UNIVERSIDADE FEDERAL DO PARANÁ

ANAMARIA CEQUINEL

FATORES QUE AFETAM A SUBSTITUIÇÃO DE ESPÉCIES DURANTE A SUCESSÃO EM FLORESTA ATLÂNTICA

CURITIBA
2017

ANAMARIA CEQUINEL

FATORES QUE AFETAM A SUBSTITUIÇÃO DE ESPÉCIES DURANTE A SUCESSÃO EM FLORESTA ATLÂNTICA

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Botânica, no curso de pós-graduação em Botânica, Setor de Ciências Biológicas, da Universidade Federal do Paraná.

Orientadora: Márcia Cristina Mendes Marques

CURITIBA
2017

UNIVERSIDADE FEDERAL DO PARANÁ
Setor de Ciências Biológicas
Programa de Pós-Graduação em Botânica

"FATORES QUE AFETAM A SUBSTITUIÇÃO DE ESPÉCIES DURANTE A SUCESSÃO EM FLORESTA ATLÂNTICA".

por

ANAMARIA CEQUINEL

**Dissertação aprovada como requisito parcial
para obtenção do grau de Mestre no Programa
de Pós-Graduação em Botânica, pela Comissão
formada pelos doutores**

Drª Márcia Cristina Mendes Marques (UFPR)

Drª Isabela Galarda Varassin (UFPR)

Luciana de C. Franci
Drª Luciana de Campos Franci (UFPR)

Curitiba, 29 de junho de 2017.

Dedico à minha mãe!

AGRADECIMENTOS

Agradeço a todos que colaboraram de alguma forma para a realização desse trabalho, em especial:

À Márcia Marques, pela oportunidade e pela orientação. Agradeço também a paciência ao longo desses dois anos e meio e pelos imensos ensinamentos ecológicos e científicos que levarei para vida.

À banca, principalmente à professora Isabela Varassin e à Luciana Franci que foram extremamente solicitas e queridas, além das valiosas contribuições ao manuscrito. Também agradeço aos suplentes, Victor Zwiener e Guilherme Seger. A banca não poderia ter tido melhores membros.

Ao Vinícius Marcílio-Silva, por suas contribuições principalmente no processo analítico (me encorajando no R) e pela empolgação com meus resultados.

À Elivane Capelesso, por ter deixado o trabalho árduo muito mais agradável; tornou-se de companheira de “parcelas perdidas” a uma grande amiga.

À Fernanda Cardoso, por ter disponibilizado seus dados.

Ao Rudá Pereira, Júlio Bastos, Tamires Burda, Emanuel Fischer, Israel Schneiberg, Fabiano Maia, Mayron Escárraga, Fabian Gavíria, Fernanda Lima e Fernanda Cardoso, nossos ajudantes de campo, por terem disponibilizado seus tempos preciosos para sofrerem um pouquinho com a gente.

À Thais Zanatta e ao Israel Schneiberg pela ajuda com a seleção de modelos.

A todos os colegas do Laboratório de Ecologia Vegetal (LEVianos), seja por um script ou artigo, como também pela troca de ideias sempre muito valiosas.

À SPVS, por nos permitir trabalhar nas suas reservas. Em especial ao Reginaldo Ferreira, que aturou nossos “chororôs”, “Seu” Pontes e “Seu” Luís, e aos guardas-parque Vando, Toninho, Jandir e Fernando, sempre dispostos a nos ajudar.

À CAPES, pela bolsa de auxílio.

Ao PPG-Botânica e todos seus integrantes que foram sempre acolhedores comigo e com meu trabalho “ecológico”.

Aos poucos, mas muito valiosos amigos, que fizeram essa caminhada mais agradável, sendo com uma palavra de conforto ou com um abraço afetuoso. A distância não impediu que sempre me fizessem companhia.

À minha mãe, a mulher mais incrível do mundo, e ao meu irmão, com os quais aprendi a ser forte diante da vida. Ao meu pai, avós, tios e todos meus familiares, até aos que nunca entendiam direito o que eu fazia, mas sempre me apoiaram.

Ao meu amor, Emanuel, que foi meu porto-seguro, aguentando minhas ausências, meus autoquestionamentos e angústias ao decorrer de todo o mestrado, além de toda ajuda como “estagiário particular”. Não tenho palavras para agradecer todo seu apoio.

“Outras vezes ouço passar o vento,
E acho que só para ouvir passar o vento vale a pena ter nascido.”

Alberto Caeiro (Fernando Pessoa)

RESUMO

Mesmo sendo foco de estudos a mais de 100 anos, a sucessão ecológica ainda não foi totalmente compreendida e permanece uma teoria em expansão. A sucessão pode ser considerada como a montagem da comunidade em progresso e as mudanças na composição de espécies e no *turnover* de indivíduos podem ser afetadas por processos estocásticos e determinísticos. Além destes, fatores bióticos e abióticos agem estruturando as comunidades durante a sucessão. Assim, quantificar a importância dos processos e fatores que atuam na estruturação das comunidades ao longo da sucessão é essencial para ações que visem a manutenção da biodiversidade em ambientes naturais e a restauração de áreas degradadas. Neste estudo, avaliou-se o efeito relativo de processos determinísticos e estocásticos na estruturação de comunidades de árvores ao longo da sucessão secundária de uma floresta tropical. Com base em uma análise de indicadores estruturais de filtragem biótica e abiótica sobre a demografia, buscou-se identificar os fatores que atuam na estruturação das comunidades. Avaliamos a demografia (recrutamento, sobrevivência e substituição de espécies e indivíduos) das árvores (DAP≥5cm) que ocorrem em um gradiente edáfico-sucessional (florestas com idades entre 7-17, 20-30, 30-55 e >80 anos, em dois tipos de solo) em Floresta Atlântica em Antonina, Paraná, sul do Brasil. Testamos a estocasticidade a partir da construção de modelos nulos para cada intervalo de idade da floresta e utilizamos a abordagem de seleção de modelo (AICc) para avaliar a importância relativa da filtragem ambiental (indiretamente medida pelo tipo de solo e idade da floresta) e as interações das espécies (medidas por área basal, densidade individual, diversidade taxonômica, funcional e filogenética) para prever taxas de recrutamento, sobrevivência, *turnover* de indivíduos e espécies. A composição e abundância de plantas em todas as comunidades diferiram das esperadas pelos modelos nulos, indicando determinismo. Os resultados revelaram também que a filtragem abiótica e biótica afetou de diferentes formas a montagem da comunidade ao longo do gradiente sucessional. A filtragem ambiental (possivelmente através do estresse do solo e das limitações relacionadas à complexidade estrutural) pareceu ser mais importante para recrutamento, sobrevivência e *turnover* de indivíduos. A filtragem biótica (possivelmente por dependência de densidade, capacidade competitiva e complementaridade de nicho) foi mais importante para sobrevivência, recrutamento e *turnover* de espécies. Sendo assim, a montagem das comunidades durante a sucessão é o resultado de um processo multifatorial com efeitos distintos no estabelecimento, sobrevivência, substituição das espécies e indivíduos. Nossos resultados adicionam achados importantes para teoria sucessional, separando os múltiplos fatores que atuam temporalmente na montagem da comunidade.

Palavras-chave: cronossequência; demografia; diversidade funcional; diversidade filogenética; Mata Atlântica; recrutamento; regeneração natural; restauração; sobrevivência.

ABSTRACT

Even being the focus of studies over 100 years, the succession has not yet been fully understood and remains a theory in expansion. Knowing that succession can be considered as the assembly of the community in progress, the changes in the composition of the species and in the turnover of individuals can be affected by stochastic and deterministic processes. In addition, biotic and abiotic factors act to structure communities during the succession. Thus, quantifying the relative importance of the processes and the factors that act on the patterns found throughout the succession are essential for the maintenance of biodiversity in natural environments and restoration of degraded areas. This study evaluated the relative effect of deterministic and stochastic processes along the secondary succession of a tropical forest, and based on a proxy analysis of biotic and abiotic filtering on demography, to identify the factors that structure communities. We assessed the demography (recruitment and survival rates, species and individual turnover) of trees (DHB≥5cm) occurring in a edaphic-successional gradient (forests aged 7-17, 20-30, 30-55, and >80 years; two soil tipes) of Atlantic Forest in Antonina, Paraná State, southern Brazil. Stochasticity was tested by building null models (randomizing species composition and abundance) for each forest age interval. Also, model selection approach (AICc) was used to assess the relative importance of environmental filtering (indirectly measured by soil type, forest age) and species interactions (measured by basal area, individual density, taxonomic, functional, and phylogenetic diversity) to predict recruitment, survival, individual and species turnover rates. The composition and abundance of plants in all communities differed from the expected by the null models, indicating determinism. The results also showed that the abiotic and biotic filtering affected in different ways the community assembly in successional gradient. Environmental filtering (possibly via soil stress and limitations related to structural complexity) seemed to be more important for recruitment, survival, and individual turnover. Biotic filtering (possibly via density-dependency, competitive ability and niche complementarity) was more important for survival, recruitment and species turnover. Thus, the community assemblage during the succession is the result of a multi-factor process with distinct effects in the establishment, survival, substitution of species and individuals. This study adds some important findings on the successional theory, by disentangling the multi-factors acting temporarily in community assembly.

Keywords: Atlantic Forest; chronosequence; demography; functional diversity; phylogenetic diversity; recruitment; regeneration; restoration; survival.

LISTA DE FIGURAS

LISTA DE FIGURAS – Capítulo 1

LISTA DE TABELAS – Capítulo 1

LISTA DE ABREVIATURAS

BA – basal area
Fdiv – functional diversity
MPD – mean pairwise distance
Pdiv – phylogenetic diversity
Rao – Rao's quadratic entropy
Tdiv – Taxonomic diversity
Tind – Individual turnover
Tsp – Species turnover
y - years

SUMÁRIO

INTRODUÇÃO GERAL

Mesmo sendo foco de estudos desde o século XIX, a sucessão ecológica ainda é um dos temas centrais em ecologia e não foi totalmente compreendida. Atualmente as discussões acerca da teoria sucessional ganharam força, pois a ideia recente sobre a sucessão ser considerada como a montagem de comunidades em progresso deu maior respaldo a essa teoria (LEBRIJA-TREJOS et al. 2010; MEINERS et al., 2015).

Vários autores foram precursores da teoria da sucessão, mas foi Henry Chandler Cowles, em 1899, o primeiro a descrever uma série sucessional completa, através da construção da evolução temporal das associações de plantas das dunas da região de Chicago (EUA) (TANSLEY, 1935). Durante a primeira década do século XX, Cowles foi o pesquisador a produzir maior conhecimento sobre sucessão e deduzir suas leis gerais (OLIVEIRA e JÚNIOR, 2011).

Posteriormente, o estudo da sucessão vegetal foi desenvolvido e consolidado principalmente por Clements (1916), que defendia que a sucessão ecológica em comunidades vegetais era preditiva e direcional, sendo um processo ordenado e determinístico no qual a comunidade seria uma unidade integrada para, ao final, chegar ao clímax. Clements acreditava que os fatores ambientais eram os responsáveis pelos processos da sucessão (CLEMENTS, 1936). Seus *insights* são reconhecidos como uma forma abrangente e contemporânea de entender a dinâmica da vegetação (PICKETT et al., 2009), e deram origem para a visão determinista da sucessão.

Gleason (1926) e Tansley (1935) contribuíram com ideias diferentes das de Clements. Gleason explicou a sucessão ecológica como um processo estocástico, onde cada espécie influencia as mudanças na composição da comunidade (GLENN-LEWIN e VAN DER MAAREL, 1992). Colaborou para a teoria sucessional abordando temas como o ambiente, migração e seleção natural. Sua visão ganhou força apenas após 1950, quando muitos ecólogos deixaram o pensamento holístico de Clements para seguir o individualismo de Gleason (PIQUERAS e BRANDO, 2016).

Tansley (1935) desenvolveu a teoria sucessional baseada em um policlímax, onde argumentava que fatores ambientais locais, como rocha de origem e posição topográfica, seriam peças chaves para determinar o desenvolvimento de vegetação. Mas, diferente da visão de monoclímax associada a Clements, Tansley defendia que era possível existir diferentes estados de clímax em uma mesma região (TANSLEY, 1935). Apenas mais tarde, em 1953, Robert Whittaker formulou o clímax padrão, onde há várias possibilidades de ápice ecológico e a comunidade varia ponto a ponto dependendo de ações abióticas e bióticas.

Outra teoria importante é de Frank Egler (1954), que descreveu a hipótese da composição florística inicial, focando na colonização e nas diferenças das formas e ciclos de vida das espécies. Assim, espécies herbáceas e arbóreas chegam praticamente no mesmo momento ao local a ser colonizado, mas como possuem ciclos de vida diferentes, o panorama de dominância muda ao longo do tempo. Assim, toda a sequência da sucessão será determinada pela composição inicial da comunidade (EGLER, 1954).

Na década de 1960 Ramón Margalef e Eugene Odum procuraram desenvolver uma teoria unificada da sucessão onde sugeriram padrões sucessionais, assumindo vários princípios já estudados, principalmente os de Clements. Margalef sugeriu a teoria de acúmulo, onde a sucessão partiria de um sistema mais simples para um mais complexo, com maior número de níveis tróficos e diversidade de espécies (MARGALEF, 1963). Odum publicou uma lista de tendências da sucessão, sugerindo que ao longo da sucessão haveria o aumento da densidade de teias tróficas, biomassa, especialização de nichos, entre outros (ODUM, 1969).

Picket, em 1976, propôs uma interpretação evolutiva da sucessão, que é tida como base de muitas abordagens contemporâneas (MIRANDA, 2009). Descreveu a sucessão como um gradiente no qual os processos de interação de estratégias evolutivas regem a substituição de espécies e onde as espécies sempre serão substituídas por melhores competidoras.

Connell e Slatyer (1977), para descrever como as populações locais interagiam, apresentaram três modelos atuantes: a facilitação, a tolerância e a inibição. De forma geral, no modelo de facilitação, as espécies pioneiras modificariam o ambiente, sendo essencial para o estabelecimento e crescimento das espécies tardias. No modelo de tolerância, o estabelecimento e o desenvolvimento das espécies tardias ocorreriam devido à capacidade de crescer em níveis mais baixos de recursos. Já no modelo de inibição, a presença das espécies colonizadoras tardias dificultaria ou impediria o desenvolvimento das outras espécies. Esses modelos de interações até hoje são usados como base de estudos em ecologia vegetal, tanto em áreas sucessionais, como em outros contextos (NUCHE e ALADOS, 2017).

Nas décadas de 1980 e 1990 a ecologia de comunidades se desenvolveu mais em abordagens mecanicistas, que refletiu nos estudos de sucessão. Buscou-se a compreensão dos processos por trás dos padrões ecológicos, o que levou os estudos a focarem em respostas a características morfológicas, fisiológicas e comportamentais dos organismos (VAN ANDEL et al., 1993).

Glenn-Lewin, Peet e Veblen, em 1992, propõem a definição mais completa e atualmente aceita sobre sucessão que fundamenta a visão contemporânea da dinâmica da vegetação. Nesta abordagem não se assume estabilidade nem uma definição de um estágio final da sucessão, dando ênfase à observação de distúrbios frequentes e repetidos e da variação contínua da vegetação, em várias escalas de tempo e de espaço.

Muitos foram os avanços no estudo de sucessão nestes 100 anos, mas ainda há muitas lacunas na compreensão deste processo (MEINERS et al., 2015). Afim de refinar o conhecimento, frequentemente muitas das teorias já mencionadas são revisitadas, tais como a composição florística inicial de Egler (1954) (VAN BREUGEL et al., 2007; CHAZDON, 2008), os mecanismos de tolerância, inibição e facilitação de Connell and Slatyer (1977) (RESS et al., 2001) e o equilíbrio entre os processos determinísticos (baseada na visão “clementiana”) e estocásticos (baseada na visão “gleasoniana") na montagem das comunidades (CHAZDON, 2008).

Sabendo que os processos de montagem da comunidade são capazes de dirigir o curso de sucessão e produção da estrutura de comunidade (DRAKE, 1990), estudar os padrões ao longo da sucessão é estudar a montagem das comunidades (LEBRIJA-TREJOS et al., 2010). O objetivo do estudo em montagem de comunidade é, principalmente, prever quais processos atuarão sobre um *pool* regional de espécies (banco de espécies de uma região específica) que determinarão as estruturas das comunidades em um habitat específico (KEDDY, 1992). Os dois processos frequentemente estudados, considerados responsáveis pela montagem das comunidades ecológicas, são a estocasticidade (neutros) e o determinismo (baseado em nicho) (VAMOSI et al., 2009).

A perspectiva estocástica prediz que todas as espécies são ecologicamente equivalentes e todos os indivíduos teriam a mesma capacidade de consumir recursos e sobreviver; colonizar determinada área dependeria de eventos estocásticos, resultando em taxas demográficas análogas. As migrações locais e a especiação regional seriam os responsáveis pela manutenção da diversidade, onde a deriva ecológica agiria distribuindo as abundâncias (HUBBELL, 2001). Eventos de dispersão e coocorrência de espécies em ambientes tropicais são frequentemente atribuídos a eventos estocásticos (CHAZDON, 2008).

Processos determinísticos são aqueles em que a capacidade de estabelecimento em uma área depende das características particulares de cada espécie para o uso de recursos (CHESSON, 2000). Neste contexto, as restrições no estabelecimento e desenvolvimento de espécies que não possuem características necessárias ao meio são considerados filtros abióticos, bem como os efeitos das interações locais podem ser considerados filtros bióticos (CAVENDER-BARES et al., 2006).

A filtragem ambiental é um dos fatores que agem estruturando as comunidades durante a sucessão. As mudanças na disponibilidade de luz, associadas ao uso anterior da terra, as características do solo, entre outros, afetariam as espécies e os indivíduos durante a sucessão (BOUKILI e CHAZDON, 2016). Mesmo sendo um mecanismo sempre observado dentro de sucessão e em montagem de comunidades foi Keddy, em 1992, quem trouxe a definição de filtros ambientais como fatores agindo dentro dos processos determinísticos. Entre os filtros ambientais que atuam na montagem ao longo de gradientes sucessionais, o aumento da complexidade da vegetação, ligada à variação na disponibilidade de luz, é um forte estruturador (BAZZAZ e PICKET, 1980). O estabelecimento de espécies tolerantes à sombra ao longo da sucessão contribui para o fechamento do dossel, diminuído a disponibilidade de luz e dificultando o estabelecimento de espécies intolerantes à sombra. Ao mesmo tempo o sombreamento facilita o desenvolvimento de espécies tolerantes que ocupam tanto o dossel quanto o sub-bosque, aumentando assim a complexidade estrutural (CHAZDON, 2008). As características do solo, como a drenagem e a disponibilidade de nutrientes, também podem restringir o estabelecimento e desenvolvimento de várias espécies, caracterizando a filtragem ambiental (ROBINSON et al., 2015). Um forte filtro edáfico é a saturação hídrica, pois mecanicamente se torna difícil o estabelecimento e desenvolvimento nesses ambientes, assim como a falta de oxigenação do solo leva a menores taxas de decomposição da matéria orgânica que, por sua vez, leva a alterações na disponibilidade de nutrientes (MELLO et al. 2015).

