organização das mesmas em relação a gradientes ambientais. As medidas mais utilizadas para estas avaliações são a amplitude de variação dos atributos funcionais (*e.g.* diversidade funcional) e a média dos atributos na comunidade, ponderada pela biomassa das espécies (*e.g.* hipótese da razão de biomassa) (Grime 1977; Tilman 1999; Díaz & Cabido 2001; Lavorel & Garnier 2002; Garnier 2004).

Dentre os processos ecológicos importantes para a dinâmica e manutenção das comunidades estão os processos demográficos, os quais correspondem ao crescimento, recrutamento e mortalidade de indivíduos na comunidade (Rozendaal & Chazdon 2015; Poorter et al. 2015; Prado Junior et al. 2016; van der Sande et al. 2017). Estes processos podem ser avaliados pela quantificação da biomassa de sobreviventes, mortos e recrutados nas comunidades ao longo do tempo, e tem se reconhecido a importância de variáveis bióticas, como relações de competição, por exemplo, mediadas por atributos funcionais, e abióticas, como variáveis edáficas, conduzindo esses processos (Finegan et al. 2015; Lohbeck et al. 2015; Poorter et al. 2015; Prado-Junior et al. 2016; van der Sande et al. 2017) (Fig.1).

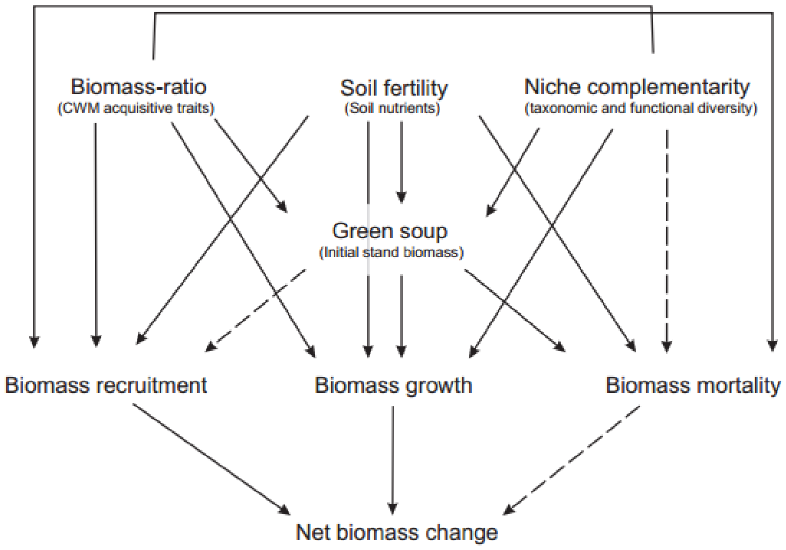

Fig 1: Modelo conceitual indicando algumas das possíveis relações entre variáveis bióticas e abióticas sobre os processos demográficos em comunidades. Figura extraída de Prado-Junior et al. 2016. *Biomass-ratio, niche complementarity* e *green soup* representam as variáveis bióticas, enquanto que *soil fertility* representa o componente abiótico. *Biomass recruitment, growth, mortality* e *net biomass change* representam os componentes da dinâmica de biomassa em comunidades. Linhas contínuas representam efeitos positivos e linhas tracejadas efeitos negativos.

Para a região tropical, especialmente amazônica, estas relações entre variáveis bióticas e abióticas conduzindo os processos demográficos têm sido estudadas nos últimos anos, fornecendo informações sobre os principais condutores da dinâmica de biomassa na região tropical (Finegan et al. 2015; Poorter et al. 2015; Prado-Junior et al. 2016; van der Sande et al. 2017; Poorter et al. 2017). Contudo, para as florestas da região subtropical, a dinâmica é pouco compreendida. Neste sentido, a região sul do Brasil se configura como uma região em potencial para tais estudos. As características da região tropical diferem da subtropical em termos de clima (*i.e.* filtro climático relacionado às baixas temperaturas), considerando condições médias e de sazonalidade, bem como em diversidade e composição de espécies. A temperatura e a precipitação são maiores na tropical, mas em termos de sazonalidade a região sul tem um clima sazonal para temperatura e a tropical tem sazonalidade em precipitação. As florestas da região tropical (como a floresta amazônica) são marcadas pela alta diversidade de espécies, enquanto que a floresta atlântica (tanto na porção tropical quanto subtropical) é marcada pelo endemismo de espécies, conferindo-lhe a caracterização de *hotspot* (Myers et al. 2000).

Neste sentido, estudos com comunidades de árvores com dados de longo prazo permitem conhecer de que forma variáveis bióticas e abióticas atuam sobre as espécies e comunidades as respostas que as mesmas apresentam diante destas condições. Por exemplo, podem ser acessados o potencial de acúmulo de carbono nestas florestas, especialmente em escala temporal (Phillips et al. 1998). Espera-se que os condutores da dinâmica nas florestas subtropicais estejam ligados às condições ambientais (*i.e.* variáveis edáficas) e aos atributos funcionais das espécies. Este trabalho discorre sobre a dinâmica de uma floresta subtropical, em estado avançado de desenvolvimento, num intervalo de 18 anos entre os levantamentos de árvores. Dados de séries temporais como estes são ainda muito escassos para a região sul do Brasil e regiões subtropicais de modo geral; contudo, são muito promissores, haja vista as respostas que podem fornecer acerca da dinâmica dos processos demográficos de comunidades florestais. Conhecer os mecanismos condutores destes processos demográficos é fundamental para ampliar o conhecimento teórico acerca da estruturação e organização de comunidades biológicas, bem como para fornecer ferramentas de predição e manejo considerando as respostas das comunidades diante das perspectivas futuras de mudanças no clima, por exemplo.

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CAPÍTULO 1

How biotic and abiotic factors drive the biomass dynamics in a subtropical forest?

Demographic processes are influenced by many biotic and abiotic factors, and mediate forest community dynamics. Community biomass changes, for example, may be positively related to diversity, but it depends on the competitive ability and the resource partitioning of coexisting species (Carroll et al. 2011). The species coexistence is mediated by equalizing mechanisms (minimizing average fitness differences between species) and stabilizing mechanisms (reducing niche overlapping and promoting resource partitioning between species) (Chesson 2000; Wright 2002; Cadotte 2007; HilleRisLambers et al. 2012). Recent developments of the coexistence theory have allowed the study of relations between stabilizing niche differences and average fitness differences due to the use of species functional traits (Carroll et al. 2011; Kraft et al. 2015).

The functional traits correspond to morphological, physiological or phenological features that influence the species fitness (Violle et al. 2007) but also constitute good predictors of ecosystem functioning (Diaz & Cabido 2001; Lavorel & Garnier 2002; Díaz et al. 2004; McGill et al. 2006; Díaz et al. 2007). Plant traits are related to ecosystem productivity, maintenance or stability face disturbances, and also to resources acquisition and carbon storage (Wright et al. 2010; Adler et al. 2014; Poorter et al. 2015; Poorter et al. 2017). Temporal changes on such ecosystem properties might be thus influenced by traits of coexisting species at the community level (Escudero & Valladares 2016), which characterizes the *vegetation quality hypothesis* (Lohbeck et al. 2015). This community level trait information can arise from mean values, representing mainly the state of dominant species (biomass-ratio hypothesis), or from the amplitude of the trait state, which is associated to the niche complementarity hypothesis.

* The references are formatted according to Journal of Vegetation Science

In this way, the *biomass-ratio hypothesis* postulates that traits of species affect the ecosystem properties based on their biomass in community (Grime 1977; Garnier et al. 2004). It can be accessed by the community-weighted mean (CWM) of traits, which represents the mean trait in a community weighted by species biomass or abundance (Garnier et al. 2004; Garnier et al. 2015). In general, this parameter allows the evaluation about community responses to environmental conditions, regarding their investments in resources acquisition (by improving the photosynthetic rates) and/or in resources conserving (by improving investment in stem structures, for example) (Wright et al. 2010; Adler et al. 2014; Levine 2016; Prado-Junior et al. 2016). The *niche complementarity hypothesis* postulates that high functional diversity is closely related to the niche differentiation of species; the use of resources is more efficient and productivity may increase (Diaz & Cabido 2001; Chisholm et al. 2013; Ruiz-Benito et al. 2016; van der Sande, Peña-Claros, et al. 2017; Mori 2018). It can be accessed by many distinct indices, such as the Rao's quadratic entropy (RaoQ), a measure that integrates the functional richness (resources use) and functional divergence (niche differentiation and resources competition) (de Bello et al. 2007; Villéger et al. 2008; Mouchet et al. 2010).

