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A ESTRUTURAÇÃO DE COMUNIDADES VEGETAIS EM ÁREAS
SUCCESIONAIS DA FLORESTA ATLÂNTICA EM DIFERENTES TIPOS
DE SOLO

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RESUMO GERAL

O século XX culminou uma fase de desmatamentos de origem antrópica sem precedentes nas florestas tropicais do planeta. Com o desaparecimento de quase a totalidade das florestas primárias pelo mundo, houve um grande aumento na importância das florestas secundárias, já que estas podem oferecer *habitats* para imensa biodiversidade, participam do equilíbrio climático do planeta e prestam os mais variados serviços ecossistêmicos, incluindo o sequestro de carbono. Quando uma floresta passa por um distúrbio, há uma série de fatores que influenciam na sua capacidade de regeneração e quão rápido isso irá acontecer, tais como características da paisagem, histórico de uso da área, tipo de manejo e fatores edáficos. Neste trabalho abordamos os efeitos de diferentes fatores sobre a estruturação de comunidades vegetais em áreas sucessionais da Floresta Atlântica, em Antonina, Paraná (25°19'15"S e 48°42'24"W). As áreas florestais foram transformadas em pastagens para búfalos e depois abandonadas em diferentes períodos ao longo dos últimos 80 anos. As áreas estão sendo restauradas por meio de regeneração natural (isolamento do gado) e de plantio direto de mudas de espécies nativas, em um projeto de larga escala (20 mil hectares) desenvolvido pela Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental (SPVS). No primeiro capítulo desta tese, analisamos a importância relativa dos seguintes fatores: técnicas usadas no manejo de pastagem, características do solo e da paisagem, idade e estratégia usada na restauração destas áreas. Para tanto, foram estabelecidas 93 parcelas circulares (total de 5,7 ha) distribuídas ao longo de áreas de restauração, onde foram amostradas todas as árvores e arbustos compondo o dossel (diâmetro à altura do peito, $DAP_{\geq} 5,0$ cm) e o sub-bosque ($DAP < 5,0$ cm e altura $\geq 1,3$ m). Utilizamos o método de seleção de modelos para descobrir

qual combinação de fatores tem maior influência na estrutura e riqueza das florestas em restauração. Foram amostrados um total de 7378 indivíduos em 93 parcelas, sendo 5144 indivíduos de 234 espécies no dossel e 2234 indivíduos de 220 espécies no sub-bosque. Os resultados mostraram que idade, distância da área de floresta mais próxima e espécies de pasto utilizadas anteriormente à restauração são os fatores que mais fortemente influenciam riqueza, abundância, área basal e altura média das comunidades de sub-bosque e dossel. No segundo capítulo, utilizamos uma sub-amostra de 45 parcelas, apenas em áreas de regeneração natural, de 3 a 80 anos de idade, ocorrendo em dois tipos de solo (Cambissolo:bem drenado e Gleissolo:periodicamente alagado) para testar possíveis efeitos do tipo de solo sobre a sucessão. Encontramos um gradiente claro de riqueza, abundância, área basal e altura ao longo da sucessão. Áreas de Cambissolo acumularam espécies mais rapidamente que as de Gleissolo no dossel, mas este padrão não se repetiu para o sub-bosque, o qual teve curvas de acumulação de espécies coincidentes para os dois tipos de solo. Concluiu-se que as características do solo desempenham um papel complementar ao forte gradiente de idade para explicar as trajetórias sucessionais em florestas tropicais, e também devem ser levadas em consideração no planejamento do manejo florestal. No terceiro capítulo, analisamos as diversidades taxonômica e funcional neste mesmo gradiente de solo e idade (Capítulo 2) para entender como são estruturadas as comunidades ao longo do processo de sucessão em dois tipos de solos contrastantes. Compilamos nove atributos funcionais de espécies do dossel do sub-bosque e utilizamos técnicas analíticas (correlação de matrizes) que permitem diferenciar convergência e divergência de atributos. Encontramos padrões de convergência e divergência atuando na estruturação das comunidades em nosso gradiente idade-solo, maximizados por diferentes atributos. No dossel, os atributos polinização por vertebrados e abiótica, tolerância à sombra, esbelteza da folha e folha do tipo composta foram diferentes entre os tipos de solo,

enquanto que no sub-bosque a interação com solo foi encontrada nos atributos tolerância à sombra e esbelteza da folha. As diversidades taxonômica e funcional aumentaram com a idade da floresta em ambos os estratos, embora apenas algumas destas métricas de diversidade tenham se diferenciado entre os tipos de solo (entropia de Rao no dossel; riqueza de espécies e redundância funcional no sub-bosque; H' e riqueza funcional em ambos). Concluimos neste capítulo que as comunidades em desenvolvimento no gradiente idade-solo são estruturadas por uma combinação de filtros abióticos e interações bióticas. Os resultados dos três capítulos permitem concluir que características do solo podem ocasionar diferenças estruturais, florísticas e funcionais em áreas florestais em sucessão, e podem fornecer subsídios para acelerar o processo de regeneração em florestas tropicais, identificando suas principais barreiras.

ABSTRACT

During the last century, tropical forests on the planet experienced a period of unprecedented deforestation of anthropogenic cause. With the disappearance of almost all primary forests in the world, secondary forests largely increased in importance, as these can provide habitats for vast biodiversity, contribute with the climatic balance of the planet and provide a variety of ecosystem services, including carbon sequestration. When a forest undergoes disturbance, there are a number of factors that influence its ability to regenerate and how fast this will happen, such as landscape features, historical land use, type of land management and edaphic factors. In this paper we address the effects of soil characteristics on the structure of plant communities in successional areas of the Atlantic Forest in Antonina, Paraná (25°19'15" S and 48°42'24" W). Over the last 80 years, many forest areas in the region have been converted into pasture for buffalos and then abandoned in different periods. The areas are now being restored through natural regeneration (isolation of the cattle) or direct planting of seedlings of native species, as part of a large-scale project (20,000 hectares) developed by the Society for Wildlife Research and Environmental Education (SPVS). In the first chapter of this thesis, we analyze the relative importance of different factors (age, pasture management techniques, soil and landscape characteristics; and restoration strategy) that influence the restoration in this area. We selected 93 circular plots (5.7 ha total) distributed along restoration areas and sampled all canopy trees (diameter at breast height, $DBH \geq 5.0$ cm) and all understory individuals (trees and shrubs, $DBH \leq 5.0$ cm and $height \geq 1.3$ m). We used a model selection approach to find out which combination of factors have greater influence on the structure and richness of forests undergoing restoration. A total of 7378

individuals were sampled, with 5144 individuals of 234 species in the canopy, and 2234 individuals of 220 species in the understory. The results revealed that age, distance from the nearest forest area and species of pasture previously used in the restoration are the factors that most influence richness, abundance, basal area and mean height of understory and canopy communities. In the second chapter, we considered a sub-sample of 45 plots, only of natural regeneration areas, with ages varying from 2 to 80 years, occurring in two types of soil (Cambisol: well drained and Gleysol: periodically flooded) to test possible effects of soil type on the succession. We found a clear gradient of species richness, abundance, basal area and height along succession age. Cambisol areas accumulated species faster than Gleysol areas in the canopy, but this pattern was not recurrent in the understory, where accumulation curves in the two soil types were coincident. We concluded that soil characteristics play a supporting role in the strong age gradient in explaining the successional trajectories in tropical forests, and should also be taken into consideration in forest management planning. In the third chapter, we analyzed the taxonomic and functional diversity in the same gradient of soil and age (Chapter 2) to understand how communities are structured along the succession process in two contrasting soil types. We compiled nine functional traits of canopy and understory species and used analytic techniques (correlation of matrices) that allow the distinction between convergence and divergence of traits along the gradient. We found significant patterns of convergence and divergence structuring communities in our soil-age gradient, maximized by different traits. In the canopy, the traits abiotic and vertebrate pollination, shade tolerance, leaf slenderness and leaf type (composed leaves) revealed interactions with soil type, while in the understory, soil type was important for the traits shade tolerance and leaf slenderness. Taxonomic and functional diversities increased with age in both forest strata, although only some of these metrics were different between types of soil (Rao entropy in the

canopy, species richness and functional redundancy in the understory; H' and functional richness in both). We conclude in this chapter that plant communities under development are structured by a combination of abiotic filters and biotic interactions. The overall results show that soil characteristics can cause structural, floristic and functional differences in successional forest areas, and should be taken into account in the implementation of restoration plans and management actions.