As interações biológicas também agem de diferentes formas ao longo do gradiente sucessional, podendo inibir a coexistência ou contribuir para isso (CHESSON, 2000). Fatores dependentes da densidade agem negativamente à sobrevivência (ex. *self-thinning*; mortalidade dependente de densidade), pois impedem o crescimento populacional excessivo através da disputa de recursos (nutrientes, luz, espaço, etc), que são mediados pela densidade de indivíduos (FRICKE e WRIGHT, 2017). Além disso, a similaridade entre espécies pode ter ação negativa, levando à limitação em sua coexistência (VOLTERRA, 1926; GAUSE, 1934), ou positiva, quando há complementaridade de nicho (LOREAU, 1998). A similaridade limitante é uma das hipóteses mais utilizadas para explicar padrões na estruturação das comunidades. Entre espécies que coocorrem em um mesmo habitat, existe um limite máximo de similaridade entre a suas características para obtenção de recursos, ou seja, as espécies coexistentes devem diferir em um mínimo na morfologia, ou competirem por um mesmo recurso (GAUSE, 1934). Esse processo, ao longo da história evolutiva, pode levar ao deslocamento de caracteres ou exclusão competitiva. A complementaridade de nicho é uma das explicações usadas para a alta diversidade nos trópicos; dentro dessa definição estão incluídos processos de diferenciação de nicho e facilitação (LOREAU, 1998). Dentro de uma mesma espécie os indivíduos compartilham características que refletem as estratégias para obtenção de recursos. Quando as estratégias se diferenciam, as espécies conseguem usar os recursos do ambiente de diferentes maneiras (diferenciação de nicho) (KRAFT et al., 2008). De maneira análoga, espécies podem se beneficiar direta ou indiretamente uma das outras, facilitando o estabelecimento e desenvolvimento (CONNELL e SLATYER, 1977). Portanto, a complementariedade de nicho permite que as espécies coexistam, evitando uma forte concorrência, ou que sejam facilitadas por outras e, consequentemente, desempenhem seus processos com eficiência (TILMAN et al., 2001).

Uma forma de entender os mecanismos atuantes na montagem das comunidades é medir os efeitos de diferentes processos sobre as performances das espécies (através das taxas demográficas) e as consequências que elas trazem para a estrutura da comunidade (LASKY et al., 2014). Os estudos demográficos surgiram no século XVIII, movidos pela preocupação com o crescimento desenfreado da população humana, mas seus princípios estatísticos cabem para todas as populações vivas (MALTHUS, 1798). A partir dos anos de 1970 a demografia ganhou também força em estudos com comunidades vegetais (HARPER e WHITE, 1974). O objetivo da demografia é monitorar as flutuações das populações no tempo e no espaço e suas taxas podem fornecer respostas sobre os processos que atuam na estruturação, dinâmica e funcionamento das comunidades (REES, 2001).

A regeneração natural das florestas tropicais proporciona um sistema ideal para acessar a dinâmica da vegetação durante a sucessão (LETCHER et al., 2012). A interferência natural geralmente desencadeia processos de regeneração e sucessão, mas a ação antrópica tem sido a principal causa de perturbação e fragmentação das florestas tropicais nos últimos séculos (CHAZDON, 2008).

Uma das florestas tropicais mais ameaçadas e altamente fragmentadas do planeta é a Floresta Atlântica. Considerada *hotspot* de biodiversidade, apresenta alta riqueza de espécies, alto nível de endemismo e muitas espécies na lista de ameaçadas de extinção (MYERS et al., 2000). A devastação desse bioma data dos tempos coloniais, onde o desenvolvimento do Brasil se deu principalmente ao longo da costa leste, local de ocorrência da Floresta Atlântica (FERRETTI e BRITEZ, 2006). Suas áreas atualmente somam no máximo 11,7% da extensão original (RIBEIRO et al*.,* 2009) e os principais remanescentes estão localizados na Serra do Mar e na Serra da Mantiqueira, regiões Sul e Sudeste do Brasil, onde o relevo acidentado dificultou o processo de ocupação (CAPOBIANCO, 2001). Uma das áreas remanescentes mais importantes está o litoral do estado do Paraná, na região da Área de Proteção Ambiental de Guaraqueçaba. Estas áreas apresentam grande continuidade de vegetação conservada, com mais de 300 mil hectares (Figura 1) (FERRETTI e BRITEZ, 2006).

Parte dessas áreas foi explorada com corte raso da vegetação nativa, muitas vezes utilizando o método coivara (LIEBSCH et al., 2008) e posterior uso para a agricultura de banana, mandioca, café e cana-de-açúcar, pastagens para criação de búfalos, além de áreas que sofreram com corte seletivo de espécies nativas comercializáveis, sendo o palmito-jussara (*Euterpe edulis* Mart.) o principal exemplo. Esses diversos níveis de interferência, frequentemente formam manchas intercaladas com regiões abandonadas, em processo de regeneração e em diferentes estágios sucessionais (CARDOSO, 2014). Neste contexto, estudos sobre os processos estruturadores de comunidades vegetais durante a sucessão secundária se tornam favoráveis nestas áreas. Identificar quais os fatores importantes para manejo dessas paisagens, podem intensificar a conservação e os esforços de restauração.

Neste trabalho avaliamos comunidades vegetais em um gradiente edáfico-sucessional em áreas da Floresta Atlântica no litoral do Paraná, com o objetivo de identificar os processos envolvidos na montagem de comunidades.

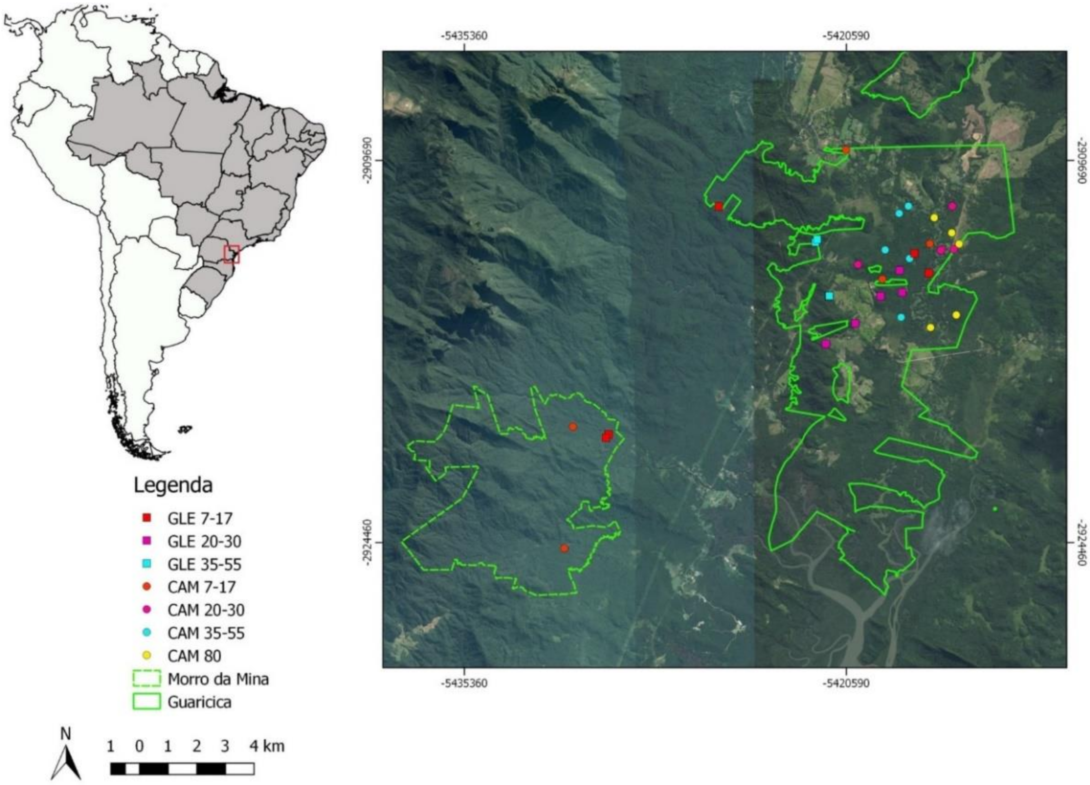

Figura 1. Localização das áreas de estudo em Antonina-Paraná, Sul do Brasil. Parcelas de diferentes idades (cores) e em dois tipos de solo (Cambissolos: quadrados; Gleissolos círculos), localizadas em duas reservas pertencentes à Sociedade de Pesquisa em Vida Silvestre e Educação Ambiental (SPVS).

REFERÊNCIAS BIBLIOGRÁFICAS

BAZZAZ, F.A. e PICKETT, S.T.A. Physiological ecology of tropical succession: a comparative review. **Annu. Rev. Ecol. Evol. Syst.** v.11, p.287-310, 1980.

BOUKILI, V.K. e CHAZDON, R.L. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. **Perspect. Plant Ecol. Evol. Syst.** v.24, p.37–47, 2016.

CARDOSO, F. A estruturação de comunidades vegetais em áreas sucessionais da Floresta Atlântica em diferentes tipos de solo. **Tese de doutorado** - Universidade Federal do Paraná, 2014

CAVENDER-BARES, J., KEEN, A. e MILES, B. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. **Ecology** v.87, p.109–122, 2006.

CHAZDON, R.L. Chance and determinism in tropical forest succession. In: **Tropical forest community ecology** (Eds. W. P. Carson & S. A. Schnitzer), Oxford, UK: Blackwell Scientific, p. 384–408, 2008.

CHESSON, P. Mechanisms of Maintenance of Species Diversity. **Annu. Rev. Ecol. Syst** v.31, p.343–66, 2000.

CLEMENTS, F.E. **Plant Succession: An Analysis of the Development of Vegetation.** Carnegie Institution of Washington, Washington, DC, 1916.

CLEMENTS, F.E. Natural and Structure of the Climax. **J. Ecol.** v.24, p.252-284, 1936.

CONNELL, J. H. e SLATYER, R. O. Mechanisms of succession in natural communities and their role in community stability and organization. **Am. Nat.** v.111, p.1119-1144, 1977.

CAPOBIANCO, J. P. R. (Org) Dossiê Mata Atlântica. **Instituto socioambiental.** São Paulo, 2001.

COWLES, H.C. The ecological relations of the vegetation on the sand dunes of lake Michigan. **Bot. Gazet.** v.27, p.361-391, 1899.

DRAKE, J. A. The mechanics of community assembly and succession. **J. Theor. Biol.** v.147, p.213–233., 1990.

EGLER, F.E. Vegetation science concepts I. Initial floristic composition – a factor in old-field vegetation development. **Vegetatio** v.4, p.412–417, 1954.

FERRETTI, A. R. e BRITEZ, R. M. Ecological restoration, carbon sequestration and biodiversity conservation: The experience of the Society for Wildlife Research and Environmental Education (SPVS) in the Atlantic Rain Forest of Southern Brazil. **J. Nat. Conserv.** v.14, p.249–259, 2006.

FOLEY, J. A.; DEFRIES, R.; ASNER, G. P.; BARFORD, C.; BONAN, G.; CARPENTER, S. R.; CHAPIN, F. S.; COE, M. T.; DAILY, G. C.; GIBBS, H. K.; HELKOWSKI, J. H.; HOLLOWAY, T.; HOWARD, E. A.; KUCHARIK, C. J.; MONFREDA, C.; PATZ, J. A.; PRENTICE, I.C.; RAMANKUTTY, N.; SNYDER, P. K. Global Consequences of Land Use. **Science** v.309, p.570-574, 2005.

FRICKE, E.C. e WRIGHT, S.J. Measuring the demographic impact of conspecific negative density dependence. **Oecologia** v.184, p.259–266, 2017.

GAUSE, G.F. The struggle for existence. **Williams and Wilkins**, Baltimore. 1934

GLEASON, H. A. The individualistic concept of the plant association**. J. Torrey Bot. Soc.** v.53, p.7-26, 1926.

GLENN-LEWIN, D.C.; MAAREL, E. VAN DER. Pattern and process of vegetation dynamics. In: **Plant Succession: theory and prediction**, Glenn-Lewin, D.C.; Peet, R.K.; Veblen, T.T. (Eds). Chapman & Hall. pp.11-59, 1992.

HARPER, J. L. e WHITE, J. The demography of plants. **Annu. Rev. Ecol. Syst.** v.5, p.419-463, 1974.

HUBBELL, S.P. Neutral theory in community ecology and the hypothesis of functional equivalence. **Funct. Ecol** v.19, p.166–172, 2005.

KEDDY, P. A. Assembly and response rules: Two goals for predictive community ecology. **J. Veg. Sci.** Uppsala, v. 3, n. 2, p.157-164, 1992.

KRAFT, N.J.B.; VALENCIA, R. e ACKERLY D.D. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. ***Science*** *v.322, p.580-582; 2008.*

LASKY, J.R., URIARTE, M., BOUKILI, V.K. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. **Proc. Natl. Acad. Sci.** v.111, p.5616–5621, 2014.

LEBRIJA-TREJOS, E.; PÉREZ-GARCÍA, E.A.; MEAVE, J.A.; BONGERS, F.; POORTER, L. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. **Ecology** v.91, p.386–398, 2010.

LETCHER, S.G., CHAZDON, R.L., ANDRADE, A.C.S., BONGERS, F., VAN BREUGEL, M., FINEGAN, B., LAURANCE, S.G., MESQUITA, R.C.G., MARTÍNEZ-RAMOS, M., WILLIAMSON, G.B. Phylogenetic community structure during succession: Evidence from three Neotropical forest sites. **Perspect. Plant Ecol. Evol. Syst.** v.14, p.79–87, 2012.

LIEBSCH, D.; GOLDENBERG, R.; MARQUES, M. C. M. Florística e estrutura de comunidades vegetais em uma cronoseqüência de Floresta Atlântica no Paraná. **Acta Bot. Brasilica** v.21, n.4, p.983-992, 2007.

LOREAU, M. Biodiversity and ecosystem functioning: a mechanistic model. **Proc. Natl. Acad. Sci**. v.95, p.5632–5636, 1998.

MALTHUS, T.R. An essay on the principle of population. **J. Johnson,** London, 1798.

MARGALEF, R. On certain unifying principles in ecology. **Am. Nat.,** v.97, p.357-374, 1963.

MEINERS, S. J., Cadotte, M.W., Fridley, J.D., Pickett, S.T.A., Walker, L.R. Is successional research nearing its climax? New approaches for understanding dynamic communities. **Funct. Ecol.** v.29 p.154–164, 2015.

MELLO, J. M., COUTO, E.G., AMORIM, R.S.S., CHIG, L.A., JOHNSON, M.S., LOBO, F.A. Dinâmica dos atributos físico-químicos e variação sazonal dos estoques de carbono no solo em diferentes fitofisionomias do pantanal norte mato-grossense. **Rev. Árvore**, Viçosa, v. 39, n. 2, p. 325-336, Apr. 2015.

MIRANDA, J.C. Sucessão ecológica: conceitos, modelos e perspectivas. **Rev. Saúde e Biol.,** v.4, n.1, p 31-37, Jan/Jun 2009

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., da FONSECA, G.A., KENT, J. Biodiversity hotspots for conservation priorities. **Nature** v.403, p.853–858, 2000.

NUCHE, P. e ALADOS, C.L. Shrub interactions drive vegetation succession of subalpine grasslands under two climatic conditions. **J. Plant Eco.** v. p.1-11, Jan 2017.

RIBEIRO, M. C. METZGER, J.P., MARTENSEN, A.C., PONZONI, F.J., HIROTAET, M.M. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biol. Conserv.** v.142, p.1141–1153, 2009.

ODUM, E.P. The strategy of ecosystem development. **Science** v.164, p.262-270, 1969.

OLIVEIRA, M. C. e JÚNIOR, M. C. S. Evolução Histórica Das Teorias De Sucessão Vegetal E Seus Processos. **CEPPG** v.24, p.104-118, 2011.

PICKETT, S.T.A. Succession: an evolutionary interpretation. **Am. Nat.** v.110, p.107-119, 1976.

PICKETT, S.T.A., CADENASSO, M.L., MEINERS, S.J. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. **App. Veg. Sci.** v.12, n.1, p.9-21, february 2009.

PIQUERAS, M.M. e BRANDO, F.R. As contribuições do americano Henry Allan Gleason (1882-1975) para a Ecologia no início do século XX. **História da Ciência e Ensino**, v.13, p. 48-68, 2016.

REES, M.C.R. Long-Term Studies of Vegetation Dynamics. **Science** v.293, n.5530, p.293-650. Jul, 2001.

ROBINSON, S.J.B., BERG, E., MEIRELLES, G., OSTLE, N. Factors influencing early secondary succession and ecosystem carbon stocks in Brazilian Atlantic Forest. **Biodivers. Conserv.** v.24, p.2273–2291, 2015.

TANSLEY, A.G. The use and abuse of vegetational concepts and terms. **Ecology** v.16, p.284-307; 1935.

TILMAN, D. REICH, P.B. KNOPS, J. WEDIN, D. MIELKE, T. & LEHMANN, C. Diversity and productivity in a long-term grassland experiment. **Science** v.294, p.843–845, 2001.

VAMOSI, S.M., HEARD, S.B., VAMOSI, J.C. & WEBB, C.O. Emerging patterns in the comparative analysis of phylogenetic community structure. **Mol. Ecol**. v.18, n.4, p.572-592, Nov. 2009.

VAN ANDEL, J., BAKKER, J.P., GROOTJANS A. P. Mechanisms of Vegetation Succession: a review of concepts and perspectives. **Acta Bot. Neerlandica** v. 42, n. 4, p. 413-433, Dec., 1993.

VAN BREUGEL, M., BONGERS, F., MARTÍNEZ-RAMOS, M. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. **Biotropica** v. 35, p. 610–619, 2007.

VOLTERRA, V. Fluctuations in the abundance of a species considered mathematically. Nature v.118, p.558-60, 1926. In Real, L. A.; Brown, J. H. **Foundations of ecology – classic papers with commentaries.** The University of Chicago Press, 1991.

WHITTAKER, R. A consideration of climax theory: the climax as a population and pattern. **Eco. Monog.** v.23, p.41-78, 1953.

CAPÍTULO 1

Determinism in tree turnover along the succession of a tropical forest[1]

---

[1] Artigo formatado de acordo com as normas da revisa OIKOS

Determinism in tree turnover along the succession of a tropical forest

Anamaria Cequinel, Vinicius Marcilio-Silva, Elivane S. Capellesso, Fernanda C. G. Cardoso, Márcia C. M. Marques

Abstract: *Abstract:* During forest succession, changes in species composition and individual turnover may be affected by deterministic and stochastic processes. In this study, we used both population and community approaches to assess the relative effects of deterministic and stochastic processes along the secondary succession of a tropical forest. Based on an analysis of proxy factors of biotic and abiotic filtering on demography, we aimed to identify the drivers that structured the communities. We assessed the demography (recruitment and survival rates) of trees occurring in an edaphic-successional gradient (forests aged 7-17, 20-30, 30-55, and >80 years; two soil types) of regenerating forests in southern Brazil. We first tested for stochasticity by building null models (randomizing species composition and abundance) for each forest age interval. The composition and abundance of plants in all communities differed from the expected results of the null models, indicating determinism. We then used a model selection approach (AICc) to assess the relative importance of environmental filtering (indirectly measured by soil type and forest age) and species interactions (measured by basal area, individual density, and taxonomic, functional, and phylogenetic diversity) to predict recruitment, survival, and individual and species turnover rates. We found that both abiotic and biotic filtering affected the community assembly in a successional gradient. Environmental filtering (possibly via soil stress and limitations related to structural complexity) seemed to be more important for recruitment, survival, and individual turnover. Biotic filtering (possibly via density dependency, competitive ability and niche complementarity) was more important for survival, recruitment and species turnover. The drivers in which the filtering affected demography and species turnover were very distinctive, indicating that community assemblage during succession is the result of a multi-factor process acting on individual and species turnover. Our results add some important findings on the successional theory, by disentangling the multi-factors acting temporarily in community assembly.

Keywords: Atlantic Forest; chronosequence; demography; functional diversity; phylogenetic diversity; recruitment; regeneration; restoration; survival.

Introduction

Although succession is one of the oldest ecological theories (Cowles 1899), determining which factors affect the changes in plant species composition over time is still a challenge for ecologists (Sutherland et al. 2013). The recent ideas of succession as a community assembly in progress (Lebrija-Trejos et al.

2010) have improved the applicability of successional theory because understanding the processes that determine species turnover can be a tool for assessing assembly mechanisms (Meiners et al. 2015). Furthermore, the knowledge of assembly structuring mechanisms is also essential for restoration activities, biodiversity conservation, and mitigation of problems caused by climate change (McGill et al. 2006, Chazdon 2008).