Instead of the vegetation quality, however, community dynamics can be related only to the *vegetation quantity hypothesis* (Lohbeck et al. 2015). This hypothesis postulates that the vegetation quantity in a site, as the tree initial forest structure, is the major driver of changes in the community, and the vegetation quality (*i.e.* CWM, RaoQ) has a secondary importance for the community structuring (Finegan et al. 2015; Lohbeck et al. 2015; Prado-Junior et al. 2016). The vegetation quantity can contribute or not with the dynamic of ecosystems processes, by improving carbon stocks at community or provisioning less light availability for smaller species growth or for recruits, for example (Lohbeck et al. 2015; Prado-Junior et al. 2016).

Besides the influence of processes mediated by plant-plant interactions, there are many abiotic factors that may influence community structure and dynamic. In forest ecosystems, the physical and chemical characteristics of the soil (soil fertility, for example) are determinant to shape plant species composition and growth patterns (Sollins 1998; Quesada et al. 2012). Soil fertility has been pointed as the main driver of biomass increment in tropical moist forests (Laurance et al. 1999; Bellingham & Tanner 2000; Castilho et al. 2006; Peña-Claros et al. 2012), but in dry forests it was negative related to productivity (Prado-Junior et al. 2016).

Studies about forest dynamics are interested on the biomass variation of communities, for example, which underlies the community net biomass change that influences ecosystem functions as productivity and nutrient cycles (Bowman et al. 2013; Poorter et al. 2015). Net biomass change is the result of three demographic processes: recruitment, growth and mortality (Finegan et al. 2015; Lohbeck et al. 2015; Poorter et al. 2015; Prado-Junior et al. 2016; Poorter et al. 2017; van der Sande, Peña-Claros, et al. 2017; van der Sande, Arets, et al. 2017). These processes might be influenced by biotic and abiotic factors, as above-mentioned, which in turn can operate in distinct scales. Forest tree communities with high mortality rates associated to species with conservative characteristics (*e.g.* wood density (hereafter “WD”), with higher values) may represent a negative effect of such traits on plant survival face shifts in environmental conditions, such as a lower mechanical strength and resistance to drought-induced embolisms (Westoby & Wright 2006; Chave et al. 2009). On the other hand, communities with high recruitment and growth rates, when associated to the dominance of species with acquisitive values (*e.g.* specific leaf area, leaf nitrogen and phosphorous content (hereafter “SLA”, “LNC and “LPC”), with higher values, respectively), indicate a positive effect of such traits on the productivity of the system, by promoting higher photosynthetic rates, for example (Poorter et al. 2008; Wright et al. 2010; Finegan et al. 2015).

Little is known for biomass change patterns in subtropical forests (Lin et al. 2012). The subtropical forests have different climatic filters (related to minimum temperatures) and it might reflect on the biodiversity and forest dynamics (Oliveira-Filho et al. 2014). For tropical forests, however, there is more information about the effect of biotic and abiotic variables on the processes underlying the biomass change. For example, tree species diversity in tropical forests have positive relationships with biomass stocks (Poorter et al. 2015; Poorter et al. 2017), lower nutrient soils have several limitations on vegetation growth, specially related to phosphorous limitations (Quesada et al. 2012), and vegetation quantity is positively related to mortality and negatively related to recruitment (Chao et al. 2008; Prado-Junior et al. 2016; van der Sande, Peña-Claros, et al. 2017).

This study aimed to evaluate the effect of biotic (following the *vegetation quantity* and *vegetation quality* hypotheses described above) and abiotic (soil fertility) drivers on the tree demographic processes in a subtropical forest, and to evaluate the effect of demographic processes on the net biomass change of the forest, as many uncertainties about the effects still exist (Martínez-Vilalta et al. 2010; Lin et al. 2012; Chen et al. 2017) and most part of the studies is related to tropical forests. We expect (i) a greater effect of community-weighted means (the biomass-ratio hypothesis) than of niche complementarity on community biomass increment, with acquisitive and conservative trait values driving the community in terms of recruitment and growth (van der Sande, Arets, et al. 2017); (ii) a positive effect of soil variables associated with fertility on the biomass of survivors and recruits (van der Sande, Peña-Claros, et al. 2017; van der Sande, Arets, et al. 2017); and (iii) a positive effect of initial vegetation quantity on the biomass loss from mortality (Chao et al. 2008; Prado-Junior et al. 2016).

Methods

Study area and sampling design

This study was carried out in a subtropical forest of Santa Catarina, southern Brazil. This region is characterized by the Atlantic forest *s.l.*, which corresponds to the second largest forest of Brazil, over tropical and subtropical latitudes, from the latitudes 6° to 30°(Oliveira-Filho & Fontes 2000; Neves et al. 2017). The study area is located on the subtropical portion of the Atlantic forest *s.l.*, in a transitional region between the Araucaria forest (a forest formation of the Atlantic forest *s.l.* characterized by presence of the conifer *Araucaria angustifolia* (Bertol.) Kuntze) and the Seasonal forest (another formation characterized by the deciduousness of many canopy trees, with 20-50% of trees losing the leaves in winter season).

The study area corresponds to a protected area (Chapecó National Forest) with a total area of 1590.6 hectares that did not suffer disturbance for the past 60 years but suffered selective logging at some extent before this period. The forest area suffers the effects of fragmentation, with the surroundings being extremely deforested (Ribeiro et al. 2009).

According to Köppen's climate classification, the region is represented by the Cfa climate, which is characterized by hot summer and cold winter (Nimer 1989; Alvares et al. 2013). The mean annual precipitation for the period from 1999 to 2016 was 2000 mm (± 374 mm) and the mean temperature for the same period ranged from 18 to 20 °C (www.inmet.gov.br). The soil formation is derived from basalt and the soil characterization comprehends ferrasols and cambisols (ICMBio 2013), related to older geomorphic surfaces and deeper soils (Klamt & Reeuwijk 2000).

For this study, we used 24 permanent forest monitoring plots (50 m x 10 m, distant at least 50 m and at most 250 m apart) installed in the core of the forest, totalizing 1.2 ha of sampling area. The first census (*t0*) was carried out in 1999, when all trees with stem circumference at breast height (c.b.h, 1.30 m) $\geq$ 30 cm were tagged, had the diameter measured, the height estimated and the individuals identified to the species level. In the second census (*t1*), 18 years later (2017), all trees were re-measured and the growth, mortality, and recruitment were evaluated.

Forest structure, estimation of above-ground biomass and demographic processes

The initial forest structure (FS_i, m^2 ha^{-1}) represents the *vegetation quantity* hypothesis (Lohbeck et al. 2015; van der Sande, Peña-Claros, et al. 2017) and it was obtained by the estimation of tree basal area (m^2 ha^{-1}) per plot sampled in the first census (*t0*).

For each plot (operational community), we estimated the above-ground biomass (AGB) using allometric equations considering the tree stem diameter at breast height (d.b.h.) information (obtained from c.b.h. transformations), wood density (g/cm^3) and maximum plant height (m) (based on Chave et. al 2014, Eq. 1).

Eq. 1: $AGB = 0673 \text{ x } (WD \text{ x } d.b.h.^2 \text{ x } H)^{0.976}$

The demographic processes (annual rate of growth, recruitment, and tree mortality) observed in each plot were calculated based on the biomass estimation. The AGB growth of survivors (AGB_{surv}, Mg ha^{-1} yr^{-1}), which represents the biomass increment of survivors in the community, was based on the growth of the trees that were present at *t0* and survived until *t1*. It was calculated as *t1-t0* divided by the census length (18 years), and corresponds to the annual rate of biomass gain per plot overall the time. The AGB Recruitment (AGB_{recr}, Mg ha^{-1} yr^{-1}) is related to the biomass gain by the community across the time and it was based on the annual rate of amount of biomass from the recruited trees (*i.e.* trees that reached 30 cm c.b.h. after the first census). Finally, the AGB Mortality (AGB_{mort}, Mg ha^{-1} yr^{-1}) represents the biomass lost from the community along time and it was based on the annual rate of biomass lost from those trees that dead between the first and last census.