1. INTRODUÇÃO GERAL

A teoria da sucessão tem sido um grande foco da ecologia, desde seus primeiros estudos no século XVIII em comunidades de dunas, até os dias de hoje, em todos os tipos de ecossistemas e com diferentes abordagens. Originalmente, em comunidades vegetais, a teoria da sucessão ecológica era vista como preditiva e direcional por Clements (1904, 1916), que descrevia a sucessão como um processo ordenado e determinístico, no qual a comunidade atua como uma unidade integrada que ao final chegaria ao clímax. No entanto, Gleason (1926) descreveu a sucessão ecológica como um processo estocástico, no qual cada espécie individualmente influencia as mudanças na composição da comunidade, ideia que ainda permanece dentre as mais atuais (Glenn-Lewin *et al.* 1992). Ao contrário de Clements, Egler (1954) acreditava que a sucessão secundária seria mais fortemente determinada pela composição florística inicial de uma área, sendo resultado das histórias de vida dos organismos que compõem a comunidade. Whittaker (1953) sugeriu que a vegetação varia continuamente ao longo da paisagem, e que a dinâmica de uma comunidade clímax é determinada pelas características bióticas e abióticas do ecossistema. Já nos anos 70, ecólogos substituíram as ideias de equilíbrio com as teorias alternativas de não-equilíbrio e começaram a enfatizar a base mecanicista dos processos ecológicos (Chazdon 2008), onde eram destacadas as mudanças na disponibilidade de recursos durante a sucessão (Odum 1959, Drury & Nisbet 1973, Noble & Slatyer 1980). Juntamente com essas ideias, também surgiu a teoria do distúrbio intermediário, que prediz que a diversidade atinge um pico durante fases

intermediárias da sucessão e decresce a níveis mais baixos numa comunidade tardia, com pouco distúrbio (Connell 1978).

Atualmente, estudos de dinâmica da vegetação durante a sucessão em florestas tropicais têm considerado três estruturas conceituais. A primeira examina o papel de fatores determinísticos *versus* fatores estocásticos na dinâmica da vegetação (Chazdon 2008). A segunda, baseada no tempo de colonização das espécies durante a sucessão, compara a composição florística inicial (espécies de todos os estágios sucessionais colonizam uma área ao mesmo tempo, mas chegam a picos de abundância em diferentes épocas) com a substituição da composição florística (primeiramente as espécies iniciais da sucessão colonizam a área para mais tarde dar espaço para as mais tardias) (Bazzaz & Pickett 1980, Chazdon 2008). A terceira estrutura foca na importância relativa de atributos da história de vida de cada espécie na determinação do balanço entre mecanismos de tolerância, inibição e facilitação durante a sucessão, no qual espécies mais tardias poderão se estabelecer somente após uma facilitação pelas espécies pioneiras ou por características próprias como taxa de crescimento e longevidade (Connell & Slatyer 1977, Rees *et al.* 2001, Chazdon 2008).

Nas florestas tropicais em geral, o processo sucessional tende a uma progressão de estágios durante os quais florestas apresentam um enriquecimento gradual de espécies e um aumento em complexidade estrutural e funcional (Chazdon 2012). No entanto, as mudanças que ocorrem na comunidade durante a sucessão florestal podem apresentar inúmeras variações e múltiplas trajetórias sucessionais, muitas vezes refletindo diferenças no uso anterior do solo (Mesquita *et al.* 2001). Há uma série de fatores que influenciam a regeneração de uma floresta determinando sua capacidade e velocidade de desenvolvimento (Uhl 1987, Aide & Cavellier 1994; Rodrigues *et al.* 2009). No início da sucessão, os fatores mais importantes são aqueles que determinam a colonização (tipo de substrato, chuva de sementes, banco de sementes,

rebrotos), até chegar a etapas mais avançadas onde a habilidade competitiva das espécies e suas tolerâncias às condições ambientais determinam os padrões de substituição de espécies (Guariguata & Ostertag 2001). A estrutura da vegetação que se estabelece após um distúrbio é variada e depende de fatores como a intensidade e o tipo do distúrbio, o período em que a área foi perturbada, o tamanho da clareira, características do solo, presença de espécies invasoras e a disponibilidade de matriz de recolonização (Swaine & Whitmore 1988; Gunderson 2000; Chazdon 2003, Myster 2004, Chazdon 2008). Geralmente, as áreas em regeneração natural em estádios iniciais da sucessão secundária são primeiramente colonizadas por espécies herbáceas pioneiras e espécies arbóreas de ciclo vital curto e crescimento rápido (Budowski 1965). Posteriormente, a vegetação herbácea declina e as espécies pioneiras que se estabeleceram irão fornecer melhores condições para o surgimento de espécies secundárias iniciais e mais tarde, secundárias tardias, que se estabelecem em ambiente sombreado e, crescem quando as condições de luz são favoráveis. O estágio avançado de sucessão é caracterizado pela ocorrência de espécies arbóreas secundárias (Brokaw 1985, Swaine & Whitmore 1988, Finegan 1996). Com o crescimento das espécies secundárias tardias, ocorre o fechamento do dossel, que acaba por suprimir as espécies intolerantes à sombra, enquanto espécies tolerantes no continuam a se estabelecer sub-bosque (Chazdon 2012).

O processo de sucessão secundária ocorre naturalmente nos ecossistemas, possibilitando sua recuperação após distúrbios (Schulze *et al.* 2005). Entretanto, há casos onde o processo de regeneração é muito lento ou onde o ecossistema não consegue se recuperar naturalmente, quando faz-se necessária uma intervenção humana, através de uma atividade de restauração (Parrotta *et al.* 1997, Aide *et al.* 2000, Martinez-Garza & Howe 2003). Desta forma, a recuperação de um ecossistema que sofreu distúrbio pode ocorrer por

processos naturais (regeneração natural) ou através de outros métodos como plantio direto de mudas, semeadura direta, nucleação ou adensamento da vegetação (Rodrigues *et al.* 2009). A opção por um ou outro modelo depende de inúmeros fatores que interferem no grau de resiliência do ecossistema.

A implantação de planos de restauração ecológica, preparados a partir de bases ecológicas precisas, é essencial para garantir a funcionalidade das comunidades florestais restauradas (Young 2000, Hobbs & Harris 2001). Dados sobre a fenologia, reprodução, características da semente (incluindo modo de dispersão e predação), mecanismos de regeneração (chuva e banco de sementes, rebrotos), taxas de crescimento (Parrotta *et al.* 1997, Guariguata & Pinard 1998, Holl 1999, Aide *et al.* 2000, Vieira & Scariot 2006), entre outros, são essenciais para estabelecer uma prática de restauração ecológica eficiente.