In the plant community assembly, both deterministic (Clements 1916) and stochastic (Gleason 1926) processes affect species turnover along the succession gradient (Chazdon 2008; Swenson & Enquist 2009). In the deterministic process, the ability to establish in an area depends on the resource use of each species (Chesson 2000). In this context, if a given species does not fit the environmental conditions and is restricted from establishing, this can be considered an abiotic filter; establishment restrictions due to local interactions can be considered a biotic filter (Webb 2000; Cavender-Bares et al. 2006). In stochastic processes, all individuals are considered ecologically equivalent; the establishing in a given area depends only of dispersal limitation and random events (Hubbell 2001). Both deterministic and stochastic processes can act individually or synergistically in structuring communities (Kraft et al. 2008; Swenson & Enquist 2009). Determining whether these processes are driving the community assembly and quantifying their relative importance are essential steps for understanding the patterns of biodiversity in natural and altered environments (Cavender-Bares et al. 2004).

These processes in along the community assemblage act differently depending on the ecological scale studied (Morris 1987); these different effects can be assessed through species demography (Lasky et al. 2014b). Individual recruitment and survival can reflect the performance of species that shape the population dynamics (Violle et al. 2012) and, ultimately, the stochastic and deterministic events acting on communities (Hubbell 2001; Rees 2001; Condit et al. 2006). Additionally, the change in composition of communities through the turnover of individuals and species (considered migrations) can reveal the distribution of abundances and permanence of populations in the communities over time (Swenson et al. 2012). Thus, this coupled population-community approach might reveal how specific drivers affect the dynamics of communities during succession.

The habitat characteristics and the elements of the community structure along the succession gradient can be used as proxies to analyse the feedback between vegetation–environment and vegetation interactions (Lebrija-Trejos et al. 2010). Among the environmental filters that act in community assemblies along successional gradients, soil characteristics, such as drainage and nutrient availability, can restrict the establishment of several species (Ulrich et al. 2014; Robinson et al. 2015). Additionally, forest age can be used as a proxy for the change in structural complexity, linked to light limitation, and potentially affects plant growth and survival (Bazzaz & Picket 1980; van Breugel et al. 2006). In addition, the performances of individuals and species populations are determined by biotic interactions, such as density-dependence processes (e.g., self-thinning) and limited similarity. Density-dependent factors prevent excessive population growth that could lead to resource (nutrients, light, space, etc.) disputes and are mediated by the density of individuals (Fricke & Wright 2017). Additionally, the similarity between individuals and between species leads to limitations on their coexistence (Chesson 2000) and niche complementarity (Loreau 1998). Both processes are usually assessed using community characteristics, such as basal area (Lasky et al. 2014a), individual density and taxonomic diversity (at the individuals/species level) (Macarthur and Levins 1967), phylogenetic diversity (at the clades level) (Webb et al. 2002), and functional diversity (at the functional groups level) (Tilman et al. 1997), as proxies. The basal area and individual density and taxonomic diversity are classical structural metrics that can measure direct plant-plant interactions and are reflected in the coexistence patterns of species and individuals (Aakala et al. 2013; Cui & Zheng 2016). In contrast, functional and phylogenetic dispersion can be related to interactions between species and provide insights on the impacts of the ecological processes in terms of evolutionary history and community functioning (Chalmandrier et al. 2015).

The natural regeneration of tropical forests provides an ideal system to assess the vegetation dynamics and community assembly during succession (Kraft et al. 2008; Letcher et al. 2012). Natural interference often triggers regeneration and successional processes, but anthropogenic actions have been major causes of disturbance and fragmentation of tropical forests (Chazdon 2008). In southern Brazil, the Atlantic Forest encompasses a mosaic of conserved areas (~68% of total area) interspersed with abandoned pastures, where natural regeneration led to areas in different successional stages (Cardoso 2014). Previous studies in the region have shown that the regeneration of these abandoned pastures is relatively fast (Cheung et al. 2010, Zwiener et al. 2014) and is positively affected by the forested landscape (Kauano et al. 2012). In this region, dispersal limitation is less important (Cheung et al. 2010), and other deterministic and/or stochastic factors affect species turnover and community assembly. Thus, studies targeting the community-structuring dynamics of secondary succession in the southern Atlantic Forest can provide important information about the theories associated with community structuring while also providing important information that can be used for the conservation, management, and restoration of these systems.

In this study, we assessed the demographic rates along a successional and edaphic gradient in the Atlantic Forest. Based on an analysis of proxy factors of biotic and abiotic filtering on demographic rates, we aimed to identify the processes that aid in structuring the communities along the secondary succession. As such, we developed the following hypotheses. 1) If stochastic effects are primarily responsible for structuring communities during succession, demography will not be determined by interactions between species or between species and the environment. Thus, the observed community patterns should not differ from random expectations (Figure 1). 2) If deterministic processes affect assemblages, there will be a relationship between the abiotic (forest age and soil type) and biotic filters (taxonomic, phylogenetic and functional diversities, basal area, and individual density) and the demographic rates during succession (Figure 1). Therefore, the younger forests with more restrictive soils should present greater environmental filtering, leading to lower taxonomic, phylogenetic and functional diversity values and higher rates of species and individual turnover.

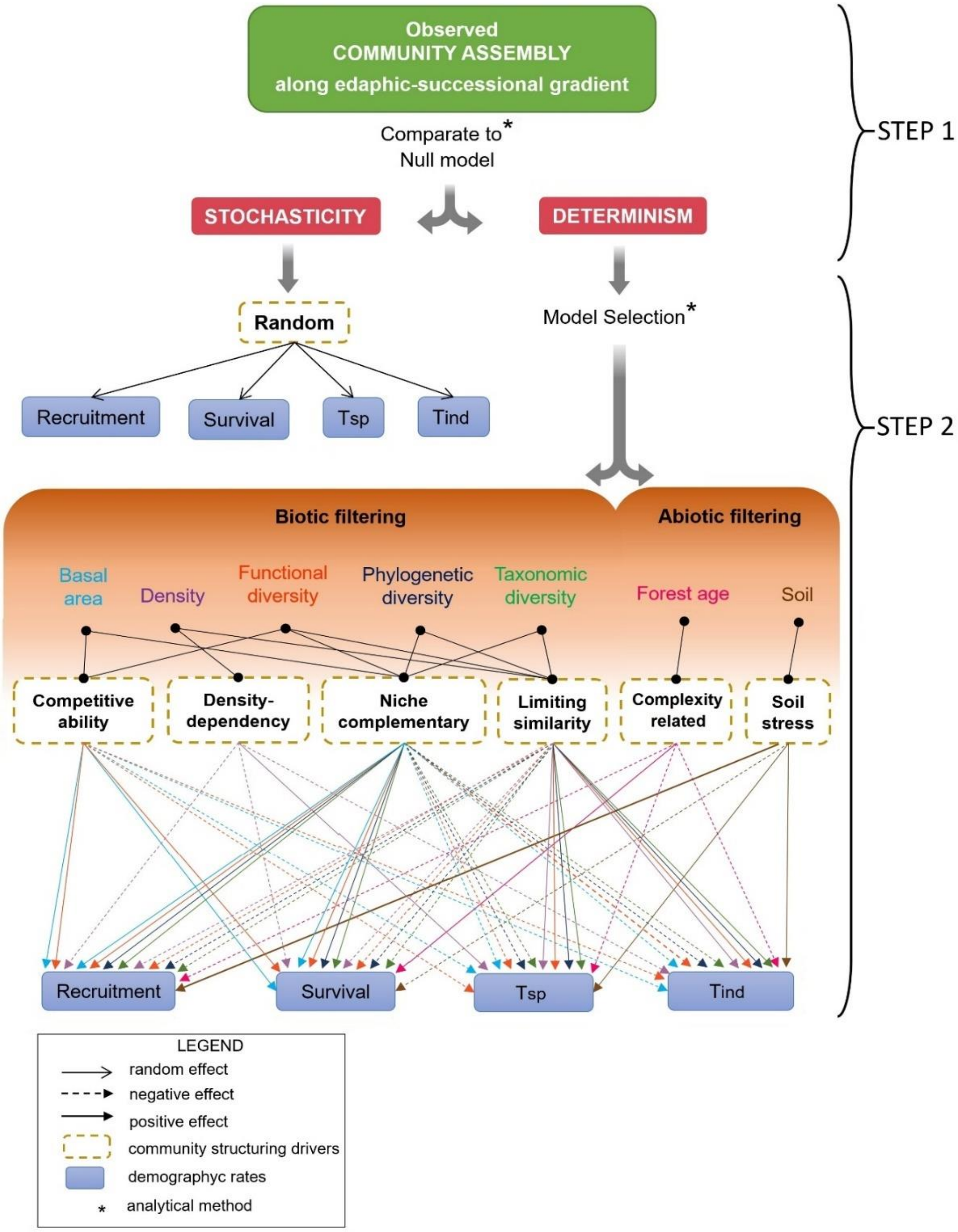

Figure 1. Conceptual and analytical framework of factors affecting community assembly along the edaphic-successional gradient. The demographic rates survival, recruitment, individual turnover (T_{ind}) and species turnover (T_{sp}) express the structuring mechanisms of community assemblages. In the Step 1 the observed communities are tested for stochasticity. If the observed community is not different from the null model, stochasticity is assumed, and species are randomly assembled, affecting demography. If the observed community differs from the null model, determinism is assumed and the Step 2 is followed: through a model selection approach, the variables related to biotic filtering (basal area, density, functional diversity, taxonomic diversity, phylogenetic diversity) and abiotic filtering (soil constrains, forest age gradient) are used to infer mechanisms affecting demography and community assembly.

Material and Methods

Study area

The Atlantic rain forest is a hotspot for biodiversity conservation, characterized by high plant and animal species richness, high levels of endemism, and high levels of threat (Myers et al. 2000). The Atlantic Forest currently encompasses only ~11% of its original area (Ribeiro et al. 2009). The devastation of this forest dates back to colonial times, when Brazil's development occurred mainly along the eastern coast, in the Atlantic Forest region (Ferretti & Britez 2006). The study area is specifically located in the dense rain forest (one of the Atlantic Forest formation types), which extends through the states of Rio de Janeiro, São Paulo, Paraná and Santa Catarina (IBGE 2012).

The studied region is part of the Guaraqueçaba Environmental Protection Area, with more than 300,000 ha, and is considered one of the most important remaining areas of the Atlantic Forest in Brazil (Ferretti & Britez 2006). The data were collected in two protected areas within this region, the *Guaricica* Natural Reserve and the *das Águas* Natural Reserve, both owned by the non-governmental organization Society for Wildlife Research and Environmental Education (SPVS). The climate in the region is humid subtropical, with an average annual temperature range between 20.8 °C and 22 °C, and the annual rainfall varies from 3,300 to 3,450 mm, with no defined dry season (Ferretti & Britez 2006).

In these reserves, there are four different types of soils: Acrisol, Fluvisol, Gleysol, and Cambisol. The study was restricted to areas with Cambisols and Gleysols, as they present contrasting characteristics and are abundant in the region (Martins et al. 2015). Cambisols are soils composed of mineral material, have an incipient B horizon, are non-hydromorphic, have variable fertility, and are frequently found on the slopes of mountains. Gleysols are composed of mineral material, have variable fertility, are hydromorphic, and are permanently or periodically saturated with water (Cardoso et al. 2012; Supplementary material Appendix 1 Table A1). In this way, Gleysols can be considered to cause more stress on trees than Cambisols.

In these reserves, forest areas (~30% of total) were converted into pasture and used for 20-30 years for buffalo ranching; then, the areas were abandoned at different periods over the last 80 years. In general, these forested areas were not disturbed among the last ~30 years, except in some regions where selective logging was detected. We used photography overlapping and interviews with locals to select areas where ranching activities were abandoned at different times to build a chronosequence.

Sample design and data collection

We conducted this study in permanent plots where the vegetation has been studied since 2010 (Cardoso 2014). A total of 35 circular plots (14 m radius, 616 m2 each plot), including 2.18 ha of second-growth forests (resulting from natural regeneration), were previously delimited (Borgo 2010). Of these forests, 20 were in Cambisol areas with abandonment ages ranging from 7 to 80 years, and 15 were in Gleysol areas aged between 7 and 55 years. Because Gleysols are distributed in lowland areas where forests were logged more intensively, there were no plots in areas aged older than 55 years for this soil type. Therefore, we built an edaphic-successional gradient (chronosequence) composed of areas representing four age classes (7-17, 20-30, 35-55 and >80 years) and two soil classes (Gleysol and Cambisol).

In each plot, we sampled all woody plant individuals with diameter at breast height (DBH) ≥5 cm. Each plant was tagged, had its DBH measured, and was identified at the species level in both 2010 and 2016. In the 2016 survey, we classified the individuals as survivors (successfully sampled in both 2010 and 2016), dead (sampled in 2010 but not located or dead in 2016), or recruits (sampled only in 2016).

Forest community structure

In order to analyze if the structure of the communities, related with biotic filters, affect the plant demography during the communities assemblage (Fig.1 Step 2), we calculated species richness (hereafter taxonomic diversity - Tdiv), individual density, and basal area of each plot (community) in the edaphic-successional gradient in each period (2010 and 2016). Comparison between soil types, forest ages, and surveys (2010-2016) were performed using a factorial ANOVA in R (R Development Core Team 2016).

Phylogenetic diversity

We considered phylogenetic diversity as a factor possibly affecting demography, related with biotic filters, acting in community assembly during the succession (Fig.1 Step 2). Thus, we followed a standard protocol to calculate the phylogenetic relationship among species. First, we built a phylogenetic relationship tree for the pool of woody species occurring in the region. We compiled a comprehensive checklist from previous studies in the region (Borgo 2010; Cardoso 2014), resulting in 435 tree species. Then, we obtained the phylogenetic relationship among these species by using the megatree R20120829mod, proposed by Gastauer & Meira-Neto (2016) and the Phylomatic algorithm implemented in the software Phylocom (Webb & Donoghue 2005). The tree nodes were dated based on estimated minimum age for genus, family and order from fossil data of Bell et al. (2010). In this method, undated nodes are equally spaced between dated nodes by the algorithm BLADJ (branch length adjustment) in the Phylocom environment (Webb & Donoghue 2005). The resulting phylogenetic tree is available in the Supplementary material Appendix 2.

Using our phylogenetic tree, we calculated the mean phylogenetic pairwise distance (MPD; in the Phylocom environment) among species for each plot for the 2010 survey. MPD (hereafter Pdiv) measures the average length of branching in the tree between each pair of taxon in a sample; it is an important metric of phylogenetic diversity because it provides an overall value of the community phylogenetic structure (Webb 2000; Webb et al. 2002). We compared the average Pdiv among communities in the edaphic-successional gradient (i.e., between soil types and forest ages) using a factorial ANOVA implemented in R (R Development Core Team 2016).

Functional diversity

To test whether function diversity affects demography, related with biotic filters, acting in community assembly during the succession (Fig. 1 Step 2), we selected eight reproductive and vegetative traits related to plant competitive ability, reproductive success and photosynthesis, as suggested by Pérez-Harguindeguy et al. (2013) (Supplementary material Appendix 3 Table A1). All species in each plot had their traits collected in the field, herbarium material or literature (see Supplementary material Appendix 3 Table A1).

To calculate functional diversity, we used the quadratic entropy of Rao, using the ‘FD’ package (Laliberté et al. 2015) for R (R Development Core Team 2016). Similar to Pdiv, the Rao’s *Q* (hereafter Fdiv) incorporates both the relative abundances of species and a measure of the pairwise functional differences between species (Rao 1982, Botta-Dukát 2005). We compared the average Fdiv among communities in the edaphic-successional gradient (i.e., between soil types and forest ages) using a factorial ANOVA implemented in R (R Development Core Team 2016).

Demographic rates

In order to assess the species and individuals performance in a gradient edaphic-successional, expressing the structuring mechanisms of community assemblages (Fig.1), individual records from 2010 and 2016 were used to calculate the annual survival (S_i) and recruitment (R_i) rates for each species in each plot. The annual survival rate was calculated from the following formula (based on Sheil et al. 1995):

$$S_i = \left(\frac{N_{i1} - N_{i0}}{N_{i1}}\right)^{1/t}$$

where N_{i0} and N_{i1} are, respectively, the number of individuals of the species *i* at the beginning and at the end of the time interval *t* (6 years). The annual mortality rate (*M*) was assumed to be the opposite of the survivor rate and was calculated as 1- S_i.

The annual recruitment rate was calculated from the following formula (Burslem et al. 2000):

$$R_i = 1 - \left(\frac{1 - n_{ir}}{N_{it}}\right)^{1/t}$$

In this calculation, n_{ir} is the number of recruits of the species *i*, and N_{it} is the number of individuals of species *i* present at the end of the time interval *t* (6 years).

We calculated the turnover of species and individuals (T_{sp}) for each plot using the formula suggested by Diamond & May (1977):

$$T_{sp} = \frac{l + g}{(S_1 + S_2)t}$$

In this formula, l is the number of extinct species at a given plot; g is the number of immigrant species; S_1 and S_2 are the total number of species in the 2010 and 2016 surveys, respectively; and t the 6-year time interval. Thus, despite an irregular demographic rate, T_{sp} was used to estimate the rate of species substitution during succession.

We also calculated individual turnover (T_{ind}), a numerical percentage expression of mortality and recruitment rates that expresses the individual substitution in the community during a given time interval. The T_{sp} formula above was then adapted to incorporate the individual substitution, as follows:

$$T_{ind} = \frac{M + R}{\left(\frac{N_1 + N_2}{2}\right)t}$$

where N_1 and N_2 are the total number of individuals in the 2010 and 2016 surveys, respectively, and t is the 6-year interval.

Null models

To analyse the possible effects of stochasticity during the structuring of community assemblages, we constructed a null model (Step 1, Fig. 1). Our null model constructed hypothetical communities at random based on a given species list (the total species occurring along the sampled gradient) and abundance range (minimum and maximum abundance values observed). We limited the abundance of each of the hypothetical communities by randomly selecting it from the abundance range. We generated 999 random communities for each age class using the independent swap algorithm (Gotelli 2000) implemented in the package ‘picante’ (Kembel et al. 2010). The independent swap algorithm restricts the row and column of the species abundance matrix while distributing species among communities using observed species occurrences in each age class. We used the ‘spaa’ package (Zhang 2016) for converting the species list into a matrix, where the rows of the output matrix are the sites (communities) and the columns are the species. The R script for the null models is presented in Supplementary material Appendix 4.

We compared null and observed communities (species composition) by Mantel tests using the ‘vegan’ package (Oksanen et al. 2017). For this comparison, we randomly selected 10 null communities (from the 999) and performed the test with the observed communities (a total of 10 per forest age), repeating the test 99 times. We calculated the mean and the standard deviation values of all 99 tests. All analyses were performed in R (R Development Core Team 2016).

Model selection

To understand the relative effects of environmental filters and species interactions on demographic rates in studied successional communities, we performed a model selection approach (Step 2, Fig. 1). This approach, based on maximum likelihood assessments, searches and selects the predictive variables that best explain the response variable (Burnham & Anderson 2002). In all models, we used the demographic rates (recruitment, survival, turnover of species and turnover of individuals) as response variables. As predictive variables, we used parameters directly and indirectly related to environmental filters (forest age and soil types) and species interactions (species richness, phylogenetic diversity, functional diversity, individual density, and basal area, calculated from the 2010 survey). Forest age was considered a proxy of the structural complexity in the successional gradient that is related to several environmental conditions that change along the succession, including conditions such as light availability, temperature, and air humidity (Bazzaz & Picket 1980). Thus, we considered forest age a structural complexity related to these environmental conditions. The two soil types indirectly reflect the stress caused by periodical water excess (in Gleysols). Individual density can reflect the negative effects of density dependence (Fricke & Wright 2017), and when combined with basal area, Tdiv, Fdiv and Pdiv reflect the biotic interactions that can influence the exclusion or coexistence of individuals of the same species, clades or functional groups (Webb et al. 2002, Lasky et al. 2014a). However, basal area also may reflect competitive ability (Goldberg 1990).