The estimation of the net biomass change was obtained by the annual rate of biomass variation during the census (Eq. 2) (Prado-Junior et al. 2016), and the total annual biomass increment (AGB_{incr}) of the time corresponds to the sum of total AGB_{surv} and AGB_{recr} (Finegan et al. 2015).

Eq. 2: $(AGB_{surv} + AGB_{recr}) - AGB_{mort}$

In order to delimit the maximum possible growth rate and lost for recruits and died trees of the community, respectively, we maintained the 30 cm c.b.h for biomass estimation, assuming that recruits had 0 cm c.b.h prior to the second census and dead trees had died immediately before the first census (Talbot et al. 2014). Following this method, we considered that there is a possibility for a new tree to grow from 0 cm c.b.h to 30 cm c.b.h from the first to the second census, and die immediately after the first census, respectively.

Soil sampling

The soil nutrient availability was determined by collecting soil samples from 0 to 20 cm depth at four sampling points distributed within each plot. The four samples were homogenized and air dried for 48h. Soil analysis was conducted at Soil Laboratory at Federal University of Rio Grande do Sul, Brazil, following the methodology of Tedesco et al. (1995). Soil variables used to infer about the potential effect on demographic processes were: pH, clay content (%), phosphorus (P, mg/dm^3), potassium (K, mg/dm^3), organic matter (OM, %) and cation exchange capacity (CEC, $cmol_c/dm^3$). Correlations between soil variables are available in Appendix 1. Mean values (and standard deviations) are described in Appendix 2.

Functional traits

We included functional traits related to growth and survival (Westoby et al. 2002; Westoby & Wright 2006; Poorter et al. 2008; Wright et al. 2010). The traits selected were specific leaf area (SLA, mm^2/mg) (related to the maximum light-capturing, photosynthetic and respiration rates, *e.g.* Poorter et al. 2008); leaf dry matter content (LDMC, mg/g) (a good predictor of net primary production and nutrient cycling, *e.g.* Fortunel et al. 2009; Smart et al. 2017); wood density (WD, g/cm^3) (long-term structures, hydraulic conductance and competitive vigor, *e.g.* Poorter et al. 2008; Chave et al. 2009); leaf nitrogen content (LNC, %) and leaf phosphorous content (LPC, %), both associated with photosynthetic assimilation (Rubisco in the case of LNC and ATP in the case of LPC) (Wright et al. 2004); maximum potential height (Hmax, m), related to competitive ability and light interception (Westoby et al. 2002; Wright et al. 2010), and deciduousness (dec, 0/1), measured as the loss of leaves during the cold season (Cornelissen et al. 2003). Most of the trait data for the species in this study were available at part of the dataset from our Plant Ecology Laboratory. For those species which trait data were not available we selected three to five individuals per species and collected at least 10 leaves for measuring leaf traits (*i.e.* SLA, LDMC, LNC and LPC), following the same procedures adopted in the Lab. For WD information, we used the information available at the world wood density database (Chave et al. 2009; Zanne et al. 2009). The trait sampling procedures followed standardized protocols (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013).

Niche complementarity and biomass-ratio hypotheses

Predicting variables associated with the *niche complementarity* hypothesis were accessed by the RaoQ's functional diversity index (hereafter, FD) (Eq. 3). We calculated FD for each trait separately, using the *rao.diversity* function, SYNCSA package.

Eq. 3: $\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\, P_i P_j$

The biomass-ratio hypothesis was accessed by the community-weighted mean (CWM) trait values, based on proportional species basal area (*functcomp* function, FD package) (Eq. 4).

Eq. 4: CWM = $\sum_{i=1}^{n} p_i * trait_i$

The species matrix used to calculate both measures contained the species sampled at the community in the first sampling (*t0*), in order to evaluate the effect of the initial composition on the community dynamics until the second sampling (*t1*). Correlations between CWMs calculated based on different traits are available in Appendix 1.

Statistical analysis

We fitted linear models considering each demographic process (response variables: annual rate of AGB_{surv}, AGB_{recr} and AGB_{mort}), as a function of the four set of predictors, separately: initial forest structure (FS_i), biomass-ratio (CWM values of each trait), niche complementarity (FD values of each trait) and soil composition (six soil variables). At end, we fitted a total of 12 models. We also verified the association between mean community diameter (predictor) and AGB_{mort} (response variable) using linear regression to better understand the dynamic of community mortality.

We further performed linear models to evaluate the effect of each component of biomass dynamic (demographic process) on the net biomass change (response variable). To proceed with these regressions, we considered the annual rate of biomass growth of survivors (AGB_{surv}), recruitment (AGB_{recr}), mortality (AGB_{mort}), and biomass increment (AGB_{incr}) as predictor variables.

Data transformation was applied when necessary: AGB_{surv}, AGB_{recr}, AGB_{mort}, and AGB_{incr} were log transformed to improve the homogeneity of residual variance. All the predictor variables were standardized previously to mean zero and unit variance using the function *decostand* (method standardize, vegan package) (Oksanen et al. 2018). We used all subsets of linear models and selected the models that had the lowest Akaike Information Criterion (AIC), considering the most parsimonious model (with the lowest number of predictor variables) (*stepAIC* function, method backward, MASS package). All statistical analyses were performed in R v3.3.3 (R Core Team 2016).

Results

In the first census we sampled 930 individuals, belonging to 59 species and 28 families, while in the second it was 800 individuals belonging to 61 species (see Appendix 3 for species identity, biomass and species trait values). Families with the largest number of species were the same in both censuses: Fabaceae (11), Lauraceae and Rutaceae (5), Salicaceae and Sapindaceae (4). Details about floristic and structural description of the forest can be seen in Bordin et al. (in review).

Overall net biomass change was slightly positive between two censuses (0.03 ± 0.09 Mg ha^{-1} yr^{-1}, ranging from -0.38 to 0.16 Mg ha^{-1} yr^{-1}). Across all communities, the average growth in biomass of survival trees (AGB_{surv}) was 0.12 ± 0.04 Mg ha^{-1} yr^{-1}, recruited trees (AGB_{recr}) was 0.01 ± 0.007 Mg ha^{-1} yr^{-1}, and mortality trees (AGB_{mort}) was 0.10 ± 0.08 Mg ha^{-1} yr^{-1}. The biomass increment (survivors + recruits, AGB_{incr}) was 0.13 ± 0.04 Mg ha^{-1} yr^{-1} and initial forest structure was 137.8 ± 31.7 m^2 ha^{-1}.

All set of the predictor variables had effect on the components of biomass dynamics (Fig. 1, Appendix 4). Functional traits were good predictors of biomass growth of survivors, soil variables influenced biomass of recruits and the initial structure predicted the biomass loss from mortality. Bivariate plots between predictors selected by the models (Fig. 1) and the respective response variables are available at Appendix 5 to see the general trends.

The best models to explain the biomass gain within the survivors included positive effect of CWM_{hmax} and negative effect of CWM_{lpc}, FD_{hmax} and FD_{ldmc} (see also the effect size results in Appendix 4). The vegetation quantity hypothesis (FS_i), $CWM_{ldmc,}$ CWM_{sla}, CWM_{dec}, FD_{sla}, FD_{lnc}, FD_{wd} were also included, but had a weak effect on AGB_{surv}. Soil variables had no effect on growth of survivals (Fig 1).

The set of variables that better explained recruitment biomass (AGB_{recr}) were the soil pH and soil K. The soil CEC, FD_{hmax} and FS_i were also included on best models selected (Fig. 1). The variables related to biomass-ratio hypothesis had no effect on biomass recruitment.