O objetivo da restauração é criar um ecossistema auto-suficiente que seja resistente às perturbações e não necessite mais de assistência após um certo período (SER 2004). Os métodos para mensurar quando esse objetivo é atingido são uma discussão frequente na ecologia, mas a maioria dos estudos normalmente utiliza medidas de estrutura da vegetação, diversidade de espécies ou processos ecossistêmicos (Ruiz-Jaen & Aide 2005). Paralelamente a estes atributos, deve-se também compará-los com ecossistemas de referência sujeitos a condições similares às das áreas restauradas, para ter uma estimativa do sucesso da restauração (Hobbs & Harris 2001, SER 2004).

Apesar do aumento no número de estudos abordando a restauração de ecossistemas em várias regiões do mundo nas últimas décadas (Sayer *et al.* 2004, Young *et al.* 2005), ainda existem muitas lacunas no conhecimento acerca dos ecossistemas florestais restaurados. Menos de 10% dos estudos que avaliaram a restauração após o plantio de mudas ou semeadura direta foram realizados em florestas tropicais, por exemplo (Ruiz-Jaen & Aide

2005). Uma maneira de ampliar nosso entendimento sobre os ecossistemas em regeneração é aproveitá-los para estudos de regras de montagem (*assembly rules*) de comunidades. Considerando que a sucessão secundária já foi descrita como a “estruturação de comunidades em ação” (Lebrija-Trejos *et al.* 2010), ela pode nos auxiliar a compreender um dos maiores desafios da ecologia, que é entender quais processos determinam a distribuição e coexistência de espécies em florestas tropicais. Cada espécie dentro de uma comunidade tem seu próprio conjunto específico de características ou atributos funcionais, que irão influenciar a forma como cada uma delas responderá às condições bióticas e abióticas do meio (Reich *et al.* 2003, Violle *et al.* 2007). A diversidade de estados de cada atributo funcional presente em uma comunidade vai determinar a sua diversidade funcional, a qual permite o entendimento da dinâmica de recursos, estabilidade e produção dos ecossistemas (Díaz & Cabido 1997, Mason *et al.* 2005).

Os atributos podem evoluir em resposta às condições ambientais e interações com outras espécies (Reich *et al.* 2003). Filtros ambientais podem selecionar espécies que ocorrem em um determinado lugar, devido às condições limitantes, como a luminosidade, temperatura e umidade (Keddy 1992). Assim, apenas as espécies que têm atributos que lhes conferem a capacidade de resistir a tais condições serão capazes de sobreviver num determinado local (Cavender-Bares *et al.* 2009). Estas adaptações às condições do ambiente devem levar a uma convergência de determinados atributos funcionais dentro da comunidade. Por outro lado, espécies que utilizam um recurso de forma semelhante não devem coexistir frequentemente, uma vez que a que é competitivamente superior irá excluir a outra quando os recursos do ambiente forem limitantes (Weiher *et al.* 1998). Desta forma, a competição implica em uma limitação de similaridade no uso de recursos (MacArthur & Levins 1967) e consequentemente, a uma divergência nos atributos funcionais entre as espécies.

O uso de atributos funcionais na restauração está apenas começando (Temperton *et al.* 2004). Nos trópicos, a alta complexidade de espécies impõe uma barreira para modelagem de tamanha diversidade, tornando difícil a utilização da diversidade taxonômica. A utilização de medidas de diversidade funcional, portanto, pode simplificar e aprimorar nosso entendimento sobre os processos de restauração. Os atributos funcionais de plântulas e árvores podem ser fortes determinantes de taxas demográficas que governam mudanças na composição de espécies durante a regeneração florestal (Chazdon 2014). A escolha das espécies para a restauração não deve ser feita apenas através das suas necessidades de luz, mas deve incluir atributos em nível de comunidade como fenologia, síndrome de dispersão, habilidade de reprodução vegetativa, habilidade de fixar nitrogênio, deciduidade, produção de serapilheira, entre outros (Sansevero 2013).

Diversos projetos de restauração e estudos de sucessão estão sendo desenvolvidos na Floresta Atlântica (Floresta Ombrófila Densa). Este bioma é considerado um dos mais ameaçados do planeta e encontra-se extremamente fragmentado, restando menos de 12% da sua cobertura original (Ribeiro *et al.* 2009). Devido à sua alta riqueza de espécies e endemismo, é atualmente um dos *hotspots* para conservação da biodiversidade (Myers *et al.* 2000, Martini *et al.* 2007). Para plantas, por exemplo, 40% de suas 8000 espécies são endêmicas (Metzger 2009) e muitas de suas espécies encontram-se entre as mais ameaçadas do planeta (Mittermeier *et al.* 2005). Assim como outros sistemas taxonomicamente diversos, a Floresta Atlântica também possui uma enorme diversidade funcional, relacionada à biologia reprodutiva das espécies e aos diversos tipos de interações, o que a torna ainda mais difícil de restaurar (Rodrigues *et al.* 2009). A destruição da Mata Atlântica do Brasil e sua biodiversidade começou juntamente com a colonização do Brasil, há mais de 500 anos (Dean 1996) e chegou em níveis alarmantes ao longo do tempo. Apenas nos últimos 30 anos, o

Brasil experimentou um progresso em ações para conservação, junto com a criação de parques e áreas protegidas (Mittermeier *et al.* 2005). Hoje, os principais remanescentes concentram-se nas regiões Sul e Sudeste do Brasil, recobrando parte da Serra do Mar e da Serra da Mantiqueira, onde o processo de ocupação foi dificultado pelo relevo acidentado e pouca infra-estrutura de transporte (Capobianco 2001).

Nos remanescentes de Floresta Atlântica do sul do Brasil, encontram-se áreas florestais com diferentes níveis de interferência, muitas vezes intercaladas por pastagens abandonadas, que estão em processo de regeneração e em diferentes estágios sucessionais, constituindo um mosaico ambiental. Desta forma, a região é favorável para o estudo da sucessão vegetal e dos padrões funcionais e estruturais das comunidades vegetais, assim como dos diversos fatores que podem afetar a restauração florestal. Neste contexto, para este trabalho de tese, foram selecionadas diferentes comunidades vegetais estabelecidas a partir da regeneração natural e do plantio direto de mudas de espécies nativas, com os seguintes objetivos:

(1) Avaliar qual a importância relativa de diferentes fatores sobre a trajetória sucessional de áreas de restauração. Os fatores estudados foram as técnicas de manejo de pastagem (espécie de pasto utilizada, destocamento, presença de árvores remanescentes), características do solo (classe de solo) e da paisagem (distância e área da floresta madura mais próxima), idade da área e estratégia de restauração (regeneração natural, plantio de árvores nativas) (abordado no Capítulo 1).

(2) Avaliar se a estrutura florestal (abundância de indivíduos, riqueza de espécies, área basal, altura média e composição de espécies) de comunidades vegetais desenvolvendo-se sobre diferentes tipos de solo (Cambissolo e Gleissolo) difere ao longo do gradiente sucessional (Capítulo 2).

(3) Analisar como são estruturadas as florestas tropicais ao longo do processo de sucessão em dois tipos de solos contrastantes (Cambissolo e Gleissolo), avaliando padrões de convergência (relacionada com filtros ambientais) e divergência (relacionada à competição) de atributos, diferenças nas diversidades taxonômica e funcional e mudanças dos padrões em atributos funcionais específicos durante a sucessão, nos dois tipos de solo (Capítulo 3).