Model selection was performed using the ‘MuMIn’ package (Barton 2016). The package ‘AICcmodavg’ was used to select the most parsimonious models based on the smallest Akaike Information Criterion (AICc), corrected for small samples (Hurvich & Tsai 1989; Burnham & Anderson 2002). Models with ΔAICc ≤2 (the difference between AICc of the best model selected with the other models) were also accepted, highlighting their weight of evidence (AICcw)

(Burnham & Anderson 2002). To check for multi-collinearity, we calculated the variance inflation factor (VIF) using the ‘car’ package (Fox et al. 2016); variables with VIF≥5 were considered multicollinear, which makes them more worrisome values (Krebs et al. 2012).

We also calculated the importance of each predictor variable measured across all models (Burnham & Anderson 2002) using the Akaike weights (AICcw), which describe the weight of evidence for a given model to be the best explanatory model from the model set included in analysis. Therefore, the importance of each predictor variable is measured by the sum of Akaike weights of models that include one variable. From this calculation, the greater the importance value of a model with a specific predictor variable is, the greater the importance of this variable (Burnham & Anderson 2002). Variables with relative values above >0.5 were considered important (Pasinelli et al. 2007). All analyses were performed in R (R Development Core Team 2016).

Results

The total individual density, taxonomic diversity (Tdiv), and basal area in plant communities varied in the six-year period along the edaphic-successional gradient. There was greater Tdiv in forests aged 35-55 y and >80 y, higher densities in forests aged 20-30 y, and a gradual increase in basal area with forest age (Supplementary material Appendix 5 Table A1; Supplementary material Appendix 5 Fig. A1). In general, there was an increase (or small decreases) in individual density, Tdiv and basal area along the succession (Supplementary material Appendix 5 Table A1).

The phylogenetic diversity (Pdiv) increased along the gradient for both soils (Supplementary material Appendix 5 Fig. A2a), with Pdiv of older areas (≥ 35-55 y) approximately 20% higher than that of younger areas (7-17 y). The amplitude of Pdiv values was higher in Gleysols than in Cambisols (Supplementary material Appendix 5 Fig. A2a). The functional diversity (Fdiv) presented no clear pattern, with higher values at the beginning and at the end of the successional gradient in Cambisols, while Fdiv values in Gleysols tended to increase (Supplementary material Appendix 5 Fig. A2b).

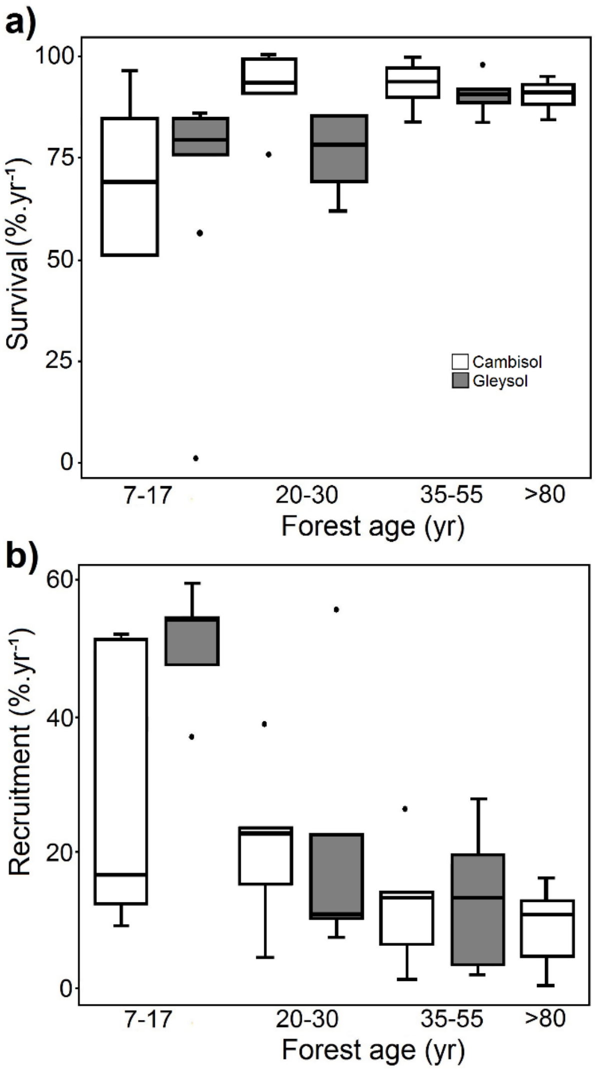

Figure 2. Boxplot of survival (a) and recruitment (b) annual rates (%) of trees occurring along edaphic-successional gradient in Southeastern Brazilian Atlantic Forest, for the period of 2010-2016.

Demography

In general, there was high individual survival (average: >60%) along the successional gradient in both soil types (Fig. 2a). Survival rates were lower in young forests (7-17 y) but displayed an increasing trend in 20-30 y, 35-55 y and >80 y forests in both soils (Fig. 2a). There was individual recruitment in all forests along the gradient (average: 9-51%). Communities in young forests (7-17 y) and with Gleysols presented higher rates of individual recruitment, while the lowest rates were in forests >80y (Fig. 2b).

In general, individual turnover (average: 6-25%) was much higher than species turnover (average: 3-7%) along the edaphic-successional gradient (Fig.s

3a, 3b). Additionally, Gleysols presented the highest turnover rates in forests of all ages. The individual turnover rate was much higher in young forests (7-17 y) for both soils, decreasing gradually along the successional gradient (Fig. 3a). The species turnover rate presented no clear pattern; the values were relatively constant along the gradient (Fig. 3b).

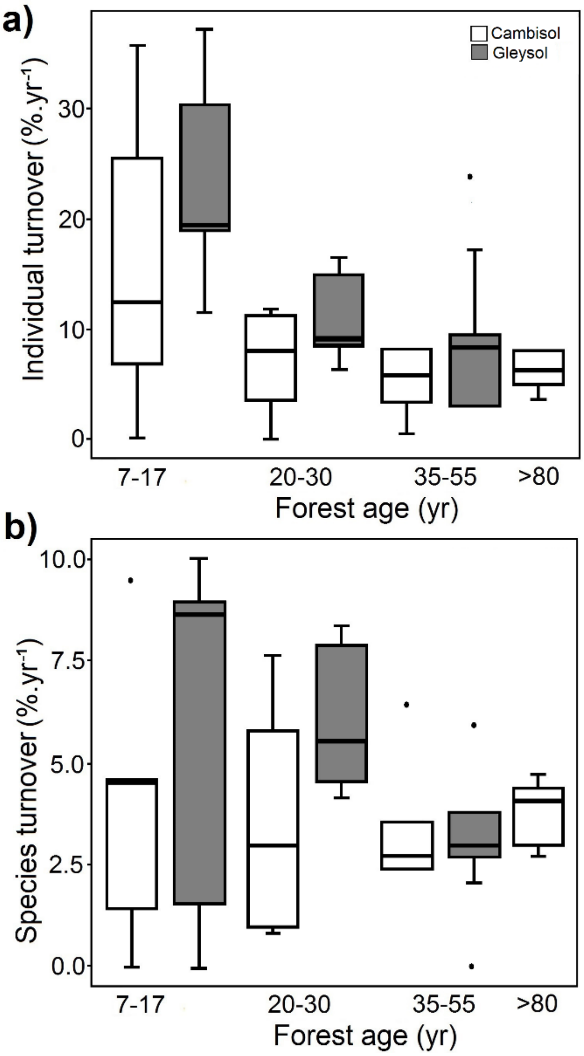

Figure 3. Boxplot of the turnover of individuals (a) and species (b) along an edaphic-successional gradient, for the period of 2010-2016. Note the differences in y axes between the two figures.

Null communities

There were no significant correlations between the observed and expected (by null model) species assemblages (all forest ages P>0.05; Table 1). This result reveals that the composition of observed assemblages differed from the expected assemblages simply by chance, indicating the absence of stochasticity in the community assemblies during succession.

Table 1. Mantel statistic based on Pearson's product-moment correlation (*r*) between the observed and expected (by null model) community composition. Mean and standard deviation of the 99 tests. *P*>0.05 reveals that predicted and observed assemblies are not correlated.

	r	***P***
07-17	0.004±0.20	0.50±0.28
20-30	0.007±0.16	0.49±0.31
35-55	-0.009±0.21	0.50±0.29
>80	0.04±0.34	0.48±0.28

Model selection

The factors affecting survival and recruitment were explained by three and two models, respectively (Supplementary material Appendix 6 Table A1). The best models explaining survival included basal area, Pdiv, Fdiv, forest age and soil, which were, in general, positively related to survival (Supplementary material Appendix 6 Table A1 and Fig. A1). The best models explaining recruitment included individual density and forest age, which were negatively related to recruitment (Supplementary material Appendix 6 Table A1 and Fig. A2). The individual turnover and species turnover rates were explained by nine and one selected model(s), respectively (Supplementary material Appendix 6 Table A1). The best models explaining individual turnover included all of the predictive variables, except for Pdiv; only soil was positively related to individual turnover (Supplementary material Appendix 6 Table A1 and Fig. A3). The model selected for species turnover included only Pdiv (Supplementary material Appendix 6 Table A1) which was negatively related to species turnover (Supplementary material Appendix 6 Fig. A4).

Considering the variables with highest importance (relative variable importance >0.50), survival was predicted by basal area, functional, phylogenetic and taxonomic diversities (biotic filtering), and forest age (abiotic). Recruitment was mainly predicted by forest age (a proxy of abiotic filtering) and by density (biotic filtering). Individual turnover was predicted by soil (abiotic filtering), and species turnover was predicted by phylogenetic diversity (biotic filtering) (Table

2; Figure 4).

Table 2. Relative variable importance for models of the predictive variables affecting demographic rates, in an edaphic-successional gradient. In bold, highest values of importance. T_{sp} = species turnover and T_{ind} = individual turnover. BA = basal area; Den = individual density; Pdiv = Phylogenetic diversity (MPD); Fdiv= Functional diversity (Rao); Tdiv = Taxonomic diversity (richness); Soil = soil type; Age = Forest age.

Predictive variables	*Response variables*			
	Recruitment	Survival	T_{ind}	T_{sp}
BA	0.35	**0.99**	0.34	0.23
Den	**0.59**	0.21	0.29	0.2
Pdiv	0.29	**0.58**	0.23	**0.64**
Fdiv	0.29	**0.58**	0.26	0.25
Tdiv	0.25	**0.67**	0.46	0.4
Soil	0.26	0.30	**0.59**	0.19
Age	**0.84**	**0.58**	0.26	0.21

Discussion

In this study, we explored the effects of structuring mechanisms on demographic rates and community assembly along a successional gradient. We found evidence of determinism in structuring plant communities. As expected in our hypotheses, the deterministic processes acted differently along the successional gradient, where environmental filtering was more important in determining recruitment and turnover of individuals, while biological filters were more important for determining species survival and species turnover. Considering that succession is an ecological theory of expansion (Miners et al. 2015), our results add some important findings to this theory by disentangling the multi-factors acting temporally on community assembly.

Demography

The high demographic rates found in this study (survival >60% and recruitment >9% per year) are a recurring pattern in tropical forests (Phillips et al.

2004), where productivity is accelerated in stable climates (Phillips 1994). Additionally, the increasing survival rates and decreasing recruitment rates along the successional gradient were previously observed (van Breugel et al. 2006; Lebrija-Trejos et al. 2010). This pattern results in communities gradually becoming more abundant, with more individuals and species but lower dynamics along successions with less turnover, which can be related to a trajectory trending towards equilibrium (Phillips et al. 2004).

The patterns of individuals and species turnover contrasted throughout the successional gradient, with higher rates of individual substitution than species substitution. Additionally, the individual turnover was greater in the early years of succession, while the species turnover was approximately constant during the succession. Communities at the beginning of the successional process are dominated by populations of short-lived species (Chazdon 2008) that are continually renewed, keeping high individual turnover rate. The species turnover occurs at a lower rate, and as the successional process continues, new species are progressively incorporated into the community. Thus, substitution of individuals can be redistributing the abundances among species, leading to species accumulation consequently increasing the community diversity (Phillips et al. 1994, Norden et al. 2012).

Succession as a deterministic process

We found evidence of determinism, but no stochasticity, in community assemblages during succession. Empirical evidence of determinism as the dominant process driving tropical forest community assemblies during succession is rare; synergic effects of deterministic and stochastic processes are much more common (Svenning et al. 2004, Norden et al. 2015). In beginning of succession, random events of seed dispersal affect the assembly of communities (Chazdon 2008), as our results from individuals turnover. After these events, stochasticity seems to have no effect and the successional process is probably more directional and predictive (Clements 1916), determined by biotic and abiotic interactions.

In our study, we used a coupled population-community approach to infer how the communities are assembled over time. From this approach, each successional phase along the gradient should be a predictable assembly of species ruled by environmental filtering and by multiple biotic interactions; despite this, stochastic events such as storms, droughts, floods, and diseases, which frequently occur in tropical areas (Feeley et al. 2011), can potentially shape the environment (by changing resources and conditions) and biotic interactions, ultimately affecting the deterministic assemblies of the succession.

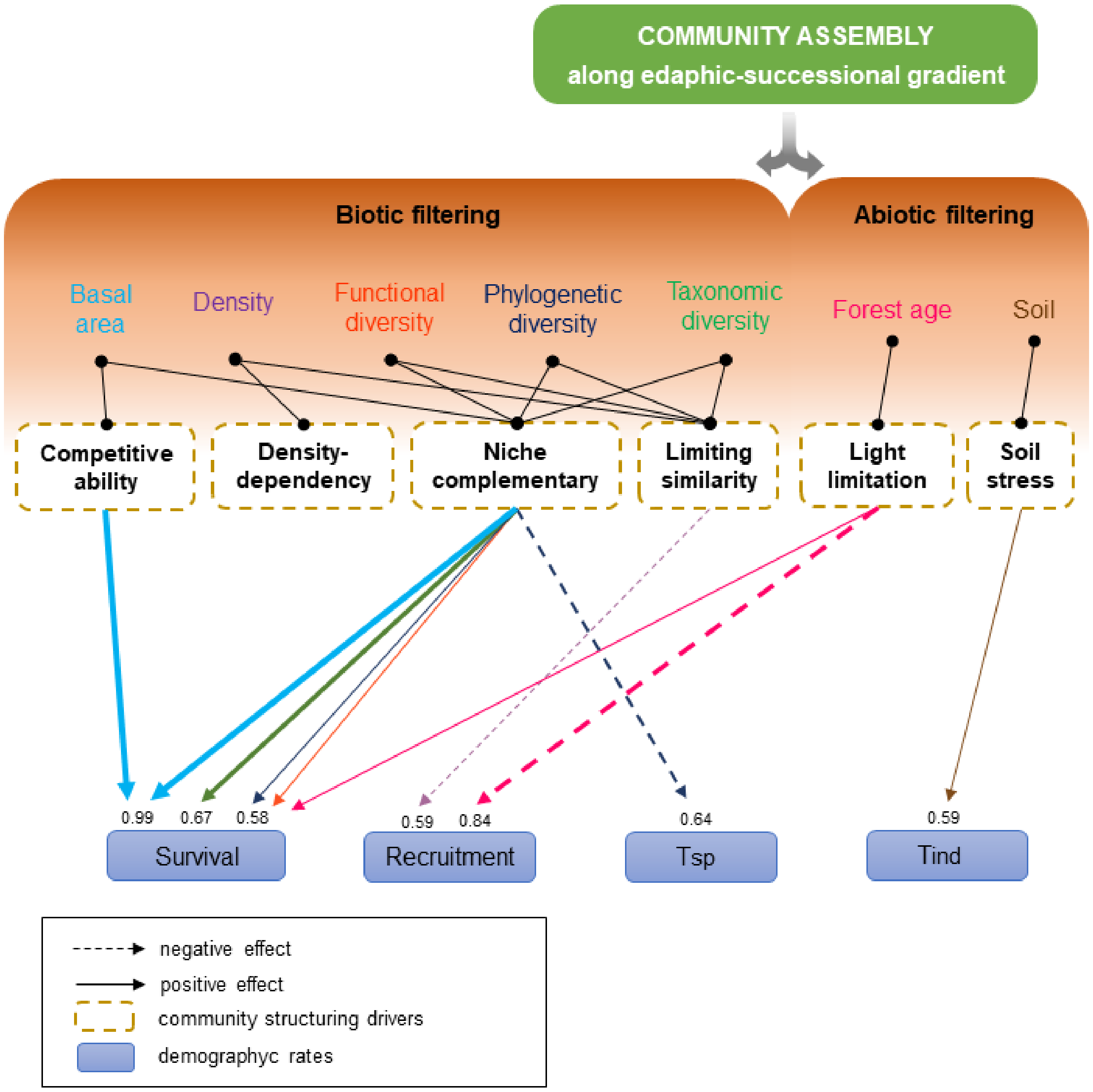

Figure 4. Deterministic factors affecting community assembly along the edaphic-successional gradient. The demographic rates survival, recruitment, individual turnover (T_{ind}) and species turnover (T_{sp}) express the structuring mechanisms of community assemblages. Through biotic filtering (expressed by basal area, density, functional diversity, taxonomic diversity, phylogenetic diversity) and abiotic filtering (soil constrains, forest age gradient) the community structuring mechanisms (density-dependency, self-thinning, niche complementarity, limiting similarity, limiting light/temperature, soil stress) affect demography and community assembly. Arrows width represent the relative variable importance, indicated at end of arrows (Table 2).

Drivers of plant community assemblies

As previously reported in other tropical forest studies (Lebrija-Trejos et al. 2010; Norden et al. 2012; Boukili & Chazdon 2016; Marcilio-Silva et al. 2016), we found that environmental and biotic filtering affect the community assembly in a region with a successional gradient. However, the mechanisms driving the filtering on demography and species turnover are very distinctive. Whereas environmental filtering (possibly via limitations related to structural complexity and soil stress) seems to more greatly affect the recruitment, survival, and individual turnover, the biotic filtering (possibly via density dependency, competitive ability and niche complementarity) more greatly affects the survival, recruitment and species turnover. Thus, the studied community assemblage during the succession is the result of a multi-mechanistic process with varying importance acting in individual and species turnover.

Individual recruitment was strongly and negatively affected by forest age possibly because of the limitations related to structural complexity and light limitation in advanced stages of succession (Bazzaz & Picket 1980). Additionally, as the density is high during the intermediate phases of succession, limiting similarity mechanisms might possibly affect the recruitment of individuals in a negative way. Thus, individual recruitment is constrained by abiotic and biotic filtering from the intermediate to the advanced phases of succession.

The individual survival was strongly and positively affected by basal area, revealing that larger individuals had higher a probability of permanence in the community. The increase in basal area along the successional gradient, coupled with the increase in diversity, might be related to niche complementarity (Lasky et al. 2014a). In addition, large individuals have a greater capacity to consume resources during their development, resulting in higher competitive ability (Goldberg 1990). This is especially relevant in the advanced phases of succession, where environmental filtering caused by an increase in structural complexity, linked with light limitation, leads to the dominance of long-lived species in these communities. These species are shade tolerant, highly competitive (Valladares and Niinemets 2004) and contribute to the canopy closure in the advanced phases of succession.

Survival is also positively affected by functional, phylogenetic and taxonomic diversities, suggesting that niche complementarity is important to the permanence of individuals in the community. A change in the availability of resources, mainly light, throughout the succession process causes changes in the mechanisms of coexistence. The initial stages of succession are dominated by pioneering and light-demanding species; during succession, these resource limitations give way to niche complementarity, as the communities are more heterogeneous in species and in resources used in advanced stages (Lohbeck et al. 2015). This complementarity occurs because tropical forests present resource heterogeneity, allowing the establishment of species with different necessities (Schnitzer and Carson 2001); this increase in taxonomic complexity and consequently, phylogenetic divergence, creates new niche spaces, leading to the coexistence of different functional groups (Meiners et al. 2015).

Individual turnover progressively decreases during the successional process and is positively affected by soil. Restrictive soils act as a strong environmental filter for plants (Ulrich et al. 2014). The stress caused by the low drainage of Gleysols can act as an intermediate disturbance, affecting the turnover by constraining the set of species that can establish in this soil (Marques et al. 2009).