For the amount of biomass lost through mortality (AGB_{mort}), the FS_i had a strong negative effect (Fig. 1) (Appendix 4). The best models selected also included CWM_{ldmc} and FD_{wd}, soil K, soil P and clay content. Communities with large diameter trees were responsible by most part of biomass lost through mortality (Fig. 2).

The net biomass change across all plots was specially influenced by the biomass mortality and biomass increment (Fig. 3, Fig. 4), as we observed more biomass gain than biomass loss (Fig. 5).

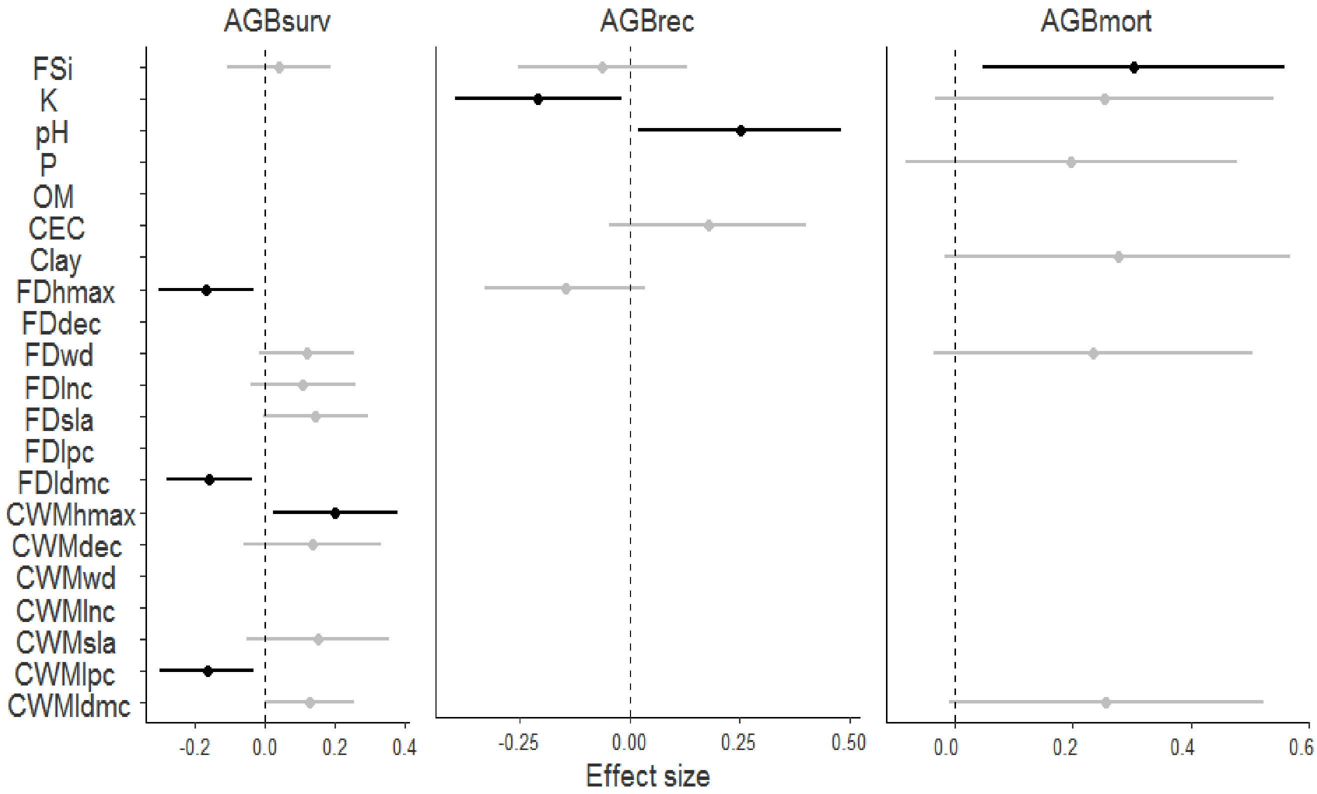

Fig. 1: Standardized coefficient (β) plots from the demographic processes models. Points are average estimates of the models and the bars correspond to the 95% confident intervals (CI). Variables without results were not selected by model selection. Significant effects are represented by the variables which did not overlap with zero.

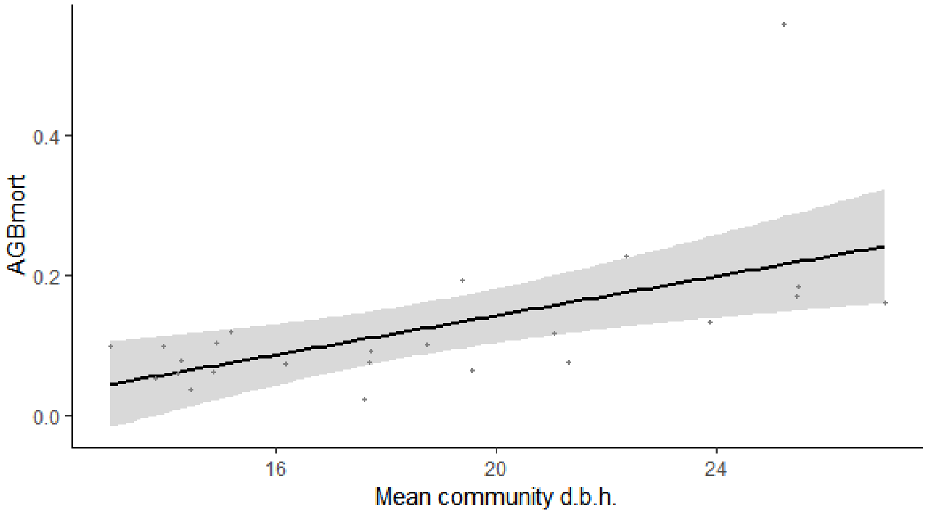

Fig. 2: Linear regression of mean community diameter and annual rate of above-ground biomass lost through mortality (AGB_{mort}). Adjusted R^2: 0.3, p= 0.002. Model 95% confident intervals: 0.005 – 0.02.

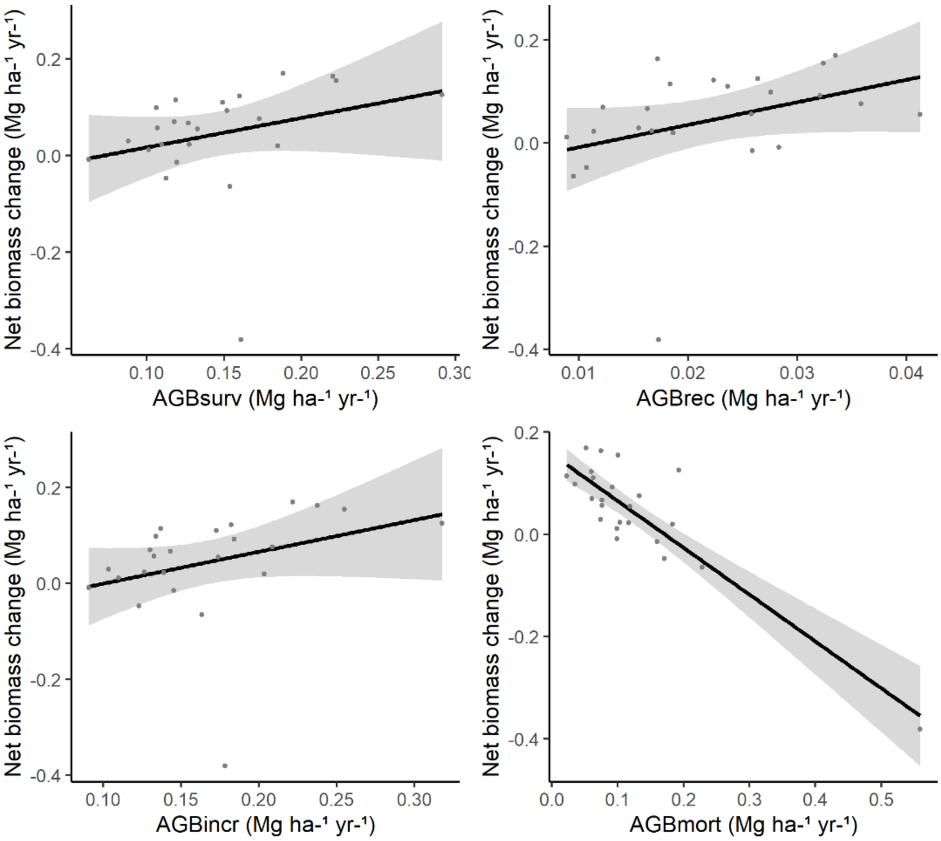

Fig 3: Biplots from the net biomass change models, using demographic processes (AGB$_{surv}$ Mg ha-¹ yr-¹, AGB$_{recr}$ Mg ha-¹ yr-¹ and AGB$_{mort}$ Mg ha-¹ yr-¹) and biomass increment (AGB$_{incr}$ Mg ha-¹ yr-¹) as predictor variables.