2. Caracterização da área de estudo

O estado do Paraná conserva em seu litoral alguns dos principais remanescentes da Floresta Atlântica, com aproximadamente 500 mil ha, sendo representado por florestas de encosta (Floresta Ombrófila Densa Alto-Montana, Montana e Sub-Montana) e de planície (Floresta Ombrófila Densa de Terras Baixas e Aluvial), juntamente com os ecossistemas associados como manguezais, restingas, campos de altitude, enclaves de campos e cerrados (Câmara 2005, IBGE 2012). As florestas são caracterizadas pela riqueza de espécies arbóreas perenifólias organizadas em estratos definidos, associadas a outras formas biológicas, igualmente diversas (Roderjan & Kuniyoshi 1988, Ravazzani *et al.* 1995). Desde o início do século XVII, a planície litorânea e o início das encostas no estado do Paraná tiveram a sua paisagem muito alterada devido à colonização e garimpo, e mais recentemente pelo cultivo da banana e da mandioca, extração de palmito e criação de búfalo (Borsatto *et al.* 2007).

O estudo foi desenvolvido no litoral norte do estado do Paraná, localizado dentro da Área de Proteção Ambiental (APA) de Guaraqueçaba (entre 48°45' e 48°00'W; e 24°50' e 25°30'S), a qual compreende os municípios de Guaraqueçaba, Morretes e Antonina, com uma área de 313 mil hectares de florestas, estuários, baías, ilhas, mangues e planícies. A amostragem foi realizada na Reserva Natural do Rio Cachoeira e na Reserva Natural Morro

da Mina, em Antonina, PR (Fig. 1), de propriedade da organização não-governamental Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental (SPVS). Nas reservas são encontradas diferentes tipologias vegetacionais, de acordo com a classificação de Veloso *et al.* (1991): Floresta Ombrófila Densa nas sub-formações Submontana, de Terras Baixas e Aluvial, além Formações Pioneiras de Influência Fluvial. Em cada uma dessas tipologias, têm-se ainda florestas em regeneração natural e em diferentes estádios de desenvolvimento (Ferretti & Britez 2006).

O clima predominante na região, segundo a classificação de Köppen, é o subtropical úmido mesotérmico (Cfa) sem estação seca definida e isento de geadas nas regiões serranas; e chuvoso tropical sempre úmido (Aft) na planície (Ipardes 2001). Os dados climáticos médios para um período de 9 anos mostram uma precipitação anual de 3016 mm e temperatura média de 21,2°C (Cardoso *et al.* 2012). A altitude varia desde o nível do mar até 900m a.s.l.

Os solos na região pertencem às classes Neossolos, Gleissolos, Argissolos e Cambissolos. Os Neossolos são solos constituídos por material mineral ou orgânico, pouco espessos, pouco desenvolvidos e não alagados. Os Gleissolos ocupam terraços adjacentes às planícies aluviais, sendo, portanto, hidromórficos, minerais, arenosos, de fertilidade variável e permanentemente ou periodicamente saturados por água. Normalmente apresentam horizonte glei dentro dos primeiros 50 cm da superfície do solo (Embrapa 2006). A gleização é causada pelo regime de umidade redutor em meio anaeróbico, com deficiência de oxigênio devido ao encharcamento do solo por longo período, o que implica no surgimento de cores acinzentadas, azuladas ou esverdeadas, devido a compostos ferrosos resultantes da escassez de oxigênio (Embrapa 2006). Os Cambissolos são constituídos por material mineral, com características que variam muito de um local para outro, podendo ser desde fortemente até imperfeitamente drenados, de rasos a profundos, de cor bruna ou bruno-amarelada até

vermelho escuro, e de alta a baixa saturação por bases e atividade química da fração coloidal. Possuem horizonte B incipiente subjacente a qualquer tipo de horizonte superficial (Embrapa 2006). Os Argissolos são solos minerais, não hidromórficos, bem a moderadamente drenados, com presença de horizonte B textural, variando de rasos a muito profundos (Embrapa 2006).

Em 2000, a organização não-governamental SPVS iniciou, juntamente com parcerias internacionais, projetos de combate ao aquecimento global (Projeto de Restauração da Floresta Atlântica; Projeto de Ação Contra o Aquecimento Global em Guaraqueçaba e Projeto Piloto de Reflorestamento em Antonina), onde antigas fazendas de búfalo foram adquiridas e convertidas em áreas protegidas. Nessas áreas os búfalos foram lentamente removidos, e as áreas restauradas através de regeneração natural e de plantios de mudas de espécies nativas (Ferretti & Britez 2006). Nas áreas de plantio, mudas de aproximadamente 15 espécies de crescimento rápido foram plantadas em grades de $1,5 \times 2,5$ m, resultando em uma densidade de 2666 plântulas por hectare. As sementes foram coletadas localmente nas reservas e as mudas foram produzidas em um viveiro local, sendo posteriormente transplantadas (com aproximadamente 5 meses de idade). A regeneração natural consistiu apenas no abandono e isolamento das pastagens com cercas. Mais informações das características da área de estudo e da restauração podem ser encontradas em Ferretti & Britez (2006) e Bruel *et al.* (2010).

Para este estudo, utilizamos estas áreas em processo de restauração (plantio e regeneração natural), juntamente com florestas adjacentes em diferentes estádios sucessionais para estabelecer 93 parcelas circulares, com 14m de raio cada, em um total de 5.7ha de área amostrada (Fig. 1). As parcelas foram selecionadas com base nas parcelas de monitoramento de carbono já existentes na reserva, as quais foram estabelecidas sobrepondo-se aerofotos, mapa de vegetação, mapa de tipo e uso do solo, a fim de otimizar as atividades de restauração

e manejo das reservas. Informações adicionais sobre o histórico de perturbação e a idade das áreas foram obtidas através de entrevistas com moradores da região. As parcelas demarcadas representam, portanto, um gradiente sucessional (Fig. 2) e edáfico da região de estudo. O levantamento de dados das parcelas ocorreu entre agosto de 2009 e dezembro de 2011, quando as áreas restauradas pelo projeto da SPVS estavam com, no máximo 12 anos.