Species turnover tends to be higher at the beginning of the successional process and decreases during more advanced phases. Therefore, the species that are still being recruited tend to be phylogenetically redundant; the stands with greater phylogenetic diversity present lower species turnover. The higher turnover at the beginning of succession leads to the coexistence of greater species diversity over time, and by the niche complementarity perspective, functional and evolutionarily distant species can coexist by resource partition (Meiners et al. 2015). Niche complementarity can lead to saturation of diversity when all niches are well occupied (Loreau 1998).

Concluding remarks

In this work, we analyzed the effects of structuring drivers in community assembly. Plant demographics proved to be an efficient approach to study these effects at different ecological scales (here population-community). Knowing that deterministic processes are important in the structuring of communities, we found different drivers acting on the performance of species and individuals throughout the assembly of communities over time. Both abiotic and biotic filtering affect community assembly along the successional gradient; however, the drivers acting on individual and species turnover are distinct. Thus, the community assembly during the successional period is the result of a multi-factor process acting mainly on individual and species turnover

Acknowledgements

We are grateful to the Society for Research in Wildlife and Environmental Education (Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental, SPVS) for allowing the research in their reserves and for their logistical support. We are also grateful to Isabela G. Varassin and Luciana Franci for their suggestions regarding the manuscript, to Thais Zanatta for statistical support on model selection, and to the Brazilian Research Council (CNPq) for financial support (Grant 577336/2008-8). AC, VMS and ESC received scholarships from the Brazilian Education Council (CAPES); MCMM received a grant from CNPq (Grant 303897/2016-3).

References

Aakala, T. et al. 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. - Forest Ecol. Manag. 308, 128–135.

Barton K. 2016. MuMIn: multi-model inference. R package ver. 1.15-6.

Bazzaz, F. A. and Pickett, S. T. A. 1980. Physiological ecology of tropical succession: a comparative review. - Annu. Rev. Ecol. Evol. Syst. 11:287-310.

Bell, C. D. et al. 2010. The age and diversification of the angiosperms re-revisited. - Am. J. Bot. 97: 1296–1303.

Borgo, M. 2010. A Floresta Atlântica do litoral norte do Paraná, Brasil: aspectos florísticos, estruturais e estoque de biomassa ao longo do processo sucessional. - PhD thesis, Universidade Federal do Paraná.

Botta-Dukát, Z. 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. - J. Veg. Sci. 16: 533-540.

Boukili, V. K. and Chazdon, R. L. 2016. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. - Perspect. Plant Ecol. Evol. Syst. 24: 37–47.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information - Theoretic Approach (2nd ed).

Burslem, D. F. R. P. et al. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. - J. Ecol. 88: 1063–1078.

Cardoso, F. C. G. et al. 2012. Stem growth and phenology of two tropical trees in contrasting soil conditions. Plant Soil 354: 269-281.

Cardoso, F. 2014. A estruturação de comunidades vegetais em áreas sucessionais da Floresta Atlântica em diferentes tipos de solo. - PhD thesis, Universidade Federal do Paraná.

Cavender-Bares, J. et al. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. - Ecology 87: 109–122.

Chalmandrier, L. et al. 2015. Effects of species’ similarity and dominance on the functional and phylogenetic structure of a plant meta-community. - Ecology 96: 143–153.

Chazdon, R. L. 2008. Chance and determinism in tropical forest succession. - In: Carson, W.P. and Schnitzer, S.A. (ed), Tropical Forest Community Ecology. Blackwell, pp. 384–408.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. - Annu. Rev. Ecol. Syst 31: 343–66.

Cheung, K. C. et al. 2010. Forest recovery in newly abandoned pastures in Southern Brazil: implications for the Atlantic Rain Forest resilience. - Nat. Conserv. 8: 66–70.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. - Carnegie Institution of Washington.

Condit, R. et al. 2006. The Importance of Demographic Niches to Tree Diversity. - Science 313: 98-101.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of lake Michigan. Bot. Gaz. 27: 361-391.

Cui, W. & Zheng, X.-X. 2016. Partitioning Tree Species Diversity and Developmental Changes in Habitat Associations in a Subtropical Evergreen Broadleaf Secondary Forest in Southern China. - Forests 7: 228.

Diamond, J. M. and May, R. M. 1977. Species turnover rates on islands: dependence on census interval. - Science 197: 266–270.

Feeley, K. J. et al. 2011. Directional changes in the species composition of a tropical forest. - Ecology 92: 871–82.

Ferretti, A. R. and de Britez, R. M. 2006. Ecological restoration, carbon sequestration and biodiversity conservation: The experience of the Society for Wildlife Research and Environmental Education (SPVS) in the Atlantic Rain Forest of Southern Brazil. - J. Nat. Conserv. 14: 249–259.

Fox, J. et al. 2016. Companion to Applied Regression. R version 3.2.0.

Fricke, E. C. and Wright, S. J. 2017. Measuring the demographic impact of conspecific negative density dependence. - Oecologia 184:259–266.

Gastauer, M. and Meira-Neto, J. A. A. 2016. An enhanced calibration of a recently released megatree for the analysis of phylogenetic diversity. - Brazilian J. Biol. 76: 619–628.

Gleason, H. A. 1926. The individualistic concept of the plant association. - Bull. Torrey Bot. Club 53: 7-26.

Goldberg, D. E. 1990. Components of resource competition in plant communities. - In: Grace, J. B. and Tilman, D. (ed), Perspectives on plant competition, Academic Press., pp 26-49.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. - Ecology 81: 2606–2621.

Hubbell SP. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. - Funct. Ecol 19: 166–172.

Hurvich, C. M. and Tsai, C. L. 1989. Regression and time series model selection in small samples. - Biometrica 76: 297–307.

IBGE 2012. Manual Técnico da Vegetação Brasileira. - Instituto Brasileiro de Geografia e estatística.

Kauano, E. E. et al. 2012. Landscape structure in the northern coast of Paraná state, a hotspot for the Brazilian Atlantic Forest conservation. Rev. Arvore 36: 961–970.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. - Bioinformatics 26: 1463–1464.

Kraft, N. J. B. et al. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. - Science 322: 580–582.

Krebs, P. et al. 2012. Modelling the eco-cultural niche of giant chestnut trees: new insights into land use history in southern Switzerland through distribution analysis of a living heritage. - J. Hist. Geog. 38: 372- 386.

Laliberté, E. et al. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Lasky, J. R. et al. 2014a. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. - Ecol. Lett. 17: 1158–1167.

Lasky, J. R. et al. 2014b. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. - Proc. Natl. Acad. Sci. 111: 5616–5621.

Lebrija-Trejos, E. et al. 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. - Perspect. Plant Ecol. Evol. Syst. 12: 267–275.

Letcher, S. G. et al. 2012. Phylogenetic community structure during succession: Evidence from three Neotropical forest sites. - Perspect. Plant Ecol. Evol. Syst. 14: 79–87.

Lohbeck, M. et al. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. - Ecology 96: 1242–1252

Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. - Proc. Natl. Acad. Sci. 95: 5632–5636.

Macarthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. - Amer. Nat. 101: 377-385.

Marcilio-Silva, V. et al. 2016. Functional turnover and community assemblage during tropical forest succession. - Community Ecol. 17: 88–97.

Marques, M. C. M. et al. 2009. Dynamics and diversity of flooded and unflooded forests in a Brazilian Atlantic rain forest: a 16-year study. - Plant Ecol. Divers. 2: 57–64.

Martins, K. G. et al. 2015. Effects of soil conditions on the diversity of tropical forests across a successional gradient. - For. Ecol. Manage. 349: 4–11.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. - Trends Ecol. Evol. 21: 178–185.

Meiners, S. J. et al. 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. - Funct. Ecol. 29: 154–164.

Morris, D. W. 1987. Ecological Scale and Habitat Use. - Ecology, 68: 362–369

Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. - Nature 403: 853–858.

Norden, N. et al. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. - Ecology 93: 70-82.

Norden, N. et al. 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. - Proc. Natl. Acad. Sci. 112: 8013-8018.

Oksanen, J. et al. 2017. Community Ecology Package. R package version 2.4-3.

Pasinelli, G. M. et al. 2007. Possible causes and consequences of philopatry and breeding dispersal in Red-backed Shrikes Lanius collurio. - Behav. Ecol. Sociobiol. 61: 1061-1074.

Pérez-Harguindeguy, N. et al. 2013. New Handbook for standardized measurment of plant functional traits worldwide. - Aust. J. Bot. 23: 167–234.

Phillips, O. L. et al. 1994. Dynamics and species richness of tropical rain forests. - Proc. Natl. Acad. Sci. 91: 2805–2809.

Phillips, O. L. et al. 2004. Pattern and process in Amazon tree turnover, 1976–2001. - Philos. Trans. R. Soc. London. Ser. B 359: 381–407.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rao, C.R. 1982. Diversity and dissimilarity coefficients: a unified approach. - Theor. Pop. Biol. 21: 24-4.

Rees, M. C. R. 2001. Long-Term Studies of Vegetation Dynamics. - Science 293: 293-650.

Ribeiro, M. C. et al. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. - Biol. Conserv. 142: 1141–1153.

Robinson, S. J. B. et al. 2015. Factors influencing early secondary succession and ecosystem carbon stocks in Brazilian Atlantic Forest. - Biodivers. Conserv. 24: 2273–2291.

Schnitzer, S. A. and Carson, W. P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. - Ecology 82: 913–919.

Sheil, D. et al. 1995. The Interpretation and misinterpretation of mortality rate measures. - J. Ecol. 83: 331–333.

Sutherland, W. J. et al. 2013. Identification of 100 fundamental ecological questions. - J. Ecol. 101: 58–67.

Svenning, J. C. 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85: 2526- 2538.

Swenson, N. G. and Enquist, B. J. 2009. Opposing assembly mechanisms in a Neotropical dry forest: Implications for phylogenetic and functional community ecology. - Ecology 90: 2161–2170.

Swenson, N. G. et al. 2012. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. - Ecology 93: 490–499.

Tilman, D. et al. 1997. The influence of functional diversity and composition on ecosystem processes. - Science 277: 1300–1302.

Ulrich, W. et al. 2014. Soil conditions and phylogenetic relatedness influence total community trait space during early plant succession. - J. Plant Ecol. 7: 321–329.

Valladares, F. and Niinemets, I. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences.- Annu. Rev. Ecol. Evol. Syst. 39:237-57

van Breugel, M. et al. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. - J. Trop. Ecol. 22: 663–674.

Violle, C. et al. 2012. The return of the variance: Intraspecific variability in community ecology. - Trends Ecol. Evol. 27: 244–252.

Webb, C. 2000. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. - Am. Nat. 156: 145–155.

Webb, C. O. and Donoghue, M. J. 2005. Phylomatic: Tree assembly for applied phylogenetics. - Mol. Ecol. Notes 5: 181–183.

Webb, C. O. et al. 2002. Phylogenies and Community Ecology. - Annu. Rev. Ecol. Syst. 33: 475–505.

Zhang, J. 2016. Species Association Analysis. R package version 0.2.2

Zwiener, V.P. et al. 2014. Disentangling the effects of facilitation on restoration of the Atlantic Forest. - Basic Appl. Ecol. 15: 34–41.

APPENDICES

Appendix 1

SOIL CHARACTERISTICS

Table A1. Means (± SE) of the nutritional and physical characteristics of two soil types in Atlantic Forest areas, Southern Brazil. ns= non-significant.

Soil parameter	**Cambisol**	**Gleysol**	***t* or *Z* test**
pH (CaCl2)	3.78 ± 0.06	3.96±0.04	*t*=2.24; *P*=0.04
Al (cmolc.dm-3)	2.36 ± 0.21	2.14± 0.28	ns
Ca (cmolc.dm-3)	0.41 ± 0.27	0.50 ± 0.18	ns
Mg (cmolc.dm-3)	0.31 ± 0.09	0.43 ± 0.09	ns
K (cmolc.dm-3)	0.15 ± 0.01	0.14 ± 0.02	ns
P (mg.dm-3)	4.64 ±1.03	3.79 ± 0.48	ns
C (g.dm-3)	4.47 ± 0.25	7.72 ± 0.43	ns
Clay (g.kg-1)	390.7± 37.59	225.14 ± 47.99	*t*=2.5; *P*=0.03
Silt (g.kg-1)	143.23 ± 50.47	318.91 ± 51.87	*Z*=2.64; *P*=0.008
Sand (g.kg-1)	463.48 ± 51.19	456.23 ± 94.24	ns

Appendix 2

PHYLOGENETIC TREE

Phylogenetic tree of plants occurring in successional areas of Atlantic forest. Building with megatree R20120829mod and dated from fossil data of Bell et *al.* (2010): Details in Methods.