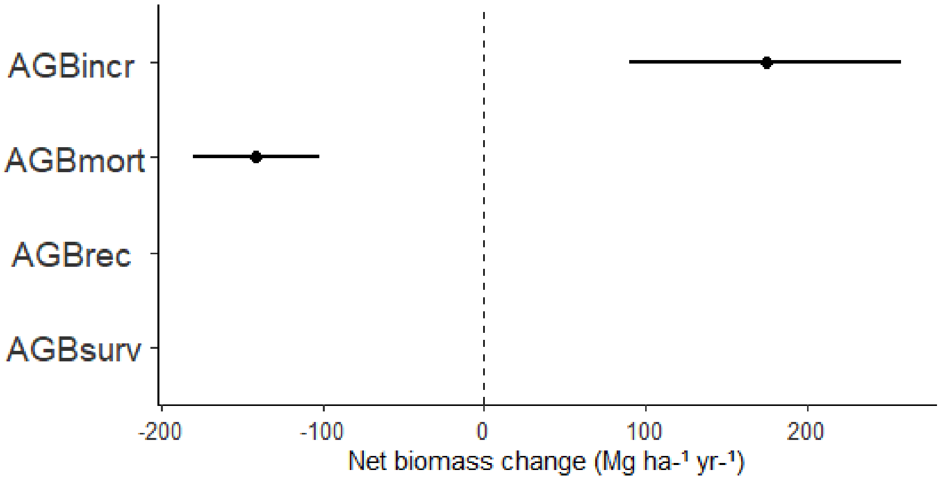

Fig 4: Coefficient (β) plot from the net biomass change model. Points are average estimates of the model and the bars correspond to the 95% confident intervals (CI). Variables without results were not selected by model selection. Significant effects are represented by the variables which did not overlap with zero.

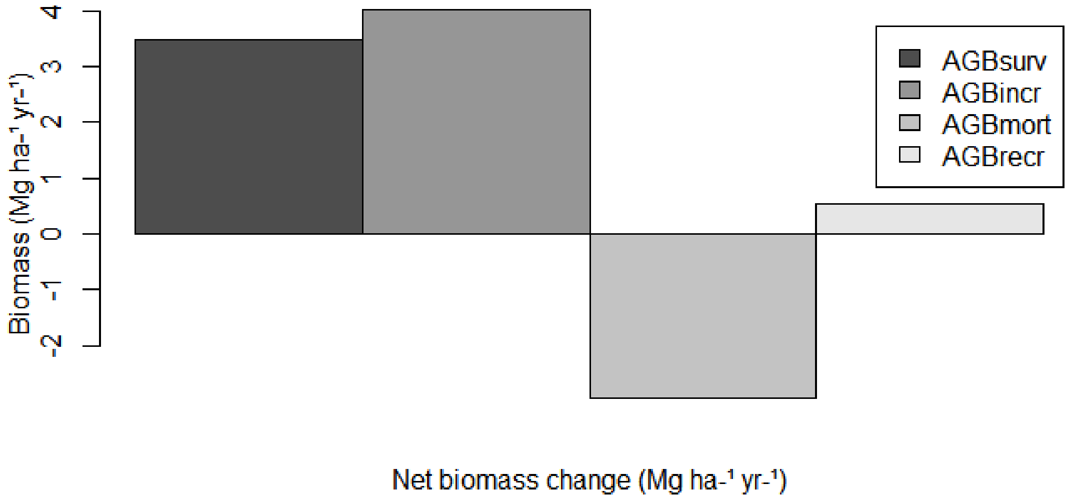

Fig 5: Contribution of each demographic process (AGB_{surv}, AGB_{recr} and AGB_{mort}, Mg ha^{-1} yr^{-1}) and AGB_{incr} to the net biomass change (Mg ha^{-1} yr^{-1}).

Discussion

We evaluated the effect of biotic (following the *vegetation quantity* and *vegetation quality* hypotheses) and abiotic (soil fertility) drivers on the tree demographic processes in a subtropical forest. We found that: i) the effect of vegetation quality included both variables related to the biomass-ratio hypothesis and the variables associated to niche complementarity hypothesis; ii) soil pH and soil K content were the most important abiotic variables, having opposing effects on biomass of recruits; iii) vegetation quantity, measured by the initial forest structure of communities, had a strong positive effect on biomass mortality; and iv) the main demographic processes driving the net biomass change of the studied forest were the tree biomass mortality rate and tree biomass increment.

Vegetation quality (CWM and FD) had effects on biomass growth at the studied subtropical forest, similarly to the influence already registered for tropical forests (*e.g.* Finegan et al. 2015; Poorter et al. 2015; Poorter et al. 2017; van der Sande, Peña-Claros, et al. 2017). A positive effect of mean Hmax values (CWM_{hmax}) and the negative effect of FD_{hmax}

reflect the importance of adult stature for resource acquisition in this old-growth forest, with closed canopy system (Poorter et al. 2008; Finegan et al. 2015). Forest communities where potential height of trees is higher are probably related to stands with the predominance of canopy trees counter to old-growth stands where understory and canopy trees might co-occur (*i.e.* higher FD_{hmax} and lower mean CWM_{hmax}), which presented lower biomass growth within the studied period. It is linked to plant economic spectrum (Wright et al. 2004; Chave et al. 2009), that trees may be investing in adult stature instead leaf acquisitive characteristics. In this way, the negative effect of CWM_{lpc} reflects that species with mean LPC values have lower growth rates, and this must be related to the leaf investments in structures and growth instead leaf nutritional compounds for fast resources acquisition. In general, conservatives characteristics such as higher LDMC values are related to protection against leaf damages and to stress tolerance (Poorter et al. 2008; Smart et al. 2017). Moreover LDMC is a good predictor of biomass productivity in grasslands (Smart et al. 2017) and in old-growth forests (Shen et al. 2016). The negative effect of FD_{ldmc} and tendency of positive effect of CWM_{ldmc} also suggest that communities characterized by species that invest in leaf conservative characteristics instead of acquisitive characteristics (Reich et al. 1992; Wright et al. 2004; Poorter & Bongers 2006; Wright et al. 2010) were more efficient in accumulate biomass within the survivals.

Surprisingly, the effect of soil variables on biomass recruitment was different from the expected for plants. In general, soil K is positive related to growth of seedlings, saplings, and forest primary productivity as well (Tripler et al. 2006; Wright et al. 2011; Wright et al. 2018), but seems to be negative for tree recruitment. The relation between soil K and soil pH is positive, such as acid soils limit the soil K, and this must reflect the availability of K for plants use (Tripler et al. 2006). However, in our forest communities soil K was negatively related to the overall fertility (CEC, Appendix 1), thus recruitment biomass was higher on stands with lower soil K and higher pH, which in turn might also potentially represent communities with more fertile soils. The amount of deciduous species may be also contributing to the soil nutrient composition due to the losing leaves, leading to biomass accumulation in litter form, which influences the soil composition (Cornelissen et al. 1999).