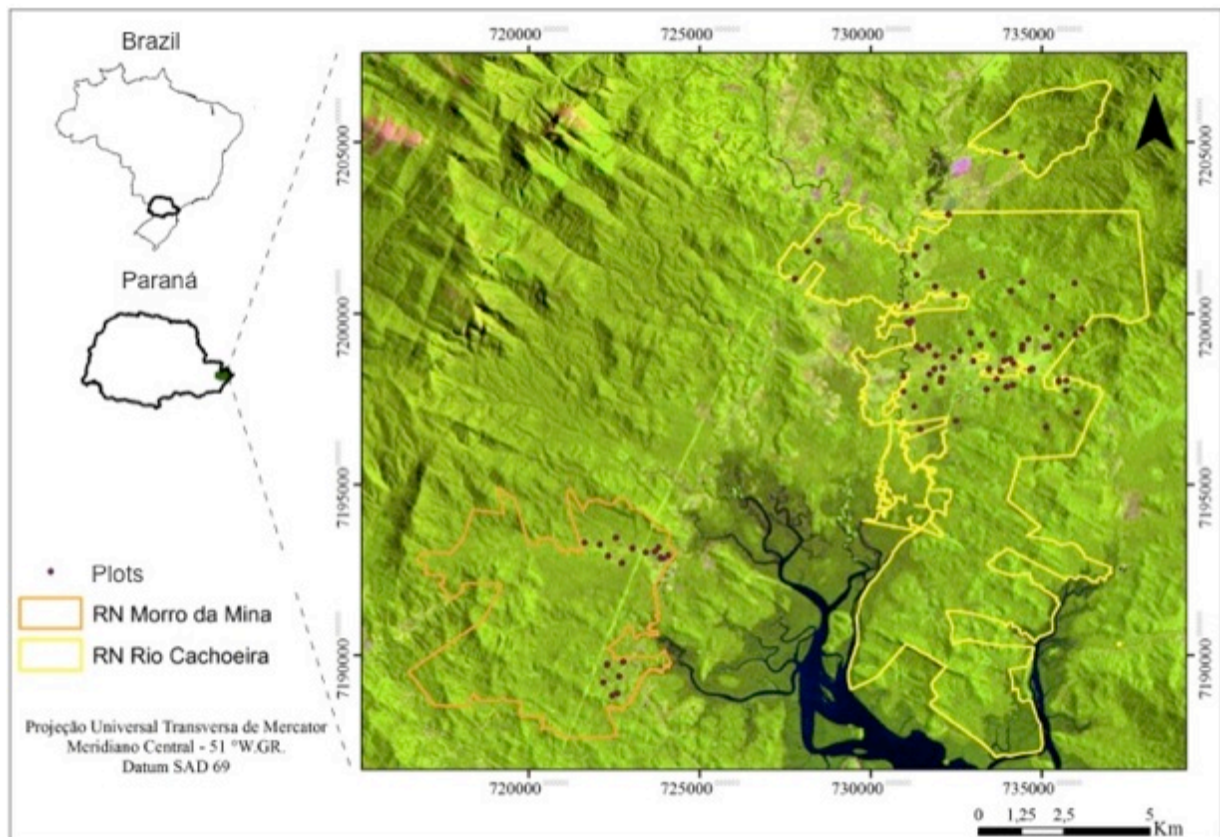


Figura 1 - Mapa da área de estudo mostrando o Brasil, o Paraná e as 93 parcelas utilizadas neste estudo, nas Reservas Naturais do Morro da Mina e do Rio Cachoeira, de propriedade da Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental (SPVS).



Figura 2 – Áreas em diferentes estádios sucessionais na Floresta Atlântica, em Antonina, Paraná. **A.** Área em processo inicial de regeneração com 4 anos de idade, com presença da gramínea exótica *Urochloa cf humidicola*; **B.** Área intermediária, de 15-25 anos de idade; **C.** Área de floresta avançada com mais de 80 anos de idade.

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FATORES QUE AFETAM A TRAJETÓRIA SUCESSIONAL EM ÁREAS DE
RESTAURAÇÃO NA FLORESTA ATLÂNTICA

Disentangling factors affecting successional trajectory in restoration areas of Atlantic Forest

Abstract

There are a variety of factors that influence the restoration of tropical forests, determining its capacity to develop, and how fast this is going to happen. A relatively large knowledge of which factors potentially affect the quality of restoration areas in the tropics has been assessed last years, but the relative importance of multiple factors determining the success of restoration is still poorly understood. In this study, we analyzed the structure of plant communities under restoration process in the Atlantic Forest in southern Brazil, aiming to evaluate the relative importance of pasture management techniques (pasture species used previously in the pasture, tree root removal before planting the pasture, presence of remnant trees), soil and landscape features (soil type, distance and area of the nearest adjacent forest, terrain relief), and restoration age and strategy (natural regeneration, native trees plantation) affecting the restoration of a tropical forest in abandoned agricultural areas. We established 93 circular plots (615.7m² each, total 5.7 ha) along restoration areas and sampled trees and shrubs from the forest canopy (diameter at breast height, DBH \geq 5.0cm) and understory (DBH \leq 5.0 and height \geq 1.3m). Plots included areas undergoing restoration with two contrasting restoration strategies (natural regeneration and native species plantation), in different ages (from 2 to 80 years old), four soil types (Cambisol, Gleysol, Acrisol and Fluvisol), four pasture types (*Urochloa cf humidicola*, *U.arrecta*, *Paspalum* sp. and mixed), two types of terrain relief (lowlands and hillsides) and at different distances from the nearest forest remnant (0 to 460m). We used the model selection approach to find which combination of factors had stronger influence in the structure and diversity of successional forests. Our results demonstrated that age, nearest-neighbor distance and the species of

fodder grass preceding restoration (all selected in 63% of the models) are the strongest factors influencing species richness, abundance, basal area and mean height of both canopy and understory communities. Other variables such as restoration strategy (38%), soil type (31%) and terrain relief (25%) also played a supporting role in explaining these response variables. Older plots and closer to forest remnants had, in general, increased richness, abundance, basal area and mean height. Restoration areas established in areas previously planted with the exotic grass *Urochloa* spp. limited canopy abundance and species richness. These results suggest that important biotic and abiotic factors strongly interact to influence successional processes in restoration areas.

Key words: grazing; natural regeneration; restoration; plantation; tropical forest

Introduction

There are a variety of factors that influence regeneration of a forest, determining its capacity to develop, and how fast this is going to happen (Uhl 1987, Aide & Cavelier 1994; Rodrigues *et al.* 2009). The vegetation that establishes after a disturbance or in newly abandoned areas is well varied and depend on such factors, like type and intensity of the disturbance, time since the area has been abandoned, size of the area, propagule availability, presence of remnant trees and proximity to forested areas (Guevara *et al.* 1986, Aide *et al.* 1995, Toh *et al.* 1999, Finegan & Delgado 2000, Steininger 2000, Gunderson 2000, Zimmerman *et al.* 2000, Chazdon 2003, Myster 2004, Kauano *et al.* 2013, Zwiener *et al.* 2014). The land use history also brings important implications to the successional trajectories. Recovery in abandoned pastures, for example, may take longer than recovery following other types of human and natural disturbances, such as hurricanes and plantations (Aide *et al.* 1995).

In abandoned pastures, different pasture species and management techniques can potentially affect restoration. Exotic grasses have been intensively used for livestock foraging in tropical pastures (Hooper *et al.* 2005). This grass cover strongly competes with recruiting vegetation by reducing light availability (Vieira *et al.* 1994; Hooper *et al.* 2002) and limits regeneration by competing with tree seedlings for water and nutrients (Nepstad *et al.* 1996). The intensity of competition, however, may depend on the species of grass present in the area, since they differ in their growth rates and competitive ability. Other than pasture species, root removal, or the process of removing all the roots from the ground prior planting the grass for pasture can influence restoration. Resprouting stems can be an important contribution to forest recovery (Chazdon 2003, Zanini *et al.* 2014), and since root removal inhibits resprouting, it potentially affects restoration. One more factor to consider in the

pasture management is the retaining of some isolated trees and shrubs in the abandoned fields. Remnant vegetation plays a critical role in forest recovery, promoting rapid increases in species richness, tree density and aboveground biomass (Chazdon 2003). Remnant shrubs and trees in pastures attract fauna that use them as perches, bringing propagules and thus, enhancing restoration (Slocum & Horvitz 2000, Zwiener *et al.* 2014). The shade generated by the crowns of remnant trees also produces an indirect facilitation effect of reducing competition with exotic pasture grasses.

In addition to pasture techniques, other factors acting in micro-scale, such as soil characteristics, may also be important in the plant community regeneration and succession (Chapter 2). Soil physical characteristics (texture), nutrient availability and moisture affect plant growth in several ways. Soil texture, for example, is one of the most important characteristics of the soil, influencing directly and indirectly a cascade of relations between organic matter, ions and soil drainage (Fearnside & Leal-Filho 2001, Silver *et al.* 2000). Therefore, it is expected that soil type will also play a role in plant community succession and dynamics in tropical forests.