(((((((((((((schinus_terebinthifolius:25.000000,tapirira_guianensis:25.000000)anacardiaceae:25.000000,protium_kleinii:50.000000)bursa_to_anaca:28.066666,(((cabralea_canjerana:39.000000,cedrela_fissilis:39.000000,(guarea_macrophylla:26.000000,(trichilia_lepidota:13.000000,trichilia_pallens:13.000000,trichilia_silvatica:13.000000)trichilia:13.000000):13.000000,meliaceae_sp:39.000000)meliaceae:14.000000,((citrus_limon:20.000000,citrus_reticulata:20.000000)citrus:20.000000,esembeckia_febrifuga:40.000000,esenbeckia_grandiflora:40.000000,metrodorea_nigra:40.000000,pilocarpus_pauciflorus:40.000000,pilocarpus_sp:40.000000,zanthoxylum_rhoifolium:40.000000)rutaceae:13.000000)meliaceae_to_rutaceae:12.533333,((allophylus_edulis:20.500000,allophylus_petiolatus:20.500000,allophylus_puberulus:20.500000,allophylus_sp:20.500000)allophylus:20.500000,cupania_oblongifolia:41.000000,(matayba_guianensis:20.500000,matayba_intermedia:20.500000,matayba_juglandifolia:20.500000,matayba_sp:20.500000)matayba:20.500000)sapindaceae:24.533333):12.533333):12.533333,(jacaratia_spinosa:82.400002,((ceiba_speciosa:66.000000,malvaceae_sp:66.000000,malvaviscus_penduliflorus:66.000000,pseudobombax_grandiflorum:66.000000)malvaceae:8.199997,daphnopsis_sp:74.199997):8.200005)malvales_to_brassicales:8.199997):8.200005,picramnia_ramiflora:98.800003):8.200000,(buchenavia_:89.000000,(((clidemia_hirta:26.969696,clidemia_urceolata:26.969696)clidemia:26.969696,(leandra_dasytricha:26.969696,leandra_fragilis:26.969696,leandra_glasiovi:26.969696,leandra_melastomoides:26.969696)leandra:26.969696,melastomataceae_sp:53.939392,melastomataceae_sp1:53.939392,melastomataceae_sp2:53.939392,(miconia_cabucu:26.969696,miconia_carthacea:26.969696,miconia_cinerascens:26.969696,miconia_cinnamomifolia:26.969696,miconia_cubatanensis:26.969696,miconia_dodecandra:26.969696,miconia_fasciculata:26.969696,miconia_jucunda:26.969696,miconia_latecrenata:26.969696,miconia_membranaceae:26.969696,miconia_pusiliflora:26.969696,miconia_tristis:26.969696)miconia:26.969696,mouriri_chamissoana:53.939392,(ossaea_amygdaloides:26.969696,ossaea_sp:26.969696,ossaea_sp1:26.969696)ossaea:26.969696,(tibouchina_pulchra:26.969696,tibouchina_trichopoda:26.969696,tibouchina_sp:26.969696,tibouchina_sp1:26.969696,tibouchina_sp2:26.969696)tibouchina:26.969696)melastomataceae:26.969696,(((calycorectes_australis:32.363636,calycorectes_sellowianus:32.363636)calycorectes:32.363636,((((((calyptranthes_conccina:10.787879,calyptranthes_grandifolia:10.787879,calyptranthes_lanceolata:10.787879,calyptranthes_lucida:10.787879,calyptranthes_strigipes:10.787879)calyptranthes:10.787879,marlierea_eugeniopsoides:21.575758):10.787878,(((marlierea_obscura:8.090909,marlierea_reitzii:8.090909,marlierea_riedeliana:8.090909,marlierea_sp:8.090909,marlierea_sp2:8.090909,marlierea_sp3:8.090909,marlierea_sylvatica:8.090909,marlierea_tomentosa:8.090909)marlierea:8.090909,myrcia_multiflora:16.181818):8.090910,

```
myrcia_racemosa:24.272728):8.090908,myrcia_bicarinata:32.363636)myrciagroup:8.090908,myrciaria_floribunda:40.454544):8.090912,(myrceugenia_miersiana:24.272728,myrceugenia_myrcioides:24.272728,myrceugenia_reitzii:24.272728)myrceugenia:24.272728):8.090908,(((campomanesia_neriifolia:14.159091,campomanesia_reitziana:14.159091,campomanesia_sp:14.159091,campomanesia_xanthocarpa:14.159091)campomanesia:14.159091,(psidium_cattleianum:14.159091,psidium_guajava:14.159091,psidium_sp:14.159091)psidium:14.159091):14.159090,(eugenia_beaurepaireana:21.238636,eugenia_brevistyla:21.238636,eugenia_burkartiana:21.238636,eugenia_candolleana:21.238636,eugenia_catharinensis:21.238636,eugenia_cerasiflora:21.238636,eugenia_cereja:21.238636,eugenia_jambos:21.238636,eugenia_leitonii:21.238636,eugenia_magnibracteolata:21.238636,eugenia_malacantha:21.238636,eugenia_melanogyna:21.238636,eugenia_mosenii:21.238636,eugenia_multicostata:21.238636,eugenia_neoglomerata:21.238636,eugenia_obovata:21.238636,eugenia_platysema:21.238636,eugenia_prasina:21.238636,eugenia_sp1:21.238636,eugenia_sp2:21.238636,eugenia_stigmatosa:21.238636,eugenia_subavenia:21.238636,eugenia_sulcata:21.238636,eugenia_umbelliflora:21.238636,eugenia_uniflora:21.238636,eugenia_unifolia:21.238636,eugenia_verticillata:21.238636)eugenia:21.238636):14.159092):8.090908,(gomidesia_brasiliensis:32.363636,gomidesia_flagellaris:32.363636,gomidesia_palustris:32.363636,gomidesia_schaueriana:32.363636,gomidesia_spectabilis:32.363636)gomidesia:32.363636,(myrcia_acuminatissima:32.363636,myrcia_floribunda:32.363636,myrcia_formosiana:32.363636,myrcia_glabra:32.363636,myrcia_grandiflora:32.363636,myrcia_insularis:32.363636,myrcia_pubipetala:32.363636,myrcia_richardiana:32.363636,myrcia_spectabilis:32.363636,myrcia_splendens:32.363636,myrcia_tenuivenosa:32.363636)myrcia:32.363636,myrtaceae_sp:64.727272,myrtaceae_sp1:64.727272,myrtaceae_sp2:64.727272,myrtaceae_sp3:64.727272,myrtaceae_sp4:64.727272,myrtaceae_sp5:64.727272,myrtaceae_sp6:64.727272,myrtaceae_sp7:64.727272,neomitranthes_glomerata:64.727272,(plinia_edulis:32.363636,plinia_trunciflora:32.363636)plinia:32.363636,(syzygium_cumini:32.363636,syzygium_jambos:32.363636)syzygium:32.363636)myrtaceae:8.090912,vochysia_bifalcata:72.818184):8.090904):8.090909)myrtales:18.000000)malvids:4.949997,((((trema_micrantha:68.000000,(((artocarpus_integrifolia:22.000000,(morus_nigra:11.000000,sorocea_bonplandii:11.000000):11.000000):11.000000,((brosimum_lactescens:19.799999,((ficus_adhatodifolia:6.600000,ficus_enormis:6.600000,ficus_gomelleira:6.600000,ficus_insipida:6.600000,ficus_organensis:6.600000,ficus_sp:6.600000)ficus:6.600000,pseudolmedia_hirtula:13.200000):6.599999):6.600000,maclura_tinctoria:26.400000):6.600000)moraceae:21.000000,(bohemeria_caudata:34.000000,(cecropia_glaziovii:17.000000,cecropia_pachystachya:17.000000)cecropia:17.000000,coussapoa_microcarpa:34.000000,pourouma_guianensis:34.000000)urticaceae:20.000000)cannabaceae_to_moraceae:14.000000):14.000000,(eriobotrya_japonica:41.000000,prunus_myrtifolia:41.000000):41.000000)rosales:17.000000,(((((albizia_edwallii:21.688889,(inga_edulis:10.844444,inga_luschnatiana:10.844444,inga_marginata:10.844444,inga_sellowiana:10.844444,inga_sessilis:10.844444,inga_striata:10.844444)inga:10.844444)ingeae:10.844444,(mimosa_bimucronata:21.688889,(piptadenia_gonoacantha:10.844444,piptadenia_paniculata:10.844444)piptadenia:10.844444,pseudopiptadenia_warmingii:21.688889)piptadenia_group:10.844444):10.844444,(senna_multijuga:21.688889,senna
```

```
_oblongifolia:21.688889,senna_pendula:21.688889,senna_sp:21.688889,senna_sylvestris:21.688889)senna:21.688889):10.844444,((((andira_anthelmia:27.111111,((centrolobium_microchaete:10.166667,pterocarpus_violaceus:10.166667):10.166667,((dalbergia_brasiliensis:6.777778,dalbergia_frutescens:6.777778)dalbergia:6.777778,(machaerium_brasiliense:6.777778,machaerium_hatschbachii:6.777778,machaerium_hirtum:6.777778,machaerium_nyctitans:6.777778,machaerium_sp:6.777778,machaerium_uncinatum:6.777778)machaerium:6.777778):6.777779):6.777777):6.777779,(dahlstedtia_pentaphylla:16.944445,erythrina_speciosa:16.944445):16.944445,luetzelburgia_guaissara:33.888889,ormosia_arborea:33.888889,(zollernia_latifolia:16.944445,zollernia_sp:16.944445,zollernia_sp2:16.944445)zollernia:16.944445):6.777779,myrocarpus_frondosus:40.666668):6.777775,swartzia_acutifolia:47.444443):6.777779):6.777778,bauhinia_forficata:61.000000,copaifera_trapezifolia:61.000000,fabaceae_sp:61.000000,plathymiscium_floribundum:61.000000,schizolobium_parahyba:61.000000)fabaceae:38.000000)nitrogenfixing:7.474998,((maytenus_alaternoides:50.500000,maytenus_gonoclada:50.500000,maytenus_schumanniana:50.500000)maytenus:50.500000,((hirtella_hebeclada:89.000000,(calophyllum_brasiliense:59.333332,(clusia_criuva:29.666666,clusia_parviflora:29.666666)clusia:29.666666,garcinia_gardneriana:59.333332)clusiaceae:29.666666,(erythroxylum_amplifolium:44.500000,erythroxylum_cuspidifolium:44.500000,erythroxylum_deciduum:44.500000,erythroxylum_sp:44.500000,erythroxylum_sp1:44.500000)erythroxylum:44.500000,(actinostemon_concolor:59.333332,(alchornea_glandulosa:29.666666,alchornea_triplinervia:29.666666)alchornea:29.666666,aparisthmium_cordatum:59.333332,maprounea_brasiliensis:59.333332,pachystroma_longifolium:59.333332,pausandra_morisiana:59.333332,pera_glabrata:59.333332,sapium_glandulatum:59.333332,tetrorchidium_rubrivenium:59.333332)euphorbiaceae:29.666666,(humiriastrum_sp:44.500000,vantanea_compacta:44.500000)humiriaceae:44.500000,(bunchosia_pallescens:61.000000,byrsonima_ligustrifolia:61.000000)malpighiaceae:28.000000,(ouratea_parviflora:49.000000,quiina_glaziovii:49.000000)ochnaceae:40.000000,(hyeronima_alchorneoides:44.500000,margaritaria_nobilis:44.500000)phyllanthaceae:44.500000,(casearia_decandra:44.500000,casearia_obliqua:44.500000,casearia_sylvestris:44.500000,casearia_sp:44.500000)casearia:44.500000)malpighiales:6.000000,(weinmannia_paulliniaefolia:47.500000,sloanea_guianensis:47.500000):47.500000):6.000000)celastrales_to_malpighiales:5.474998):5.474998):4.950001,(((((((apocynaceae_sp:21.000000,(aspidosperma_pyricollum:10.500000,aspidosperma_ramiflorum:10.500000,aspidosperma_sp:10.500000)aspidosperma:10.500000,malouetia_cestroides:21.000000,tabernaemontana_catharinensis:21.000000)apocynaceae:44.000000,(alibertia_concolor:57.000000,(((alseis_floribunda:22.799999,(bathysa_australis:11.400000,bathysa_meridionalis:11.400000)bathysa:11.400000):11.400002,posoqueria_latifolia:34.200001,randia_armata:34.200001)ixoroideae:11.399998,chomelia_brasiliana:45.599998):11.400000,amaioua_guianensis:57.000000,cordiera_concolor:57.000000,((coussarea_contracta:19.000000,coussarea_sp:19.000000)coussarea:19.000000,(psychotria_barbiflora:19.000000,psychotria_birotula:19.000000,psychotria_carthagenensis:19.000000,psychotria_dusenii:19.000000,psychotria_leiocarpa:19.000000,psychotria_mapourioides:19.000000,psychotria_nuda:19.000000,psychotria_pubigera:19.000000,psychotria_sp:19.000000,psychotria_stenocalix:19.000000,psychotria_suterella:19.000000,psychotria_vellosiana:1
```

```
9.000000)psychotria:19.000000):19.000000,hillia_parasitica:57.000000,rubiaceae_sp:57.00000
0,rubiaceae_sp1:57.000000,(rudgea_jasminioides:28.500000,rudgea_recurva:28.500000,rudge
a_villiflora:28.500000)rudgea:28.500000)rubiaceae:8.000000)gentianales:17.000000,(((((cresce
ntia_cujete:25.000000,cybistax_antisyphilitica:25.000000,jacaranda_puberula:25.000000,(tabeb
uia_cassinoides:12.500000,tabebuia_serratifolia:12.500000,tabebuia_sp:12.500000,tabebuia_u
mbellata:12.500000)tabebuia:12.500000)bignoniaceae:12.000000,citharexylum_myrianthum:37
.000000):12.000000,((aegiphila_integrifolia:19.000000,aegiphila_sellowiana:19.000000)aegiphil
a:19.000000,vitex_polygama:38.000000)lamiaceae:11.000000):11.000000,paulownia_fortunei:
60.000000):11.000000,((acnistus_arborescens:23.666666,solanum_pseudoquina:23.666666):2
3.666666,cestrum_intermedium:47.333332):23.666668):11.000000,(cordia_sellowiana:41.0000
00,cordia_silvestris:41.000000)cordia:41.000000):17.000000,(((ilex_dumosa:44.000000,ilex_int
egerrima:44.000000,ilex_pseudobuxus:44.000000,ilex_sp:44.000000,ilex_theezans:44.000000)
ilex:44.000000,(citronella_paniculata:44.000000,citronella_toledoi:44.000000)citronella:44.0000
00)aquifoliales:5.000000,((araliaceae_sp:18.000000,(schefflera_angustissima:9.000000,scheffl
era_morototoni:9.000000,schefflera_sp:9.000000)schefflera:9.000000)araliaceae:48.500000,(a
steraceae_sp:40.000000,baccharis_sp:40.000000,(eupatorium_sp:26.666666,(vernonanthura_
beyrichii:13.333333,vernonanthura_puberula:13.333333,vernonanthura_sp:13.333333)vernona
nthura:13.333333):13.333333,piptocarpha_sp:40.000000)asteraceae:26.500000):26.500000)ca
mpanulids:6.000000)lamiids_to_campanulids:5.000000,(((clethra_scabra:56.799999,(symploco
s_celastrinea:28.400000,symplocos_laxiflora:28.400000,symplocos_variabilis:28.400000)sympl
ocos:28.400000,gordonia_fruticosa:56.799999):28.399998,((diospyros_sp:66.400002,(ardisia_g
uianensis:57.000000,(myrsine_coriacea:28.500000,myrsine_gardneriana:28.500000,myrsine_g
uianensis:28.500000,myrsine_hermogenesii:28.500000,myrsine_umbellata:28.500000)myrsine:
28.500000,rapanea_hermogenesii:57.000000)primulaceae:9.400002):9.400002,((chrysophyllu
m_inornatum:25.266668,chrysophyllum_sp:25.266668,chrysophyllum_viride:25.266668)chryso
phyllum:25.266668,manilkara_subsericea:50.533337,(pouteria_sp:25.266668,pouteria_torta:25.
266668,pouteria_venosa:25.266668)pouteria:25.266668,pradosia_lactescens:50.533337)sapot
aceae:25.266666):9.399994):9.400002,cariniana_estrellensis:94.599998):9.400000)ericales_to
_asterales:4.300003,((((guapira_asperula:11.000000,guapira_opposita:11.000000)guapira:11.0
00000,pisonia_ambigua:22.000000)nyctaginaceae:38.500000,(gallesia_integrifolia:30.250000,p
hytolacca_dioica:30.250000,seguieria_langsdorfii:30.250000)phytolaccaceae:30.250000):38.50
0000,(coccoloba_sp:49.500000,coccoloba_warmingii:49.500000)coccoloba:49.500000)caryoph
yllales:9.300003):4.299995,(heisteria_silvianii:56.299999,tetrastylidium_grandifolium:56.299999
)olacaceae:56.299999):4.300001)pentapetalids:9.099998,roupala_brasiliensis:126.000000,meli
osma_sellowii:126.000000)sabiales_to_asterales:4.000000,(araceae_sp:118.000000,(((arecace
ae_sp:31.000000,astrocaryum_aculeatissimum:31.000000,attalea_dubia:31.000000,(bactris_se
tosa:15.500000,bactris_sp:15.500000)bactris:15.500000,euterpe_edulis:31.000000,(geonoma_
elegans:15.500000,geonoma_gamiova:15.500000,geonoma_schottiana:15.500000,geonoma_s
p:15.500000)geonoma:15.500000,syagrus_romanzoffiana:31.000000)arecaceae:65.000000,mu
sa_paradisiaca:96.000000)commelinids:11.000000,dracaena_fragans:107.000000):11.000000)
```

narthecidae:12.000000)poales_to_asterales:0.100006,(((((((annona_glabra:11.500000,annona_neosericea:11.500000,annona_sp:11.500000,annona_squamosa:11.500000)annona:11.500000,duguetia_lanceolata:23.000000,guatteria_australis:23.000000,(rollinia_sericea:11.500000,rollinia_sylvatica:11.500000)rollinia:11.500000,xylopia_brasiliensis:23.000000)annonaceae:28.000000,((magnolia_grandiflora:16.500000,magnolia_ovata:16.500000)magnolia:16.500000,michelia_champaca:33.000000)magnoliaceae:18.000000):18.000000,virola_bicuhyba:69.000000)magnoliales:28.000000,((aiouea_saligna:12.000000,aniba_firmula:12.000000,(cryptocarya_aschersoniana:6.000000,cryptocarya_mandioccana:6.000000)cryptocarya:6.000000,(endlicheria_paniculata:6.000000,endlicheria_sp:6.000000)endlicheria:6.000000,lauraceae_sp:12.000000,lauraceae_sp2:12.000000,(nectandra_leucantha:6.000000,nectandra_megapotamica:6.000000,nectandra_membranacea:6.000000,nectandra_oppositifolia:6.000000,nectandra_puberula:6.000000,nectandra_reticulata:6.000000)nectandra:6.000000,(ocotea_aciphylla:6.000000,ocotea_alba:6.000000,ocotea_catharinensis:6.000000,ocotea_dispersa:6.000000,ocotea_glaziovii:6.000000,ocotea_nunesiana:6.000000,ocotea_odorifera:6.000000,ocotea_puberula:6.000000,ocotea_pulchella:6.000000,ocotea_sp:6.000000,ocotea_teleiandra:6.000000,ocotea_tristis:6.000000)ocotea:6.000000,(persea_americana:6.000000,persea_sp:6.000000)persea:6.000000)lauraceae:42.500000,(mollinedia_argyrogyna:27.250000,mollinedia_blumenaviana:27.250000,mollinedia_schottiana:27.250000,mollinedia_uleana:27.250000,mollinedia_sp:27.250000)mollinedia:27.250000):42.500000):28.000000,(cinnamodendron_dinisii:83.333336,(piper_aduncum:41.666668,piper_arboreum:41.666668,piper_cernuum:41.666668,piper_dilatatum:41.666668,piper_gaudichaudianum:41.666668,piper_malacophyllum:41.666668,piper_sp:41.666668,piper_sp1:41.666668)piper:41.666668):41.666668)magnoliids:2.550003,hedyosmum_brasiliensis:127.550003):2.550003)magnoliales_to_asterales:224.899994,(araucaria_angustifolia:257.000000,(podocarpus_lambertii:128.500000,podocarpus_sellowii:128.500000)podocarpus:128.500000)araucariaceae_to_podocarpaceae:98.000000)seedplants:111.000000,((alsophila_setosa:155.333328,alsophila_steinbergii:155.333328)alsophila:155.333328,(cyathea_atrovirens:155.333328,cyathea_axillaris:155.333328,cyathea_corcovadensis:155.333328,cyathea_delgadii:155.333328,cyathea_hirsuta:155.333328,cyathea_phallerata:155.333328)cyathea:155.333328)cyatheaceae:155.333328)euphyllophyte:0.000000;

Appendix 3

FUNCTIONAL TRAITS

Table A1. Functional traits (states and functions) used for calculating functional diversity (Rao). Categorical traits were expanded to dummy variables (presence or absence of a certain characteristic). * Reitz 1975; Carvalho 2003, 2006, 2008; Borgo et al. 2011.

Trait	**State**	**Function**	**Source**
Vegetative traits			
Leaf area (cm²)	continuous	thermal balance, light interception	herbarium
Leaf margin	entire (1)	herbivore defense, light interception	herbarium
	non-entire (0)		
Leaf compoundness	simple (1)	leaf cooling, light interception	herbarium
	compound (0)		
Maximum height (cm)		competition for light	meansured in field
Maximum DBH (cm)	-	competitive ability, carbon storage	meansured in field
Shade tolerance	tolerant (1)	competitive ability	literature*
	intolerante (0)		
Reproductive traits			
Pollination	insects	reproduction	literature*
	vertebrates		
	abiotic		
Seed dispersal mode		reproduction, dispersal distance	literature*
	animal		
	abiotic		

Appendix 4.

SCRIPT FOR NULL MODELS:

```
require(spaa)
require(picante)
model.null=function(abun,spp,rnd){
res=array(0, dim=c(max(abun),1,rnd))
res.final=matrix(0,rnd,4)
colnames(res.final)=c("Iteration","s","H", "J")
com=matrix(0,(max(abun)*rnd),3)
colnames(com)=c("plot","abund","id")
for (k in 1:rnd){
abun=sample(min(abun):max(abun)) #ordering abun at random
for (i in 1:abun[1]){
spp=sample(spp) #ordering list rows at random
spp<-as.matrix(spp)
res[i,1,k]=spp[1]
}
res.final[k,1]=k
res.final[k,2]=(length(unique(res[,,k]))-1)
}
for (l in 1:rnd){
for (j in 1:length(sort(unique(res[,,l][apply(as.matrix(res[,,l]), 1, function(row) all(row !=0 ))]))))){
com[(1+(length(com[,1][apply(as.matrix(com[,1]), 1, function(row) all(row !=0 ))]))),1]<-l
com[(1+(length(com[,3][apply(as.matrix(com[,3]), 1, function(row) all(row !=0 ))]))),3]<-(sort(unique(res[,,l][apply(as.matrix(res[,,l]), 1, function(row) all(row !=0 ))]))))[j]
com[(1+(length(com[,2][apply(as.matrix(com[,2]), 1, function(row) all(row !=0 ))]))),2]<- as.numeric(table(as.matrix(sort(res[,,l][apply(as.matrix(res[,,l]), 1, function(row) all(row !=0 ))]))))[j])
}
}
```

```
comz<-(com[][apply(com, 1, function(row) all(row !=0 )),])
comz<-data.frame(comz)
comz$abund<-as.numeric(comz$abund)
com.matrix <- tapply(comz$abund, list(comz$plot, comz$id), sum)#from list to community matrix
   com.matrix[is.na(com.matrix)] <- 0
   as.data.frame(com.matrix)
H<-diversity(com.matrix)#calculating H
res.final[,3]<-H
res.final[,4]<- H/(log(length(com.matrix)))
return(list(res,comz,com.matrix, res.final))
}
```

Appendix 5

GENERAL INFORMATION ON PLANT COMMUNITIES ALONG THE EDAPHIC-SUCCESSIONAL GRADIENT

Table A1. Total individual density, species richness and basal area in a edaphic-successional gradient in two surveys.

Soil type	***Forest age***	***Individual density***		***Taxonomic diversity***		***Basal Area ($m^2.ha^{-1}$)***	
		2010	**2016**	**2010**	**2016**	**2010**	**2016**
Cambisol	**07-17**	198	217	27	32	6.36	15.48
	20-30	541	540	66	69	23.07	22.2
	35-55	414	457	90	84	26.29	32.84
	>80	464	451	115	111	34.92	35.73
Gleysol	**07-17**	237	377	25	38	6.04	16.16
	20-30	489	452	52	45	20.57	19.89
	35-55	415	421	70	73	23.04	23.11

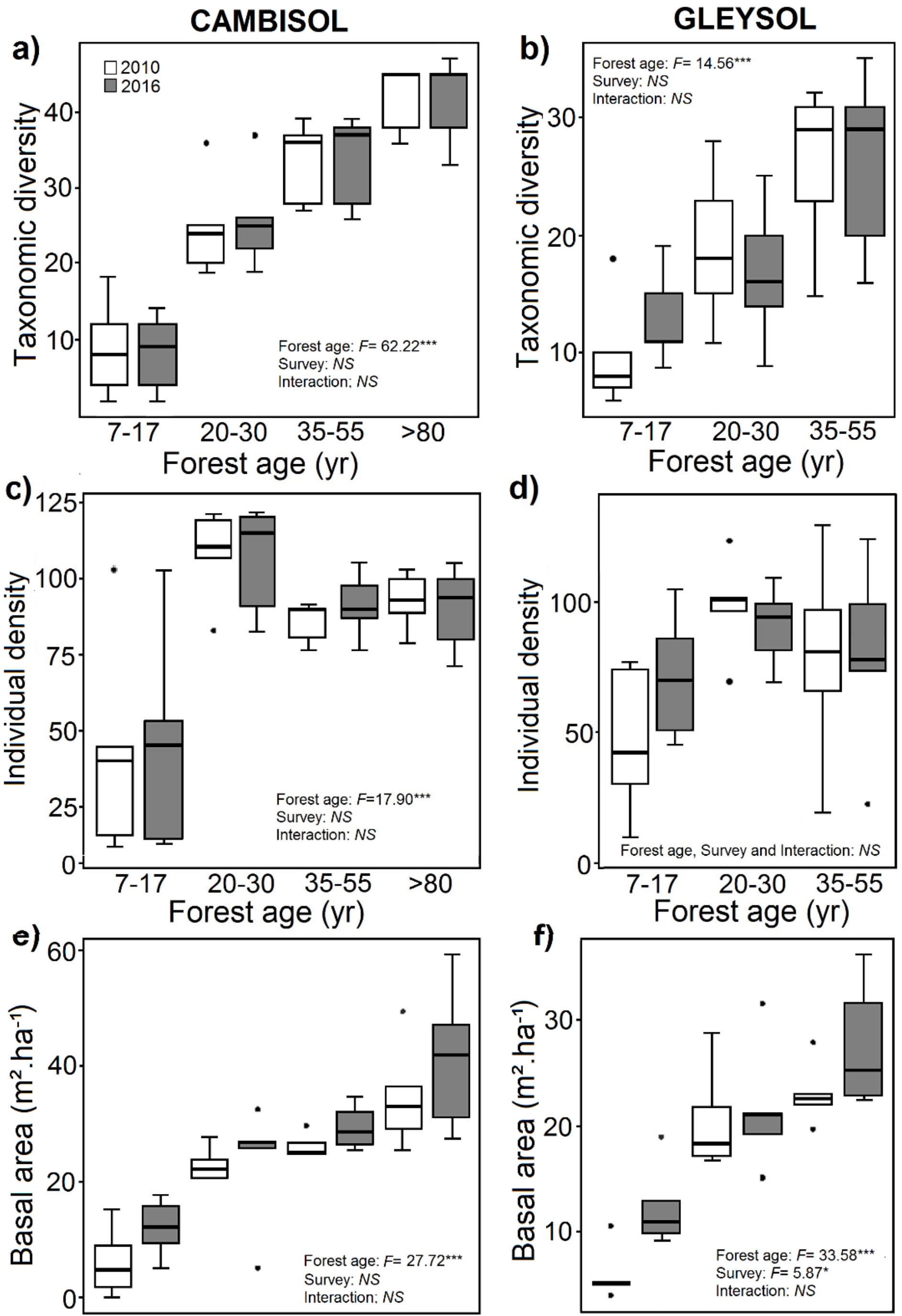

Figure A1. Boxplots of the taxonomic diversity (a, b), individual density (c, d) and basal area (e, f) alog edaphic-successinal gradient and meansured in two surveys (2010-2016). ****P*=0.0001; **P*=0.05.