There was a strong and positive effect of FS_i on biomass mortality. The influence of initial forest structure on community is related specially due to the mortality of large trees (*e.g.* negative density-dependence, senescent trees) (Chao et al. 2008; Brienen et al. 2015; Finegan et al. 2015; Lohbeck et al. 2015; Johnson et al. 2016; Prado-Junior et al. 2016; Holdaway et al. 2017; van der Sande, Peña-Claros, et al. 2017; Zhu et al. 2018). Tree mortality is expected to affect the community due to gap dynamics, especially due to large trees death, and to promote conditions for species recruitment (Yamamoto 2000; Feeley et al. 2007). However, in terms of biomass, more recruitment was not observed here, indicating a slow and long term-dynamics in subtropical forests. For next studies we suggest to account either the abundance variation of species in the community to better understand forest dynamics.

Variation of net biomass change was predicted by the biomass mortality and increment along time, but not by the biomass of survivors and recruits separately. The AGB_{mort} Mg ha^{-1} yr^{-1} can be considered a very important driver of net biomass change in tropical and subtropical forests (Delbart et al. 2010; Brienen et al. 2015; Finegan et al. 2015; Johnson et al. 2016; van der Sande, Peña-Claros, et al. 2017), as is the biomass increment (due to biomass of growth of survivors and recruitment) (Finegan et al. 2015). This biomass dynamics supports a natural process of turnover within an old-growth forest, where large individuals might die, leaving resources and space to recruits growth. These processes were observed in mature tropical forests (Feeley et al. 2007; Finegan et al. 2015), but also in regenerating forests (Lohbeck et al. 2015). At this subtropical forest, thus the mortality was predicted by FS_i, which suggests that the community dynamics has been driven by the mean biomass of large dead trees.

The effect of vegetation quality on demographic processes was important for the biomass growth of survivors at the studied subtropical forest, strengthening the evidences that species traits can shade light on the mechanisms underlying species coexistence and resources use. On the other hand, soil variables affected the biomass of recruits, and the vegetation quantity was also an important predictor of biomass mortality along the time, indicating the additional importance of abiotic variables and of forest structure in driving demographic processes of tree species. The community net biomass change was explained by the rate of biomass growth and recruitment (when combined) and by the rate of mortality, evidencing an almost stable change in forest biomass along the last 18 years. Thus, the biomass dynamic of this subtropical forest is indicating demographic processes of a mature forest most influenced by species traits, soil conditions, losing trees but also having some recruitment of new trees that will contribute to the forest biomass increment along the time. Long-term monitoring of such forest communities, ranging the temporal and/or the spatial scale, might allow for further considerations about the dynamic of subtropical forests relation to climatic conditions.

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Appendix 1

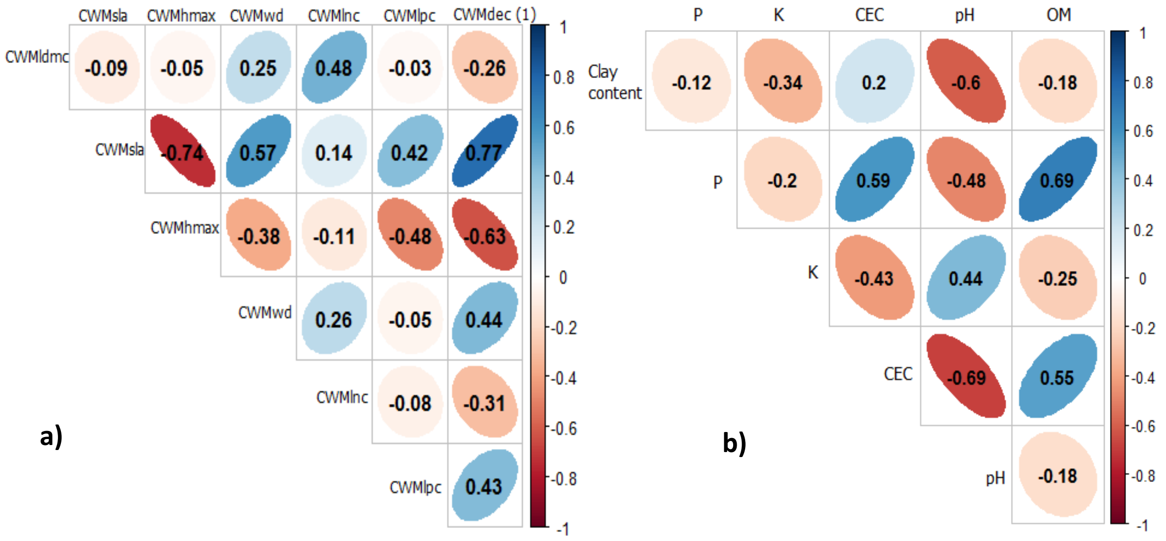

Fig 1: Correlations among a) community-weighted mean of trait values and b) soil variables. Dark blue colors indicate strong positive correlation and dark red colors indicate strong negative correlations.

Appendix 2

Table 1: Mean and standard deviation of soil variables analyzed in a subtropical forest. Clay content (%), pH, phosphorous (P, mg/dm^3), potassium (K, mg/dm^3), organic matter (OM, %), and cation exchange capacity (CEC, cmolc/dm^3).

	Clay content	**pH**	**P**	**K**	**OM**	**CEC**
Mean	50.21	4.3	3.23	68.13	4.73	21.24
SD (±)	8.57	0.31	1.36	23.93	0.84	2.98

Appendix 3

Table 2: Species identity, components of biomass dynamics estimation, abundance and species traits values, ordered by the greatest amount of initial forest structure.

Species	**FSi (m^{2}ha^{-1})**	**Biomass (Mg, t0)**	**Biomass growth**	**Biomass recruitment**	**Biomass mortality**	**Survivals number**	**Recruits number**	**Deads number**	**LDMC (mg/g)**	**SLA (mm2/mg)**	**Hmax (m)**	**WD (g/cm3)**	**LNC (%)**	**LPC (%)**	**Deciduous (0/1)**
Ocotea diospyrifolia	823.4	37.22	8.92	0.44	7.13	101	9	26	469.8	9.5	23	0.42	2.90	0.27	0
Araucaria angustifolia	443.3	27.83	12.34	0.05	1.66	44	1	9	368.5	5.3	26	0.50	0.91	0.10	0
Cupania vernalis	285.9	13.08	3.11	0.09	3.39	81	3	45	420.5	18.6	17	0.57	1.72	0.19	1
Luehea divaricata	233.7	15.03	2.77	0	0.55	12	0	1	352.8	13.3	20	0.52	1.68	0.23	1
Coussarea contracta	209.5	7.70	1.39	3.32	4.07	79	98	100	282.3	12.8	22	0.62	2.70	0.12	0
Matayba elaeagnoides	195.7	10.25	1.55	0	2.22	19	0	10	299.0	13.3	20	0.49	1.98	0.18	0
Cedrela fissilis	154.8	8.87	2.54	0	2.24	16	0	4	289.6	23.3	23	0.47	3.02	0.30	1
Cordia americana	135.9	12.13	1.65	0.03	0.88	16	1	3	422.3	14.8	23	0.69	2.30	0.16	0
Parapiptadenia rigida	130.6	12.51	2.16	0	2.66	5	0	1	458.1	14.1	25	0.68	2.51	0.16	1
Lauraceae	108.7	4.71	0	0	4.71	0	0	30	457.0	9.2	20	0.49	2.38	0.18	0
Ocotea puberula	95.8	5.35	0.44	0	4.32	2	0	3	422.7	10.2	24	0.44	3.04	0.20	0
Myrocarpus frondosus	85.1	7.57	1.69	0.34	0.58	22	5	3	396.8	12.8	25	0.82	2.90	0.18	1
Peltophorum dubium	84.8	9.34	2.94	0	0.20	7	0	1	450.7	12.0	25	0.74	2.51	0.15	1
Myrsine umbellata	79.4	3.51	0.31	0.11	2.27	14	4	22	385.4	8.2	18	0.60	1.90	0.06	0
Prunus myrtifolia	73.8	5.76	1.36	0	2.63	1	0	2	416.6	10.4	26	0.65	1.88	0.14	0
Helietta apiculata	71.0	8.27	2.00	0.12	2.85	17	2	6	357.5	10.5	25	0.81	2.20	0.17	0
Ateleia glazioviana	64.9	6.31	3.35	0	0	10	0	0	300.0	19.6	24	0.65	2.51	0.15	1
Lamanonia ternata	60.9	4.94	0.98	0	0.03	2	0	1	391.8	12.5	25	0.51	1.03	0.10	0
Diatenopteryx sorbifolia	55.3	5.80	3.17	1.47	0	12	18	0	425.7	17.9	18	0.85	2.30	0.20	1
Casearia sylvestris	52.7	3.89	1.04	1.10	1.95	17	15	20	374.5	10.1	20	0.71	2.28	0.14	1