Going further and considering also the macro-scale factors, such as landscape characteristics, we also expect that they will influence forest succession pathways. The lack of seeds was described as a major barrier to restoration (Holl *et al.* 2000), hence, the proximity to the propagule source, such as an advanced secondary forest, can be a main determinant of the speed of recovery and vegetation diversity in restored areas (Chinea 2002, Kauano *et al.* 2013). The area of this forest and the relief of the terrain in which it is inserted are also likely to influence seed dispersal, and thus, restoration.

Considering all the factors cited above, the restoration strategy to be selected to recover an area should be extensively planned, depending on the local conditions. The

plantation of native species is expected to speed up forest recovery, especially in areas of dense exotic grass cover, since planted trees suppresses grasses and ferns that may impede initial tree colonization (Otsamo 2000). In addition, planted trees can increase organic matter in the soil, prevent erosion, and enhance nutrient cycling (Montagnini & Sancho 1994). However, restoration approaches vary widely in cost and intervention and depend on goals and expectations of each particular project (Chazdon 2003).

Since the beginning of the 20th century, the Atlantic Forest in southern Brazil had its landscape greatly changed due to colonization and mining activity, and more recently due to the cultivation of banana, manioc, palm trees and buffalo farming (Borsatto *et al.* 2007). Along the remnants of the Atlantic Forest, there are areas with different levels of interference, often mingled with abandoned pastures. After changes in the local economy, many areas were abandoned are now under regeneration process and in different successional stages comprising an environmental mosaic. In this biome, plant communities recovering after a disturbance can take from 100 to 4000 years to achieve the expected proportions of forests traits of a mature forest (Liebsch *et al.* 2008). These data show that the resilience of this system is relative, therefore, measures that preserve old-growth forests and that aim to recover part of areas degraded by human activities are essential to ensure the integrity of the remnants. Understanding the factors that affect forest regeneration in tropical forests is important for improving methodologies for restoring forests and also for contributing to knowledge of successional mechanisms and theory (Zimmerman *et al.* 2000).

The goal of this study was to assess how different factors affect the restoration of the Atlantic Forest in Southern Brazil. We investigated areas undergoing restoration after pasture abandonment and asked if the pasture management techniques (pasture species used previously in the pasture, tree root removal before planting the pasture, presence of remnant

trees), soil (soil type) and landscape features (distance and area of the nearest adjacent forest, terrain relief), and restoration age and strategy (natural regeneration, native trees plantation) affect the tree abundance, species richness, basal area and height of the canopy and understory of plant communities.

Methods

Study site

This study was carried out in the Atlantic Forest of Paraná state, southern coast of Brazil, in the municipality of Antonina (25°19'15"S and 48°42'24"W). The study areas are within the Guaraqueçaba Environmental Protection Area, a large region (more than 300,000 ha) that includes forests, estuaries, bays, islands, mangroves and lowlands, and is part of one of the most important remaining areas of Atlantic Forest in Brazil (Ferretti & Britez 2006a). We collected data in two reserves within these areas, *Rio Cachoeira Nature Reserve* and *Morro da Mina Nature Reserve*. Both are property of the non-governmental organization *Society of Research in Wildlife and Environmental Education* (SPVS) and together they comprise nearly 10,000 ha.

The climate in the region is humid subtropical (Cfa), according to Köppen's classification (Ferretti & Britez 2006b), with annual precipitation of 3016 mm and mean temperature of 21.2°C over the last 25 years (Cardoso *et al.* 2012). Altitude varies from sea level to 900m a.s.l. Four soil types occur in the reserve: Acrisol, Fluvisol, Gleysol, and Cambisol (Ferretti & Britez 2006b). Acrisols are mineral soils, non-hydromorphic, moderately drained, ranging from shallow to very deep. Fluvisols consist of mineral or organic material, usually underdeveloped, shallow and well drained. Gleysols are hydromorphic, mineral, sandy, with variable fertility and are permanently or periodically

saturated with water. Cambisols comprise non-hydromorphic, mineral soils, with variable fertility and high silt content (Embrapa 2006). A general characterization of the physical and nutrient contents in these soil types can be found in the supplementary material (Table S1).

The Atlantic Forest in the region is characterized by different typologies, including Submontane, Lowland, and Alluvial Forests. In the region, 68% of the landscape is comprised of forest remnants and 9% of secondary forest areas that are mingled with buffalo grazing and agricultural areas (Kauano *et al.* 2012). With the increasing establishment of conservation areas in the region, some of these intensive use sites were abandoned and are now in a process of restoration (Ferretti & Britez 2006a), resulting in areas with vegetation in different successional stages. Other areas suffered selective logging of native commercial species, for example the native palm *Euterpe edulis* (Ferretti & Britez 2006a, Bruel *et al.* 2010, Borgo *et al.* 2011).

In 2000, a large restoration program has started in the reserves and applied passive (natural regeneration) and active (plantation of native tree seedlings) restoration strategies (Ferretti & Britez 2006a). The first plantation areas, now approximately 15 years old, are well established, with most tree species already reproductive and heights up to 15 meters. Old growth forests present in the region are an important source of seeds (Leitão *et al.* 2010) and shelter for animals (Zwiener *et al.* 2012).

Pasture and restoration characterization

The restoration program was established in lowlands and low slope areas previously used as non-intensive pasture for buffalo ranching for approximately 30 years. The pastures were established using local techniques that included slashing the forests and mechanical removing of the residuals. In some areas, farmers maintained some large trees in order to

promote shading for the cattle. The terrain was prepared by removing tree roots and stumps in some areas and seeding different African grass species. Three major grass species combinations were used in the pastures: 1) grass cover dominated by *Urochloa* cf *humidicola* (Rendle) Morrone & Zuloaga and *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga; 2) the non-invasive and less aggressive fodder grass species *Paspalum* sp.; 3) a mixture of different grasses including *Urochloa* spp. and *Paspalum* sp. *Urochloa* grasses were introduced for pasture in Brazil, and are highly adaptable to nutrient-poor and high humidity soils.

Two restoration strategies were used in the reserves: active (seedling plantation) and passive (isolation for forest regeneration) restoration. In the active restoration, seedlings of approximately 15 fast-growing species were planted in 1.5 × 2.5 m grids, resulting in a density of 2,666 seedlings.ha⁻¹. The seeds were collected locally in the reserves and seedlings were produced in a local nursery, and were transplanted when they were ~5-months old (~15 cm in height). Soil preparation included roto-tilling; fertilizers were not used. Seedlings were hand-planted in small (~800 ml) hand-made holes. Plot management included hand-weeding in the summer of the first year after seedlings were planted. The passive restoration consisted only of pasture abandonment and isolation from cattle with fences. Areas of both restoration strategies were similar prior to the restoration. Details of the study area and restoration characteristics can be found in Ferretti & Britez (2006a) and Bruel *et al.* (2010).