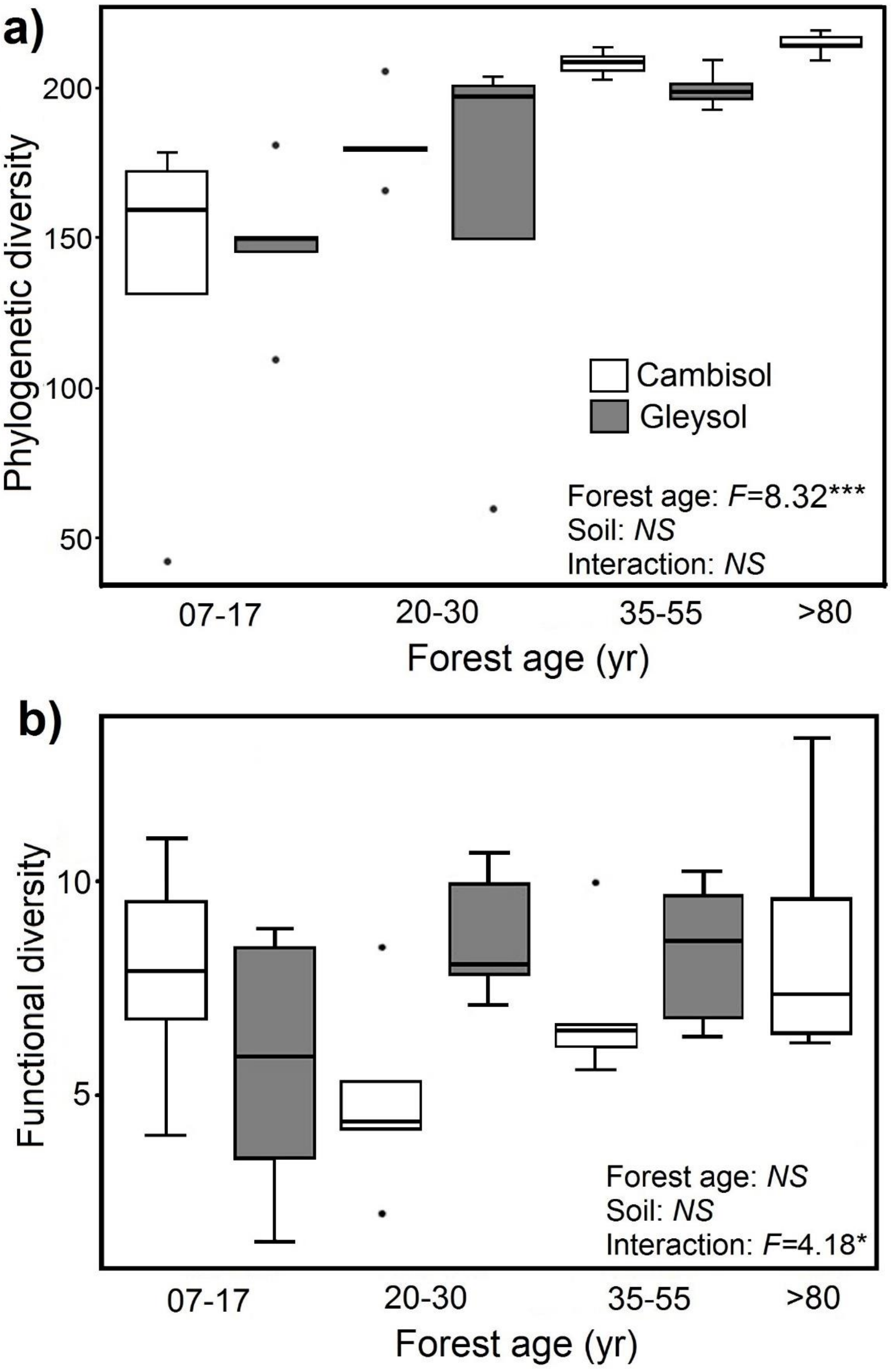

Figure A2. Boxplot of phylogenetic diversity (mensured by MPD) (a) and functional diversity (mensured by Rao) (b) along a edaphic-successional gradient in 2010 survey. ***P=0.001, *P=0.05.

Appendix 6

Additional information selection models (AICc)

Table A1. Summary of selected models for demographic rates, using the Akaike Information Criteria (AIC). Showed only models with ΔAICc <2; Akaike values (AICc - AIC with a correction for sample sizes) and weights (AICcw) of models. The effects positive (+) or negative (-) of each model was assumed from figures in Appendices S9, S10, S11 and S12. BA = basal area; Den = individual density; Pdiv = Phylogenetic diversity (MPD); Fdiv= Functional diversity (Rao); Tdiv = Taxonomic diversity (richness); Soil = soil type; Age = Forest gradient age.

Demographic rate	**Model**	**AICc**	**ΔAICc**	**AICcw**	**Effect**
SURVIVAL	BA + Pdiv + Fdiv + Soil	79.13	1.27	0.06	+/+/+/-
	BA + Age + Pdiv	79.68	1.81	0.04	+
	BA + Age + Pdiv + Fdiv + Soil	79.79	1.93	0.04	+/+/+/+/-
RECRUITMENT	Den + Age	125.27	0	0.1	-
	Age	125.52	0.24	0.09	-
INDIVIDUAL TURNOVER	BA + Soil	115.95	0	0.06	-/+
	Tdiv	115.99	0.04	0.06	-
	Tdiv + Soil	116	0.05	0.06	-/+
	Den + Soil	116.15	0.21	0.05	-/+
	BA	116.87	0.92	0.04	-
	Den	117.71	1.76	0.02	-
	Fdiv + Tdiv + Soil	117.72	1.77	0.02	-/-/+
	Fdiv + Tdiv	117.88	1.93	0.02	-
	Age + Tdiv	117.93	1.98	0.02	-
SPECIES TURNOVER	Pdiv	104.06	0	0.15	-

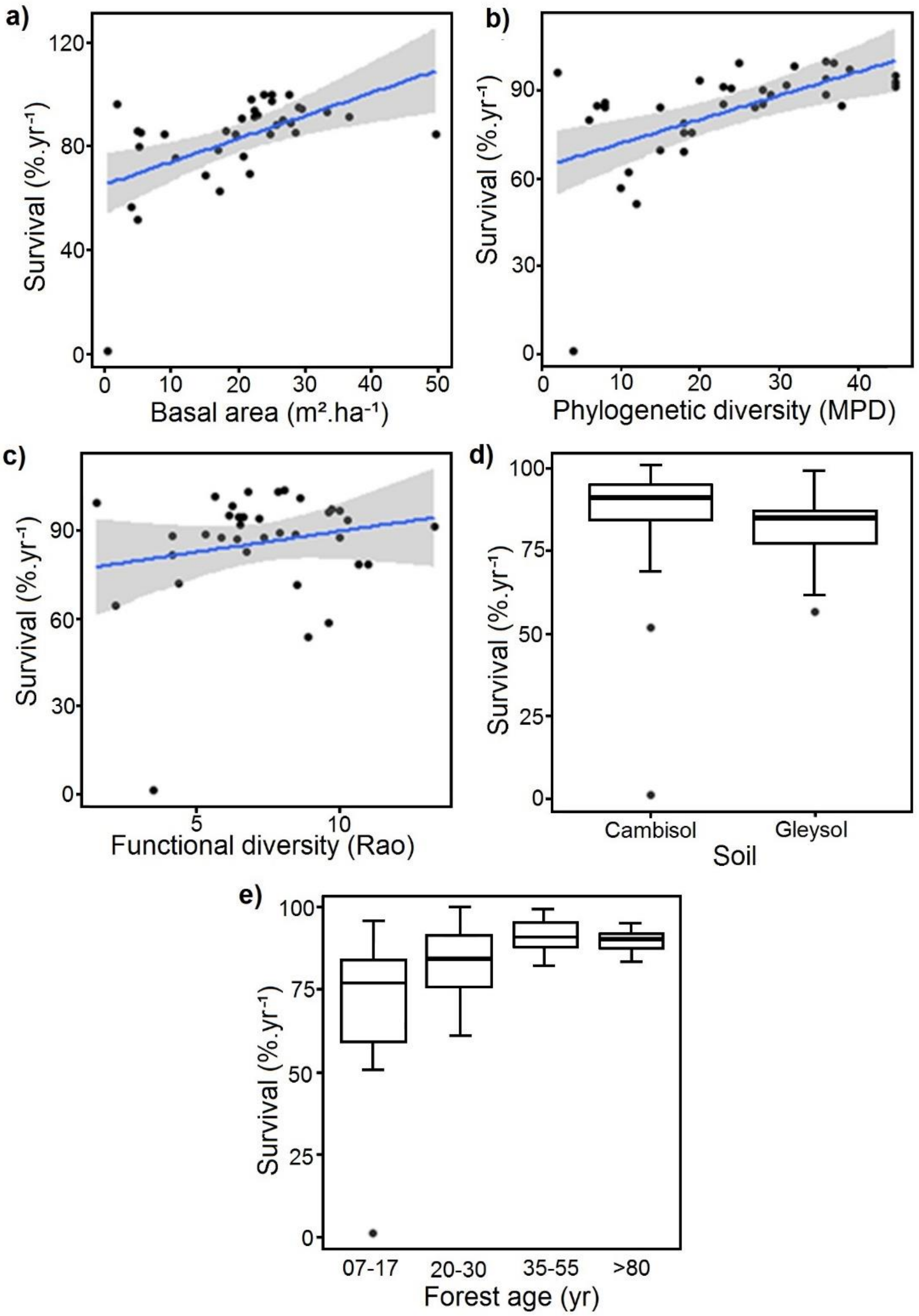

Figure A1. Relationship between the survival rate and predict variables selected in models.

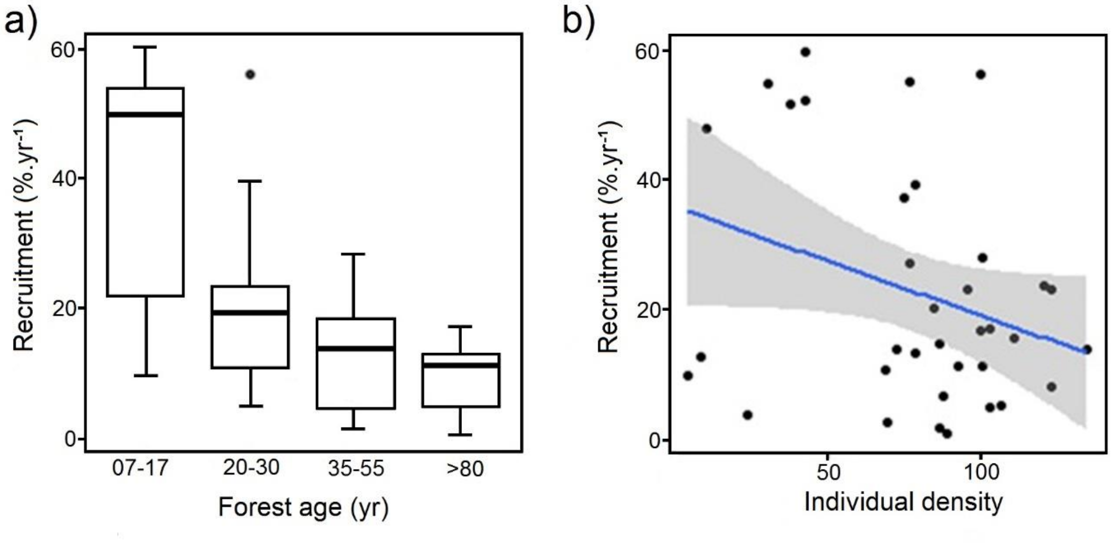

Figure A2. Relationship between the recruitment rate and predict variables selected in models.

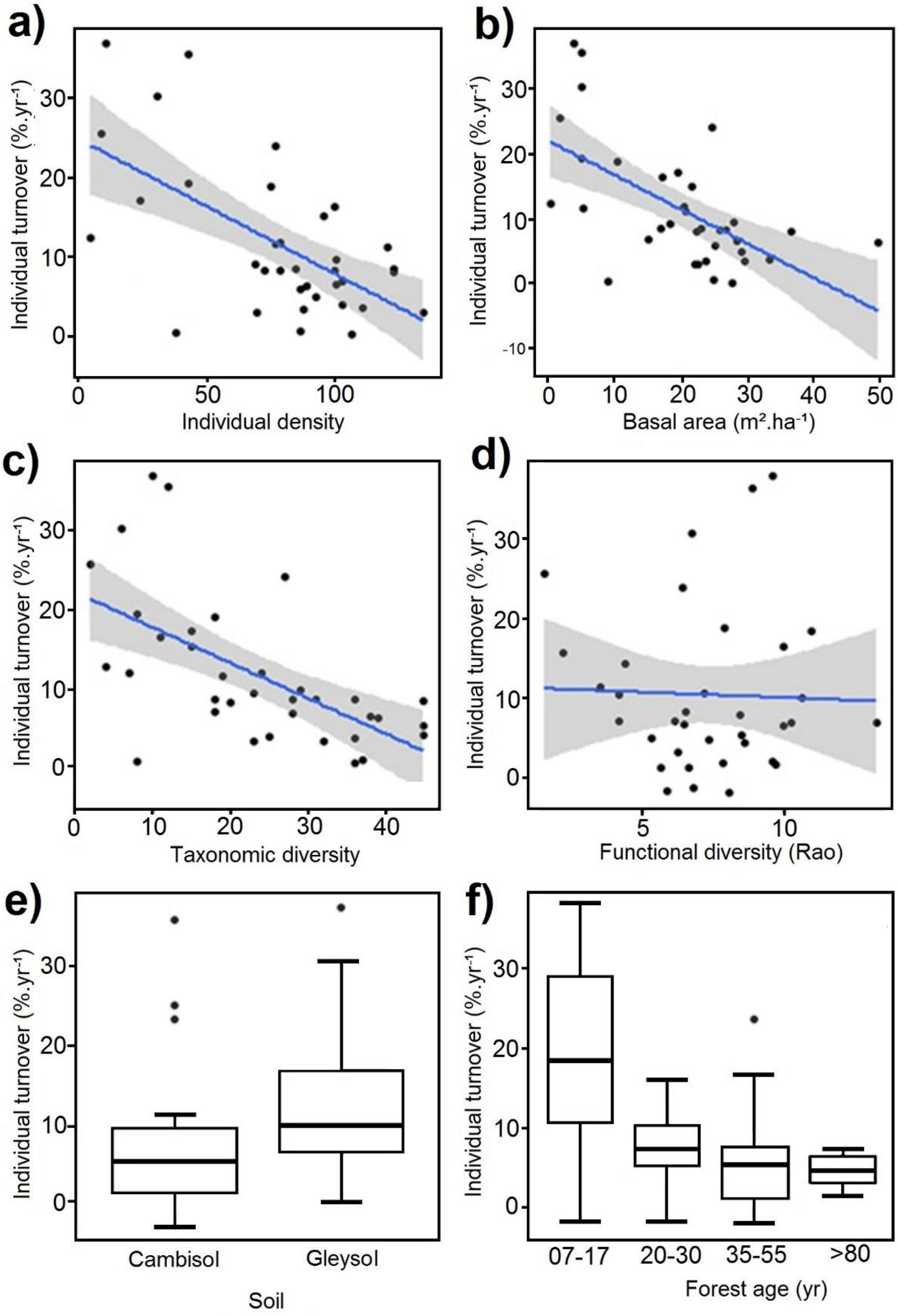

Figure A3. Relationship between the individual turnover and predict variables selected in models.

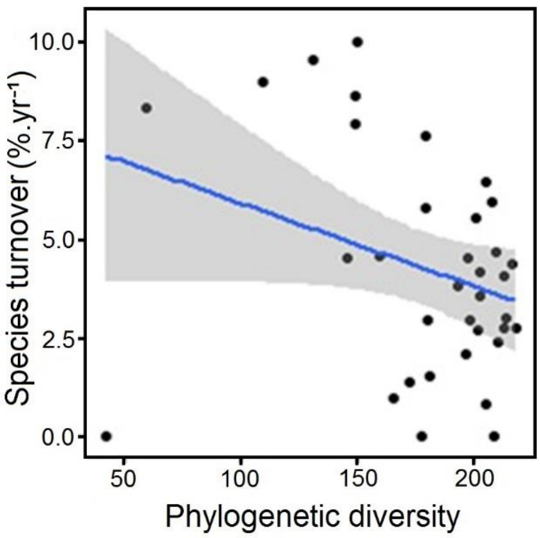

Figure A4. Relationship between the species turnover and predict variable selected in models.

Appendix 7

Relation between phylogenetic and taxonomic diversity

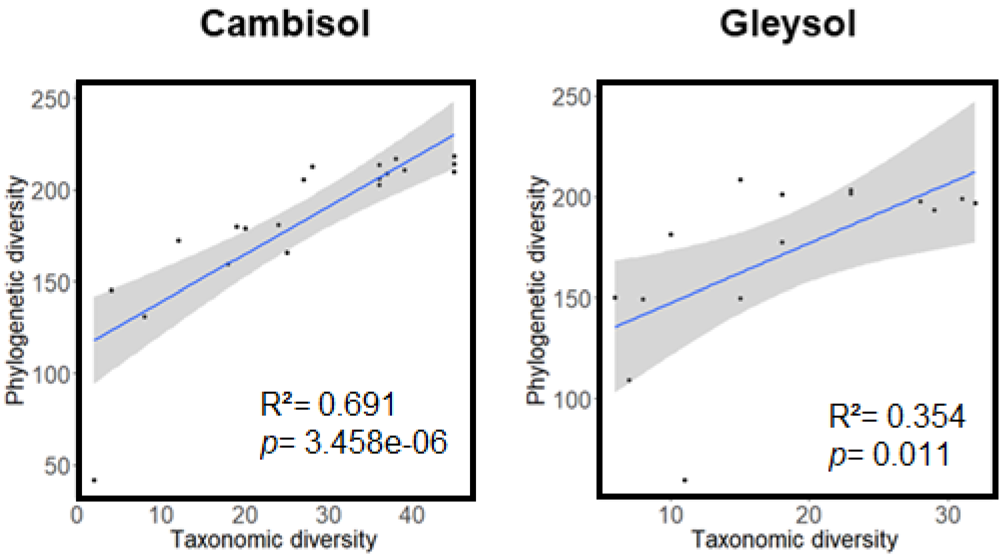

Figure A1. Positive relation between the phylogenetic diversity (mensured by MPD) and Taxonomic diversity (mensured by richness) along a successional gradient in two soil type and 2010 survey.