Species	FSi (m^{2}ha^{-1})	Biomass (Mg, t0)	Biomass growth	Biomass recruitment	Biomass mortality	Survivals number	Recruits number	Deads number	LDMC (mg/g)	SLA (mm2/mg)	Hmax (m)	WD (g/cm3)	LNC (%)	LPC (%)	Deciduous (0/1)
Chrysophyllum marginatum	52.1	4.31	0.53	0.27	1.08	12	4	8	408.3	14.5	22	0.70	1.50	0.12	1
Nectandra lanceolata	43.7	3.32	0.23	0	0.88	4	0	1	453.3	8.9	26	0.70	2.20	0.15	0
Campomanesia xanthocarpa	43.6	2.37	0.60	0.10	0.23	17	3	3	350.0	16.4	15	0.68	1.28	0.13	1
Sebastiania commersoniana	33.0	1.46	0.08	0.05	0.80	3	1	3	438.0	11.0	16	0.60	1.90	0.12	0
Nectandra megapotamica	32.0	1.39	0.59	0.08	0.58	6	3	3	414.9	10.6	17	0.41	2.06	0.12	0
Lonchocarpus campestris	25.4	2.16	0.41	0	0	3	0	0	447.8	17.1	13	0.89	2.80	0.14	1
Salicaceae	23.7	0.66	0	0	0.66	0	0	11	376.0	15.9	20	0.68	2.38	0.23	0
Strychnos brasiliensis	22.4	0.72	0.08	0.04	0.40	6	1	3	323.1	19.2	11	0.54	2.24	0.12	0
Jacaranda micrantha	20.7	1.23	0.37	0	0.46	2	0	3	331.9	25.7	24	0.48	2.40	0.13	1
Ilex paraguariensis	20.1	0.91	0.07	0.08	0.03	3	2	1	475.7	7.6	15	0.46	1.35	0.12	0
Holocalyx balansae	19.9	2.29	1.08	0	0	2	0	0	415.6	16.2	21	0.86	2.70	0.12	0
Cordia trichotoma	13.7	1.09	0.59	0	0.10	3	0	1	328.7	20.4	19	0.63	2.30	0.19	1
Banara tomentosa	12.9	0.88	0.24	0.36	0.22	8	8	3	305.7	21.2	18	0.69	2.50	0.17	1
Ilex breviscuspis	12.2	0.74	0.45	0	0.22	2	0	3	328.5	17.3	16	0.54	1.73	0.08	0
Erythrina falcata	12.0	0.63	0.39	0.02	0	1	1	0	306.9	15.2	24	0.32	3.10	0.20	1
Ocotea pulchella	11.4	0.78	0	0	0.74	1	0	2	481.6	7.2	22	0.49	1.70	0.14	0
Ruprechtia laxiflora	11.0	0.61	0.02	0	0.05	3	0	1	285.3	19.7	16	0.59	2.90	0.16	0
Allophyllus edulis	10.5	0.36	0.07	0.05	0.07	2	1	1	339.5	17.5	12	0.54	1.39	0.13	0
Aspidosperma australe	9.0	0.85	0.74	0	0	2	0	0	304.3	11.8	19	0.74	1.90	0.08	1
Ocotea sp.	8.8	0.66	0	0	0.66	0	0	1	466.5	8.9	20	0.49	2.54	0.20	0
Styrax leprosus	8.6	0.63	0.06	0	0.49	1	0	1	453.6	9.2	20	0.41	1.40	0.08	0
Erythroxylum deciduum	6.5	0.72	0.35	0	0	1	0	0	290.7	16.1	20	0.81	3.00	0.30	0
Cabralea canjerana	6.4	0.33	0.25	0	0	6	0	0	287.1	16.5	16	0.53	2.11	0.15	1
Eugenia involucrata	6.1	0.47	0.04	0.13	0.41	1	2	1	427.1	10.7	12	0.94	1.80	0.10	0
Zanthoxylum petiolare	6.0	0.57	0.27	0	0	3	0	0	355.4	15.2	18	0.90	1.50	0.29	0
Annona rugulosa	5.5	0.17	0.03	0.04	0.02	4	1	1	282.2	23.4	17	0.35	2.45	0.12	0

Species	FSi (m^2ha^{-1})	Biomass (Mg, t0)	Biomass growth	Biomass recruitment	Biomass mortality	Survivals number	Recruits number	Deads number	LDMC (mg/g)	SLA (mm2/mg)	Hmax (m)	WD (g/cm3)	LNC (%)	LPC (%)	Deciduous (0/1)
Casearia obliqua	5.4	0.37	0.31	0.07	0.03	4	1	1	453.9	9.6	24	0.67	2.76	0.50	1
Zanthoxylum kleinii	5.2	0.25	0	0.02	0.25	0	1	1	420.6	8.4	12	0.48	2.20	0.11	0
Chrysophyllum gonocarpum	4.4	0.22	0.13	0.12	0	3	3	0	443.6	10.1	12	0.67	2.60	0.14	0
Eugenia pyriformis	4.1	0.49	0.10	0	0	1	0	0	494.0	8.3	20	0.79	2.20	0.13	0
Apuleia leiocarpa	4.0	0.44	0.53	0	0	1	0	0	370.1	14.7	20	0.80	2.80	0.34	1
Piptocarpha angustifolia	3.6	0.16	0	0	0.16	0	0	1	407.1	18.8	8	0.50	1.80	0.09	0
Balfourondendron riedelianum	3.4	0.16	0.07	0.05	0.09	2	1	1	347.3	13.9	11	0.67	3.30	0.24	1
Casearia decandra	3.3	0.24	0.11	0.42	0.07	2	9	1	339.4	16.4	17	0.65	2.00	0.13	1
Tabernaemontana catharinensis	2.5	0.21	0.05	0	0	1	0	0	266.8	9.9	21	0.56	2.60	0.24	0
Sebastiania brasiliensis	2.5	0.13	0.09	0	0	2	0	0	322.4	13.6	13	0.61	1.80	0.20	1
Pilocarpus pennatifolius	2.4	0.08	0.03	0.31	0.04	1	8	1	386.1	8.8	9	0.75	2.00	0.11	0
Randia ferox	1.5	0.08	0	0	0	1	0	0	262.3	14.8	20	0.68	2.24	0.16	0
Picrasma crenata	1.0	0.04	0	0	0	1	0	0	405.2	15.2	8	0.40	2.24	0.16	1
Machaerium stipitatum	0.9	0.06	0.05	0	0	1	0	0	460.8	14.0	13	0.64	2.44	0.14	1
Inga virescens	0.9	0.05	0.01	0	0	1	0	0	448.9	13.1	12	0.58	2.78	0.14	0
Calliandra foliolosa	0.8	0.04	0	0.02	0	1	1	0	579.3	26.1	7	0.86	2.20	0.15	0
Sorocea bonplandii	0.7	0.03	0.01	0.14	0	1	4	0	422.7	10.6	11	0.62	1.23	0.10	0
Actinostemon concolor	0	0	0	0.03	0	0	1	0	348.2	5.1	20	0.90	1.14	0.07	0
Annona neosalicifolia	0	0	0	0.03	0	0	1	0	357.1	20.9	8	0.52	2.80	0.17	0

Appendix 4

Table 3: Predictor variables selected corresponding to Fig 1. Bold standardized coefficients values denote where 95% CI do not overlap with zero. 95% CI are represented by the lower and upper deviation.