Methods

The study is based on a comparative analysis of the forest restoration in different combinations of characteristics. We established a total of 93 circular plots (radius of 14m; area of 615.7m² each) resulting in a total sampled area of 5.7ha. Plots were distributed in the

two reserves and were selected in a way to account a gradient of all variables of pasture management techniques, soil and landscape characteristics, and restoration strategies (Figure 1). The plots were established in areas with age varying from 2 to 80 years. We determined the age of these forests based on aerial photographs and interviews with local people. Acrisol accounted for 6 plots, Cambisol 31 plots, Gleysol 50 plots, and Fluvisol 6 plots. A total of 70 plots were in the lowlands while 23 were in the hillsides. The distance to the closest old-growth forest remnant (nearest-neighbor distance) varied from 0 to 460m, and the area of this remnant varied between 0.09 to 40.203ha. Landscape related variables were obtained with GIS techniques from the reserves' maps and the application Vlate in ArcGIS software (see details in Kauano *et al.* 2013). 24 plots were in areas of active restoration, and 69 plots in areas of passive restoration. 21 plots were covered by the grass *Urochloa cf humidicola* and *Urochloa arrecta*, 17 with *Paspalum* sp. and 25 were mixed (*Urochloa* and *Paspalum*). For the remaining number of sites, we did not have information whether exotic grasses were used and what kind of pasture management technique was used (root removal / remnant trees), therefore, they were analyzed in a different sub-group, explained in more detail below. For these sites, we also recorded the presence of remnant trees in the plots and whether or not the plots went through root removal during the pasture establishment.

Survey and analysis of vegetation

In all 93 plots of 14m in radius we sampled all trees and shrubs with diameter at breast height (DBH; 1.3m) \geq 5cm, to characterize the canopy. In a smaller concentric sub-plot (4m in radius, 50.3 m²), we measured all individuals (tree saplings and shrubs, which will be referred hereafter as “understory”) with DBH < 5.0cm and height \geq 1.30m (or stem base diameter, for shrubs). For all sampled individuals we determined the species name and

measured the DBH and total height. We calculated total tree abundance; species richness, basal area and mean height for each plot, in each of the two plot sizes (14m and 4m), representing the canopy and understory communities, respectively.

Data Analysis

We analyzed the data in two steps. First, we used a dataset of all the 93 plots together, which includes restoration areas (up to 15 years-old) and secondary forests (15-80 years old). For this analysis, we had five explanatory variables (terrain relief, restoration age, distance from the nearest neighbor, area of the nearest neighbor and soil type). Then, we analyzed separately the subset of 61 younger restoration plots, excluding the secondary forests older than 15 years of age. In this case, we were able to add four more explanatory variables in the database of the restoration project (restoration strategy, pasture type, presence of remnant trees, use of root removal) and focus in the initial steps of restoration.

To proceed to analysis we organized the different type of variables to use in our model selection. We assigned a rank position to the categorical variables “type of pasture” and “restoration strategy”. They were ranked according to a prior analysis of the mean values of each variable in our data, and then assigned a rank position. For instance, the pasture type “*Paspalum* sp” received rank position number 3; the type “mixed” (containing both *Paspalum* sp and *Urochloa* spp.) was determined rank position number 2 and the plots containing any of the two species of *Urochloa* received rank position number 1. In this case, we expected that *Paspalum* sp. plots would have greater tree abundance, species richness, basal area and mean height than “mixed”, and these, in turn, would be ahead of the plots with *Urochloa* spp. For restoration strategy, we used 2 for active and 1 for passive restoration. This procedure of assigning rank positions to categorical variables was proposed by Padial *et al.* (2010) and

made it possible to include a larger set of variables in model selection analysis. Soil type was decomposed in four dummy variables (Legendre & Legendre 1998), representing each soil type (Cambisol, Gleysol, Fluvisol and Acrisol). We also had two presence/absence variables (root removal and presence of remnant trees). The plots where root removal was performed received number 0 and plots that did not have root removal received number 1. The plots without remnant trees received number 0 and the plots with the presence of the trees received number 1.

We then analyzed any possible spatial structure among the studied plots using Moran's I test for spatial autocorrelation (Rangel *et al.* 2006). Since Moran's I was not significant, we assumed no spatial structure in our data. Afterwards, we used a model selection approach to analyze the explanatory variables listed above, for the 93-plot dataset and the 61-plot subset. The response variables in both cases were tree abundance, species richness, basal area and mean height, separately for canopy and understory plots.

The model selection and multi-model inference approaches (Burnham & Anderson 2002) allowed us to compare the likelihood of different models. We used an exhaustive search of models comprising one explanatory variable or a combination of explanatory variables. First, competing models were compared based on Akaike Information Criterion (AIC) (Burnham & Anderson 2002). The model with minimal AIC value was selected as the best (Johnson & Omland 2004). AIC is based on the principle of parsimony, so there is a trade-off between prediction error and parameter uncertainty. Akaike weight (w_i) was also calculated for each model using the ΔAIC , which is the difference between the AIC of a given model and the AIC of the best model. These values were normalized across the set of candidate models to sum one, and each one of these values can be interpreted as the probability of a certain model to have the best fit (Johnson & Omland 2004). Coefficients of

determination (r^2) were also calculated to give the amount of variance accounted for each model. Secondly, we used multi-model inference values based on model averaging to estimate the relative importance of each explanatory variable (Johnson & Omland 2004). These values are the sum of the AIC w_i over all of the models in which a certain parameter appears (Johnson & Omland 2004).

After the best models were selected, we gathered the variables of the best selected model for abundance, species richness, basal area and height for both canopy and understory communities and performed linear regressions, ANOVAs with Tukey post-hoc or t -test for the three stronger variables in each model, in order to test relationships and differences. We used SAM software version 4.0 (Rangel *et al.* 2006) for the model selection and spatial autocorrelation analyses and R (R Core Team 2012) for all other statistical analyses.