CONSIDERAÇÕES FINAIS

Trabalhos dentro de áreas sucessionais têm se mostrado eficientes para a investigação sobre montagem de comunidades. Aliar taxas demográficas com dados estruturais das comunidades pode ser um caminho interessante para estudar os processos envolvidos durante a montagem. Neste estudo, exploramos os efeitos dos processos e fatores estruturantes sobre as taxas demográficas ao longo da sucessão. Encontramos evidências que o determinismo afeta as comunidades e que a estocasticidade não é relevante durante a sucessão. Depois de 100 anos do estudo de Clements (1916), podemos concluir que, dentro de uma escala local, como do nosso trabalho, o processo sucessional é direcional e preditivo.

Sabendo que os processos determinísticos foram os mais importantes para a estruturação das comunidades, encontramos diferentes fatores que atuam sobre o desempenho de espécies e indivíduos ao longo da montagem de comunidades. Tanto a filtragem abiótica quanto a biótica afetam em conjunto, mas de formas diferentes, as comunidades ao longo do gradiente sucessional; a sucessão é então, resultado de um processo multi-fatorial.

Mesmo nosso trabalho apresentando um enfoque teórico, nossos achados são úteis para a prática. Saber que os processos determinísticos (previsíveis) são importantes durante a montagem das comunidades e, ainda, conseguir capturar os fatores (através de indicadores estruturais mensuráveis) que estão atuando no desempenho das espécies/indivíduos, são essenciais para o manejo de paisagens, auxiliando na restauração e nos esforços para a conservação de florestas tropicais.

REFERÊNCIAS GERAIS

AAKALA, T. et al. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. **Forest Ecol. Manag.** v.308, p.128–135, 2013.

BARTON K. MuMIn: multi-model inference. R package ver. 1.15-6, 2016.

BAZZAZ, F.A. e PICKETT, S.T.A. Physiological ecology of tropical succession: a comparative review. **Annu. Rev. Ecol. Evol. Syst.** v.11, p.287-310, 1980.

BOUKILI, V.K. e CHAZDON, R.L. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. **Perspect. Plant Ecol. Evol. Syst.** v.24, p.37–47, 2016.

BELL, C. D. et al. The age and diversification of the angiosperms re-revisited. **Am. J. Bot.** v.97, p.1296–1303, 2010.

BORGO, M. A Floresta Atlântica do litoral norte do Paraná, Brasil: aspectos florísticos, estruturais e estoque de biomassa ao longo do processo sucessional. Tese de doutorado, Universidade Federal do Paraná, 2010.

BOTTA-DUKÁT, Z. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. **J. Veg. Sci.** v.16, p.533-540, 2005.

BOUKILI, V. K. e CHAZDON, R. L. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. **Perspect. Plant Ecol. Evol. Syst.** v.24, p.37–47, 2016.

BURNHAM, K. P. e ANDERSON, D. R. **Model Selection and Multimodel Inference: A Practical Information - Theoretic Approach (2nd ed),** 2002.

BURSLEM, D. F. R. P. et al. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. **J. Ecol**. v.88, p.1063–1078, 2000.

CARDOSO, F. C. G. et al. Stem growth and phenology of two tropical trees in contrasting soil conditions**. Plant Soil** v.354, p. 269-281. 2012.

CARDOSO, F. A estruturação de comunidades vegetais em áreas sucessionais da Floresta Atlântica em diferentes tipos de solo. Tese de doutorado, Universidade Federal do Paraná, 2014.

CHALMANDRIER, L. et al. Effects of species’ similarity and dominance on the functional and phylogenetic structure of a plant meta-community. **Ecology** v.96, p.143–153, 2015.

CARDOSO, F. A estruturação de comunidades vegetais em áreas sucessionais da Floresta Atlântica em diferentes tipos de solo. **Tese de doutorado** - Universidade Federal do Paraná, 2014

CAVENDER-BARES, J., KEEN, A. e MILES, B. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. **Ecology** v.87, p.109–122, 2006.

CHAZDON, R.L. Chance and determinism in tropical forest succession. In: **Tropical forest community ecology** (Eds. W. P. Carson & S. A. Schnitzer), Oxford, UK: Blackwell Scientific, p. 384–408, 2008.

CHESSON, P. Mechanisms of Maintenance of Species Diversity. **Annu. Rev. Ecol. Syst** v.31, p.343–66, 2000.

CLEMENTS, F.E. **Plant Succession: An Analysis of the Development of Vegetation.** Carnegie Institution of Washington, Washington, DC, 1916.

CLEMENTS, F.E. Natural and Structure of the Climax. **J. Ecol.** v.24, p.252-284, 1936.

CHEUNG, K. C. et al. Forest recovery in newly abandoned pastures in Southern Brazil: implications for the Atlantic Rain Forest resilience. **Nat. Conserv.** v.8, p.66–70, 2010.

CONDIT, R. et al. The Importance of Demographic Niches to Tree Diversity. **Science** v.313, p.98-101. 2006.

CUI, W. e ZHENG, X.-X. Partitioning Tree Species Diversity and Developmental Changes in Habitat Associations in a Subtropical Evergreen Broadleaf Secondary Forest in Southern China. **Forests** v.7, p.228, 2016.

DIAMOND, J. M. e MAY, R. M. Species turnover rates on islands: dependence on census interval. **Science** v.197, p.266–270, 1977.

FEELEY, K. J. et al. Directional changes in the species composition of a tropical forest. **Ecology** v.92, p.871–82, 2011.

CONNELL, J. H. e SLATYER, R. O. Mechanisms of succession in natural communities and their role in community stability and organization. **Am. Nat.** v.111, p.1119-1144, 1977.

CAPOBIANCO, J. P. R. (Org) Dossiê Mata Atlântica. **Instituto socioambiental.** São Paulo, 2001.

COWLES, H.C. The ecological relations of the vegetation on the sand dunes of lake Michigan. **Bot. Gazet.** v.27, p.361-391, 1899.

DRAKE, J. A. The mechanics of community assembly and succession. **J. Theor. Biol.** v.147, p.213–233., 1990.

EGLER, F.E. Vegetation science concepts I. Initial floristic composition – a factor in old-field vegetation development. **Vegetatio** v.4, p.412–417, 1954.

FERRETTI, A. R. e BRITEZ, R. M. Ecological restoration, carbon sequestration and biodiversity conservation: The experience of the Society for Wildlife Research and Environmental Education (SPVS) in the Atlantic Rain Forest of Southern Brazil. **J. Nat. Conserv.** v.14, p.249–259, 2006.

FOX, J. et al. Companion to Applied Regression. **R version 3.2.0.** 2016.

GASTAUER, M. e MEIRA-NETO, J. A. A. An enhanced calibration of a recently released megatree for the analysis of phylogenetic diversity. **Brazilian J. Biol**. v.76, p.619–628, 2016.

GOLDBERG, D. E. Components of resourc competition in plant communities. - In: Grace, J. B. and Tilman, D. (ed), **Perspectives on plant competition,** Academic Press., pp 26-49. 1990.

GOTELLI, N. J. Null model analysis of species co-occurrence patterns. - **Ecology** v.81, p.2606–2621, 2000.

HUBBELL S.P. Neutral theory in community ecology and the hypothesis of functional equivalence. **Funct. Ecol** v.19, p.166–172, 2005.

HURVICH, C. M. and Tsai, C. L. Regression and time series model selection in small samples. **Biometrica** v.76, p.297–307, 1989.

IBGE. Manual Técnico da Vegetação Brasileira. **Instituto Brasileiro de Geografia e estatística, 2012.**

KAUANO, E. E. et al. Landscape structure in the northern coast of Paraná state, a hotspot for the Brazilian Atlantic Forest conservation. **Rev. Arvore** v.36, p.961–970, 2012.

KEMBEL, S. W. et al. Picante: R tools for integrating phylogenies and ecology. **Bioinformatics v.**26, p.1463–1464, 2010.

FOLEY, J. A.; DEFRIES, R.; ASNER, G. P.; BARFORD, C.; BONAN, G.; CARPENTER, S. R.; CHAPIN, F. S.; COE, M. T.; DAILY, G. C.; GIBBS, H. K.; HELKOWSKI, J. H.; HOLLOWAY, T.; HOWARD, E. A.; KUCHARIK, C. J.; MONFREDA, C.; PATZ, J. A.; PRENTICE, I.C.; RAMANKUTTY, N.; SNYDER, P. K. Global Consequences of Land Use. **Science** v.309, p.570-574, 2005.

FRICKE, E.C. e WRIGHT, S.J. Measuring the demographic impact of conspecific negative density dependence. **Oecologia** v.184, p.259–266, 2017.

GAUSE, G.F. The struggle for existence. **Williams and Wilkins**, Baltimore. 1934

GLEASON, H. A. The individualistic concept of the plant association**. J. Torrey Bot. Soc.** v.53, p.7-26, 1926.

KREBS, P. et al. Modelling the eco-cultural niche of giant chestnut trees: new insights into land use history in southern Switzerland through distribution analysis of a living heritage. **J. Hist. Geog.** V.38, p.372- 386, 2012.

LALIBERTÉ, E. et al. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. **R package version** 1.0-12, 2014.

LASKY, J. R. et al. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. **Ecol. Lett.** v.17, p.1158–1167, 2014a.

GLENN-LEWIN, D.C.; MAAREL, E. VAN DER. Pattern and process of vegetation dynamics. In: **Plant Succession: theory and prediction**, Glenn-Lewin, D.C.; Peet, R.K.; Veblen, T.T. (Eds). Chapman & Hall. pp.11-59, 1992.

HARPER, J. L. e WHITE, J. The demography of plants. **Annu. Rev. Ecol. Syst.** v.5, p.419-463, 1974.

HUBBELL, S.P. Neutral theory in community ecology and the hypothesis of functional equivalence. **Funct. Ecol** v.19, p.166–172, 2005.

KEDDY, P. A. Assembly and response rules: Two goals for predictive community ecology. **J. Veg. Sci.** Uppsala, v. 3, n. 2, p.157-164, 1992.

KRAFT, N.J.B.; VALENCIA, R. e ACKERLY D.D. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. **Science** v.322, p.580-582; 2008.

LASKY, J.R., URIARTE, M., BOUKILI, V.K. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. **Proc. Natl. Acad. Sci.** v.111, p.5616–5621, 2014.

LEBRIJA-TREJOS, E.; PÉREZ-GARCÍA, E.A.; MEAVE, J.A.; BONGERS, F.; POORTER, L. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. **Ecology** v.91, p.386–398, 2010.

LETCHER, S.G., CHAZDON, R.L., ANDRADE, A.C.S., BONGERS, F., VAN BREUGEL, M., FINEGAN, B., LAURANCE, S.G., MESQUITA, R.C.G., MARTÍNEZ-RAMOS, M., WILLIAMSON, G.B. Phylogenetic community structure during succession: Evidence from three Neotropical forest sites. **Perspect. Plant Ecol. Evol. Syst.** v.14, p.79–87, 2012.

LIEBSCH, D.; GOLDENBERG, R.; MARQUES, M. C. M. Florística e estrutura de comunidades vegetais em uma cronoseqüência de Floresta Atlântica no Paraná. **Acta Bot. Brasilica** v.21, n.4, p.983-992, 2007.

LOREAU, M. Biodiversity and ecosystem functioning: a mechanistic model. **Proc. Natl. Acad. Sci**. v.95, p.5632–5636, 1998.

MALTHUS, T.R. An essay on the principle of population. **J. Johnson,** London, 1798.

MARGALEF, R. On certain unifying principles in ecology. **Am. Nat.,** v.97, p.357-374, 1963.

MEINERS, S. J., Cadotte, M.W., Fridley, J.D., Pickett, S.T.A., Walker, L.R. Is successional research nearing its climax? New approaches for understanding dynamic communities. **Funct. Ecol.** v.29 p.154–164, 2015.

MELLO, J. M., COUTO, E.G., AMORIM, R.S.S., CHIG, L.A., JOHNSON, M.S., LOBO, F.A. Dinâmica dos atributos físico-químicos e variação sazonal dos estoques de carbono no solo em diferentes fitofisionomias do pantanal norte mato-grossense. **Rev. Árvore**, Viçosa, v. 39, n. 2, p. 325-336, Apr. 2015.

MIRANDA, J.C. Sucessão ecológica: conceitos, modelos e perspectivas. **Rev. Saúde e Biol.,** v.4, n.1, p 31-37, Jan/Jun 2009

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., da FONSECA, G.A., KENT, J. Biodiversity hotspots for conservation priorities. **Nature** v.403, p.853–858, 2000.

NUCHE, P. e ALADOS, C.L. Shrub interactions drive vegetation succession of subalpine grasslands under two climatic conditions. **J. Plant Eco.** v. p.1-11, Jan 2017.

LOHBECK, M. et al. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. **Ecology** v.96, p.1242–1252, 2015.

MACARTHUR, R. e LEVINS, R. The limiting similarity, convergence, and divergence of coexisting species. **Amer. Nat.** v.101, p.377-385, 1967.

MARCILIO-SILVA, V. et al. Functional turnover and community assemblage during tropical forest succession. **Community Ecol**. v.17, p.88–97, 2016.

MARQUES, M. C. M. et al. Dynamics and diversity of flooded and unflooded forests in a Brazilian Atlantic rain forest: a 16-year study. **Plant Ecol. Divers**. V.2, p.57–64, 2009.

MARTINS, K. G. et al. Effects of soil conditions on the diversity of tropical forests across a successional gradient. **For. Ecol. Manage**. 349, p.4–11, 2015.

MCGILL, B. J. et al. Rebuilding community ecology from functional traits. **Trends Ecol. Evol.** V.21, p.178–185, 2006.

MORRIS, D. W. Ecological Scale and Habitat Use. **Ecology**, v.68, p.362–369, 1987.

NORDEN, N. et al. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. **Ecology** v.93, p.70-82, 2012.

ODUM, E.P. The strategy of ecosystem development. **Science** v.164, p.262-270, 1969.

OLIVEIRA, M. C. e JÚNIOR, M. C. S. Evolução Histórica Das Teorias De Sucessão Vegetal E Seus Processos. **CEPPG** v.24, p.104-118, 2011.

PICKETT, S.T.A. Succession: an evolutionary interpretation. **Am. Nat.** v.110, p.107-119, 1976.

PICKETT, S.T.A., CADENASSO, M.L., MEINERS, S.J. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. **App. Veg. Sci.** v.12, n.1, p.9-21, february 2009.

PIQUERAS, M.M. e BRANDO, F.R. As contribuições do americano Henry Allan Gleason (1882-1975) para a Ecologia no início do século XX. **História da Ciência e Ensino**, v.13, p. 48-68, 2016.

NORDEN, N. et al. Successional dynamics in Neotropical forests are as uncertain as they are predictable. **Proc. Natl. Acad. Sci.** v.112, p.8013-8018, 2015.

OKSANEN, J. et al. Community Ecology Package. **R package version** 2.4-3. 2017.

PASINELLI, G. M. et al. Possible causes and consequences of philopatry and breeding dispersal in Red-backed Shrikes Lanius collurio. **Behav. Ecol. Sociobiol.** v.61, p.1061-1074. 2007.

PÉREZ-HARGUINDEGUY, N. et al. New Handbook for standardized measurment of plant functional traits worldwide. **Aust. J. Bot.** v.23, p.167–234. 2013.

PHILLIPS, O. L. et al. Dynamics and species richness of tropical rain forests. - **Proc. Natl. Acad. Sci**. v.91, p.2805–2809. 1994.

PHILLIPS, O. L. et al. Pattern and process in Amazon tree turnover, 1976–2001. **Philos. Trans. R. Soc. London. Ser. B** v.359, p.381–407. 2004.

R DEVELOPMENT CORE TEAM. R: A Language and Environment for Statistical Computing. **R Foundation for Statistical Computing**, Vienna. 2016.

RAO, C.R. Diversity and dissimilarity coefficients: a unified approach. **Theor. Pop. Biol.** v.21, p.24-4. 1982.

REES, M.C.R. Long-Term Studies of Vegetation Dynamics. **Science** v.293, n.5530, p.293-650. Jul, 2001.

RIBEIRO, M. C. METZGER, J.P., MARTENSEN, A.C., PONZONI, F.J., HIROTAET, M.M. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biol. Conserv.** v.142, p.1141–1153, 2009.

ROBINSON, S.J.B., BERG, E., MEIRELLES, G., OSTLE, N. Factors influencing early secondary succession and ecosystem carbon stocks in Brazilian Atlantic Forest. **Biodivers. Conserv.** v.24, p.2273–2291, 2015.

TANSLEY, A.G. The use and abuse of vegetational concepts and terms. **Ecology** v.16, p.284-307; 1935.

TILMAN, D. REICH, P.B. KNOPS, J. WEDIN, D. MIELKE, T. & LEHMANN, C. Diversity and productivity in a long-term grassland experiment. **Science** v.294, p.843–845, 2001.

VAMOSI, S.M., HEARD, S.B., VAMOSI, J.C. & WEBB, C.O. Emerging patterns in the comparative analysis of phylogenetic community structure. **Mol. Ecol**. v.18, n.4, p.572-592, Nov. 2009.

VAN ANDEL, J., BAKKER, J.P., GROOTJANS A. P. Mechanisms of Vegetation Succession: a review of concepts and perspectives. **Acta Bot. Neerlandica** v. 42, n. 4, p. 413-433, Dec., 1993.

VAN BREUGEL, M., BONGERS, F., MARTÍNEZ-RAMOS, M. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. **Biotropica** v. 35, p. 610–619, 2007.

SCHNITZER, S. A. e CARSON, W. P. Treefall gaps and the maintenance of species diversity in a tropical forest. **Ecology** v.82, p.913–919. 2001.

SHEIL, D. et al. The Interpretation and misinterpretation of mortality rate measures. **J. Ecol.** v.83, p.331–333. 1995.

SUTHERLAND, W. J. et al. Identification of 100 fundamental ecological questions. **J. Ecol.** v.101, p.58–67. 2013.

SVENNING, J. C. Ecological determinism in plant community structure across a tropical forest landscape. **Ecology** v.85, p.2526- 2538. 2004.

SWENSON, N. G. e ENQUIST, B. J. Opposing assembly mechanisms in a Neotropical dry forest: Implications for phylogenetic and functional community ecology. **Ecology** v.90, p.2161–2170, 2009.

SWENSON, N. G. et al. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. **Ecology** v.93, p.490–499, 2012.

TILMAN, D. et al. The influence of functional diversity and composition on ecosystem processes. **Science** v.277, p.1300–1302, 1997.

ULRICH, W. et al. Soil conditions and phylogenetic relatedness influence total community trait space during early plant succession. **J. Plant Ecol.** v.7, p.321–329, 2014.

VALLADARES, F. e NIINEMETS, I. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences**. Annu. Rev. Ecol. Evol. Syst**. v.39, p.237-57. 2008.

VAN BREUGEL, M. et al. Community dynamics during early secondary succession in Mexican tropical rain forests. **J. Trop. Ecol.** v.22, p.663–674. 2006.

VIOLLE, C. et al. The return of the variance: Intraspecific variability in community ecology. **Trends Ecol. Evol.** V.27, p.244–252. 2012.

WEBB, C. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. **Am. Nat**. v.156, p.145–155. 2000.

WEBB, C. O. e DONOGHUE, M. J. Phylomatic: Tree assembly for applied phylogenetics. **Mol. Ecol. Notes** v.5, p.181–183. 2005.

VOLTERRA, V. Fluctuations in the abundance of a species considered mathematically. Nature v.118, p.558-60, 1926. In Real, L. A.; Brown, J. H. **Foundations of ecology – classic papers with commentaries.** The University of Chicago Press, 1991.

WHITTAKER, R. A consideration of climax theory: the climax as a population and pattern. **Eco. Monog.** v.23, p.41-78, 1953.

WEBB, C. O. et al. Phylogenies and Community Ecology. **Annu. Rev. Ecol. Syst**. v.33, p.475–505, 2002.

ZHANG, J. Species Association Analysis. **R package version 0.2.2**. 2016.

ZWIENER, V.P. et al. Disentangling the effects of facilitation on restoration of the Atlantic Forest. **Basic Appl. Ecol.** v.15, p.34–41, 2014.