Response variable	Explanatory variable	Standardized Coefficient	Averaged Slope 95% CI
AGBsurv	CWMldmc	0.126	(-0.0015; 0.2536)
	CWMlpc	**-0.165**	(-0.2998; -0.0309)
	CWMsla	0.152	(-0.0521; 0.3554)
	CWMdec	0.134	(-0.0618; 0.3290)
	CWMhmax	**0.201**	(0.0217; 0.3798)
	FDldmc	**-0.159**	(-0.2793; -0.0382)
	FDsla	0.145	(-0.004; 0.2939)
	FDlnc	0.107	(-0.0424; 0.2570)
	FDwd	0.120	(-0.015; 0.2547)
	FDhmax	**-0.169**	(-0.3058; -0.0314)
	FSi	0.039	(-0.1069; 0.1857)
AGBrecr	FDhmax	-0.1454	(-0.3280; 0.037)
	CEC	0.1775	(-0.0471; 0.4021)
	pH	**0.2504**	(0.0208; 0.4799)
	K	**-0.2074**	(-0.3966; -0.0181)
	FSi	-0.0615	(-0.2532; 0.1303)
AGBmort			
	CWMldmc	0.2566	(-0.009; 0.5226)
	FDwd	0.2361	(-0.0336; 0.5058)
	Clay	0.2774	(-0.0147; 0.5696)
	P	0.1982	(-0.0831; 0.4795)
	K	0.2529	(-0.0334; 0.5393)
	FSi	**0.3044**	(0.0483; 0.5603)

Appendix 5

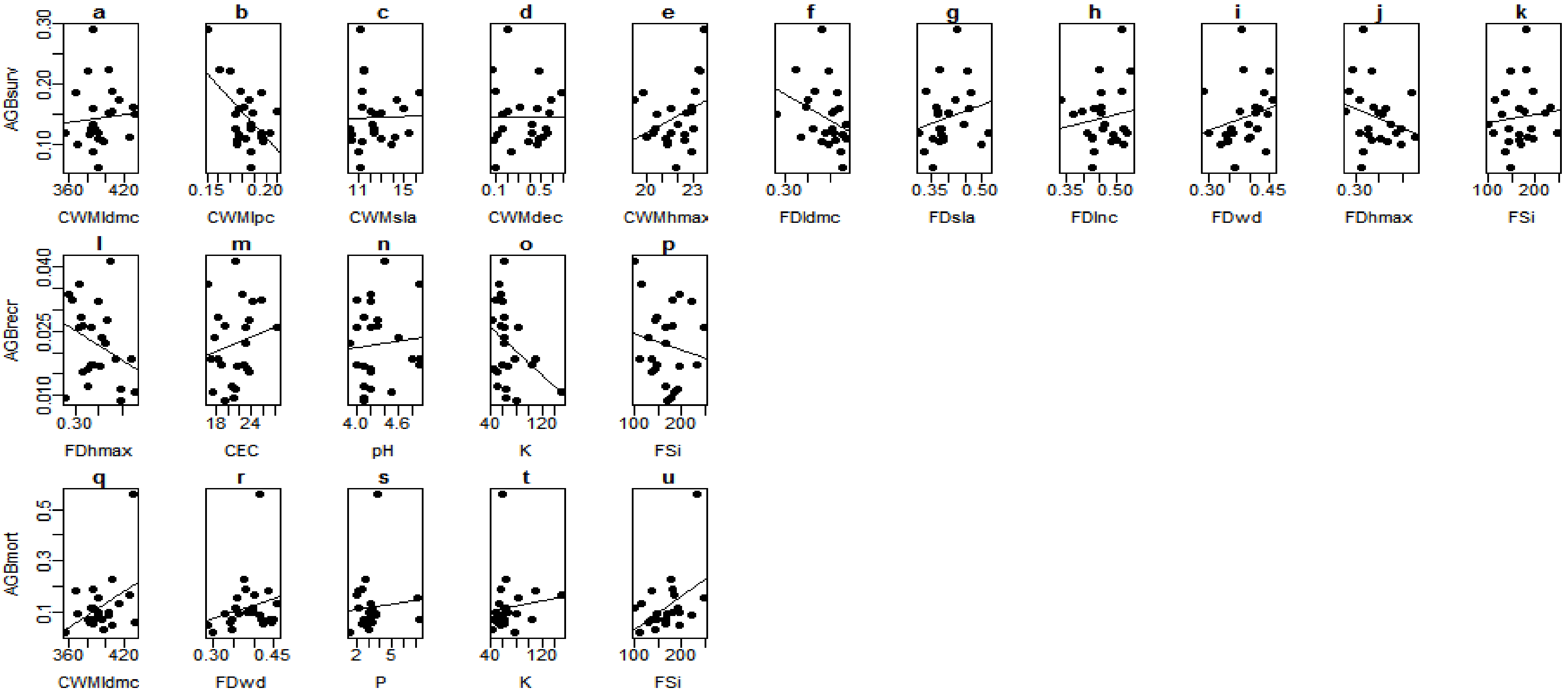

Fig 2: Bivariate relations of predictor variables of soil, biomass ratio, niche complementarity and vegetation quantity hypotheses and response variables (AGB$_{surv}$, AGB$_{recr}$ and AGB$_{mort}$). Vegetation quality variables: CWM: community-weighted means of LDMC (leaf dry matter content), LPC (leaf phosphorous content), WD (wood density); FD: functional diversity of LPC, WD, Hmax (maximum height) and SLA (specific leaf area). Soil variables: CEC: cation exchange capacity; OM: organic matter; P: phosphorous and pH. Vegetation quantity: FSi (initial forest structure).

Considerações finais

Este é o primeiro estudo que apresenta dados de dinâmica florestal numa escala de tempo relativamente longa - 18 anos, para a região sul do Brasil. Embora a escala de estudo possa ser considerada pequena, apenas 24 parcelas em uma área florestal, foi possível observar alguns indícios da importância das variáveis bióticas e abióticas sobre a dinâmica desta floresta subtropical. Em geral, os mecanismos que conduzem os processos demográficos estão relacionados aos atributos funcionais de plantas, variáveis edáficas e quantidade de biomassa presente na comunidade.

A perda de biomassa nas comunidades demonstrou ser um mecanismo chave influenciando a da mudança líquida da biomassa presente nestas comunidades de floresta subtropical, assim como o aumento em biomassa proveniente do crescimento e recrutamento de novos indivíduos. Em geral, os resultados sugerem que a floresta pouco aumentou em termos de acúmulo de biomassa, dada a elevada perda (associada à alta mortalidade) em relação ao aumento em biomassa. Dentre as explicações para esta variação, estão o alcance da maturidade nesta floresta. Neste sentido, indivíduos mais velhos e maiores, que acumularam mais biomassa ao longo do tempo, têm morrido e permitido que este espaço seja utilizado para a colonização destes locais por espécies características de estágio sucessional avançado, as quais serão responsáveis pela maior biomassa no futuro.

Estudos que relacionam estas variáveis fornecem subsídios para a compreensão de como é a dinâmica destas florestas subtropicais, as quais são pouco compreendidas quando comparadas às florestas tropicais, por exemplo. Para estudos futuros, seria importante incluir o componente filogenético associado às espécies presentes nas comunidades, a fim de considerar a história evolutiva a elas relacionadas. Além disso, estudos em escalas maiores, tanto de tempo como de espaço, também são importantes e necessários, pois envolveriam condições diferenciadas de clima e variáveis edáficas, o que também tende a influenciar as características funcionais das comunidades e consequentemente, o efeito destas variáveis sobre os processos demográficos nas comunidades florestais da região subtropical. Além de conhecer o efeito destas variáveis sobre os processos demográficos em comunidades, avaliar os efeitos da mortalidade e recrutamento sobre a composição funcional das comunidades deve ser considerado em estudos futuros, uma vez que evidenciam a recuperação das comunidades diante de distúrbios, assim como fornecem informações sobre a velocidade de mudança e recuperação das florestas subtropicais.

Estudos como este têm sua importância pautada na compreensão acerca da dinâmica de comunidades florestais na região subtropical e de como são estruturadas as comunidades de plantas em relação aos mecanismos de coexistência de espécies. Dadas às perspectivas de mudanças climáticas futuras, torna-se necessário conhecer os processos e mecanismos que atuam no presente. Assim, as respostas obtidas podem ser utilizadas para projetar as respostas destas comunidades em cenários de mudanças no clima, por exemplo.