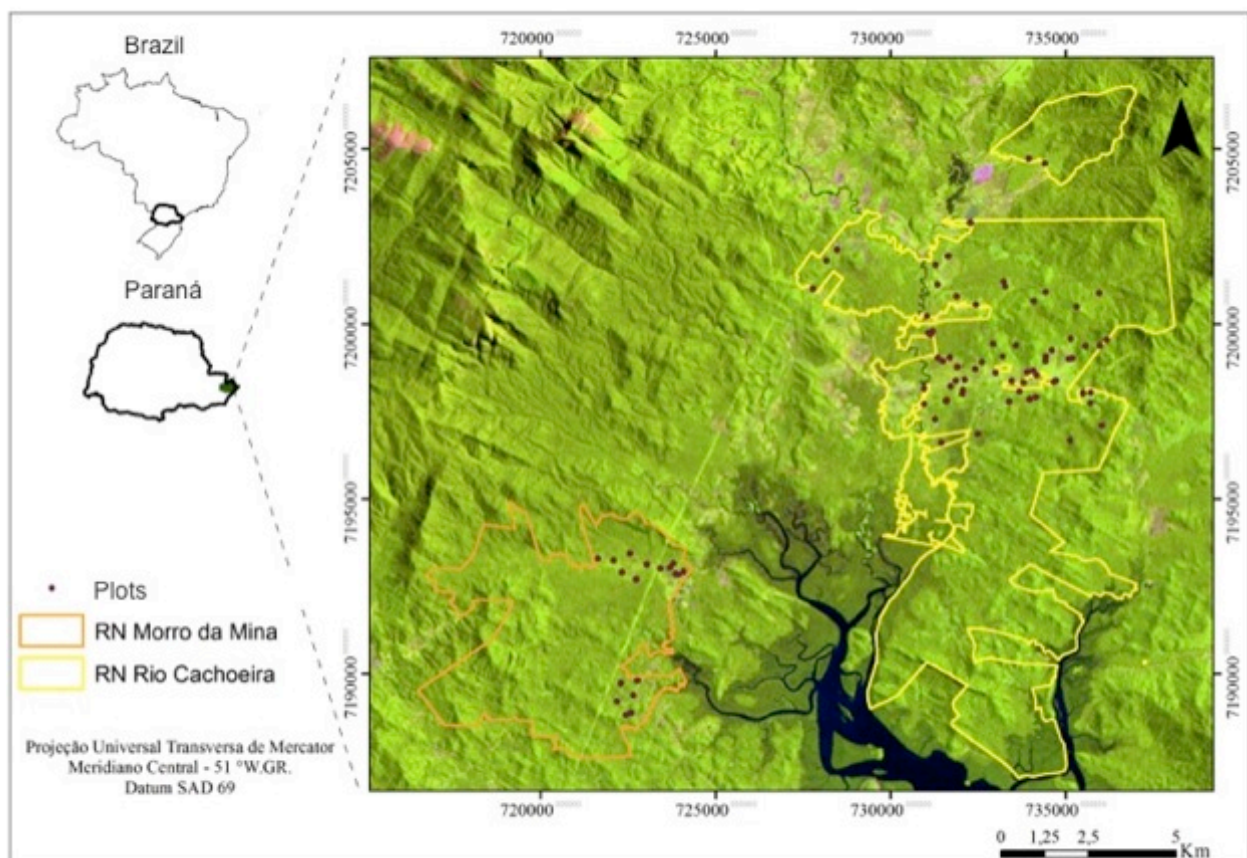


Figure 1. Map of the study area, showing Brazil, Paraná state and the 93 studied plots in two Natural Reserves (*Cachoeira* and *Morro da Mina*).

Results

Vegetation assessment

We sampled a total of 7378 individuals in 93 plots, where 5144 were canopy trees and 2234 were understory individuals, including saplings and shrubs. A total of 234 species were recorded for the canopy community and 220 species for the understory community. The most abundant species in the canopy were *Myrsine coriacea*, *Tibouchina pulchra* and *Pera glabrata*. The most abundant species in the understory were *Vernonanthura beyrichii*, *Tibouchina trichopoda* and *Myrsine coriacea* (Table 1).

Factors that affect restoration

The best models selected to describe canopy and understory abundance, species richness, basal area and height of trees included various combinations of explanatory variables. The variables that were most frequently present in our models in the canopy were nearest-neighbor distance, restoration age and pasture type, and in the understory they were nearest-neighbor distance, age and soil type (Gleysol and Fluvisol) (Table 2).

The best models were the ones that are more predictive (higher adjusted R^2) and with more explanatory power (low AIC and high AIC w_i). We list below the variables that composed the best models for both the whole dataset with 93 plots and the subset with 61 younger plots. For canopy abundance, four variables were part of the best models: restoration age, nearest neighbor distance, restoration strategy and pasture type (Table 2). Canopy tree abundance increased significantly with age in the 93-plot dataset (Fig. 2a), and showed a negative relation with nearest-neighbor distance, with plots more distant to adjacent forests with lower abundance (Fig. 2b). Plots containing the invasive grass *Urochloa* spp. (alone or mixed with the other less invasive grass) had fewer individuals than the plots containing only

the non-invasive grass *Paspalum* sp. (Fig. 2d). The explanatory variable restoration strategy was the fourth most important, so it is not represented in the figure, but it was also selected in the best model. There were significantly more trees in the canopies of plantation plots than of natural regeneration plots. In the understory, age and distance also had similar effects on abundance (Figs. 2d and 2e). Area of the nearest neighbor, soil types Fluvisol and Gleysol and relief also composed the best models in the understory (Table 2).

Species richness was explained by five main variables, which composed the best models: terrain relief, restoration age, nearest-neighbor distance, soil type (Acrisol) and pasture type (Table 2). In the same way as abundance, older areas had more species and nearest neighbor distance also had a negative relation with richness, with sites more distant to forest patches with a lower richness (Figs. 3a and 3b). Plots containing the invasive grass *Urochloa* spp. had fewer species than the plots containing only the non-invasive *Paspalum* sp. (Fig. 3e). Soil type and terrain relief were also part of the best model, although not between the three strongest variables represented in the figures. Different soil types had distinct number of species, with Cambisol with more species than Acrisol and than Gleysol. In addition, plots that were on the hillsides had significantly more species than the ones on the lowlands. In the understory, the same three variables as the canopy were more important to the models: restoration age, distance to the nearest neighbor and pasture species (Figs. 3d, 3e and 3f).

The best models for **basal area** included six variables: terrain relief, restoration age, nearest-neighbor distance, soil type (Acrisol), pasture species and restoration strategy (Table 2). Basal area increased with plot age and decreased with nearest neighbor distance, with sites more distant to forest patches with a smaller basal area (Figs. 4a and 4b). Plots with higher basal area were the ones with native species plantations (Fig. 4c). The plots on the hillsides

are not represented in the figure, but they contributed to the model and had higher basal area than the ones on the lowlands. In contrast, basal area of the plots with the three different pasture types did not differ ($P>0.05$), although considered an important variable contributing for the best model. In the understory, three variables contributed to the models: restoration age, nearest neighbor distance and the restoration technique of root removal. Older plots had increased basal area than younger plots (Fig. 4d). The other variables did not have a significant relationship with basal area ($P>0.05$).

Table 1. The five most abundant species in the canopy and understory at four different ages; in an area of Atlantic Forest in southern Brazil. N: number of individuals.

<15 years		15-25 years		30-50 years		>80 years	
Canopy							
Species	N (%)	Species	N (%)	Species	N (%)	Species	N (%)
<i>Myrsine coriacea</i>	565 (21.7)	<i>Tibouchina pulchra</i>	178 (16.2)	<i>Pera glabrata</i>	95 (9.6)	<i>Psychotria nuda</i>	40 (8.7)
<i>Senna multijuga</i>	230 (8.84)	<i>Myrsine coriacea</i>	116 (10.5)	<i>Vochysia bifalcata</i>	51 (5.2)	<i>Mollinedia schottiana</i>	23 (5.0)
<i>Mimosa bimucronata</i>	225 (8.6)	<i>Pera glabrata</i>	97 (8.8)	<i>Euterpe edulis</i>	50 (5.1)	<i>Euterpe edulis</i>	22 (4.8)
<i>Tibouchina trichopoda</i>	215 (8.3)	<i>Casearia obliqua</i>	60 (5.5)	<i>Calyptranthes grandifolia</i>	40 (4.1)	<i>Hyeronima alchorneoides</i>	19 (4.1)
<i>Tibouchina pulchra</i>	171 (6.6)	<i>Casearia sylvestris</i>	52 (4.7)	<i>Sloanea guianensis</i>	38 (3.9)	<i>Guapira opposita</i>	14 (3.0)
Total for age	2601		1100		984		460
Understory							
<i>Vernonanthura beyrichii</i>	198 (18.9)	<i>Psychotria nuda</i>	64 (11.9)	<i>Miconia cinerascens</i>	44 (9.4)	<i>Geonoma</i> sp.	15 (8.1)
<i>Tibouchina trichopoda</i>	194 (18.5)	<i>Marlierea obscura</i>	27 (5.1)	<i>Jacaranda puberula</i>	36 (7.7)	<i>Rudgea jasminioides</i>	14 (7.6)
<i>Myrsine coriacea</i>	127 (12.1)	<i>Psychotria pubigera</i>	24 (4.5)	<i>Euterpe edulis</i>	25 (5.4)	<i>Ouratea parviflora</i>	13 (7.0)
<i>Ossaea amygdaloides</i>	49 (4.7)	<i>Vochysia bifalcata</i>	20 (3.7)	<i>Psychotria nuda</i>	20 (4.3)	<i>Psychotria nuda</i>	12 (6.5)
<i>Leandra australis</i>	40 (3.8)	<i>Ouratea parviflora</i>	18 (3.4)	<i>Marlierea obscura</i>	16 (3.4)	<i>Mollinedia schottiana</i>	12 (6.5)
Total for age	1047		534		467		185

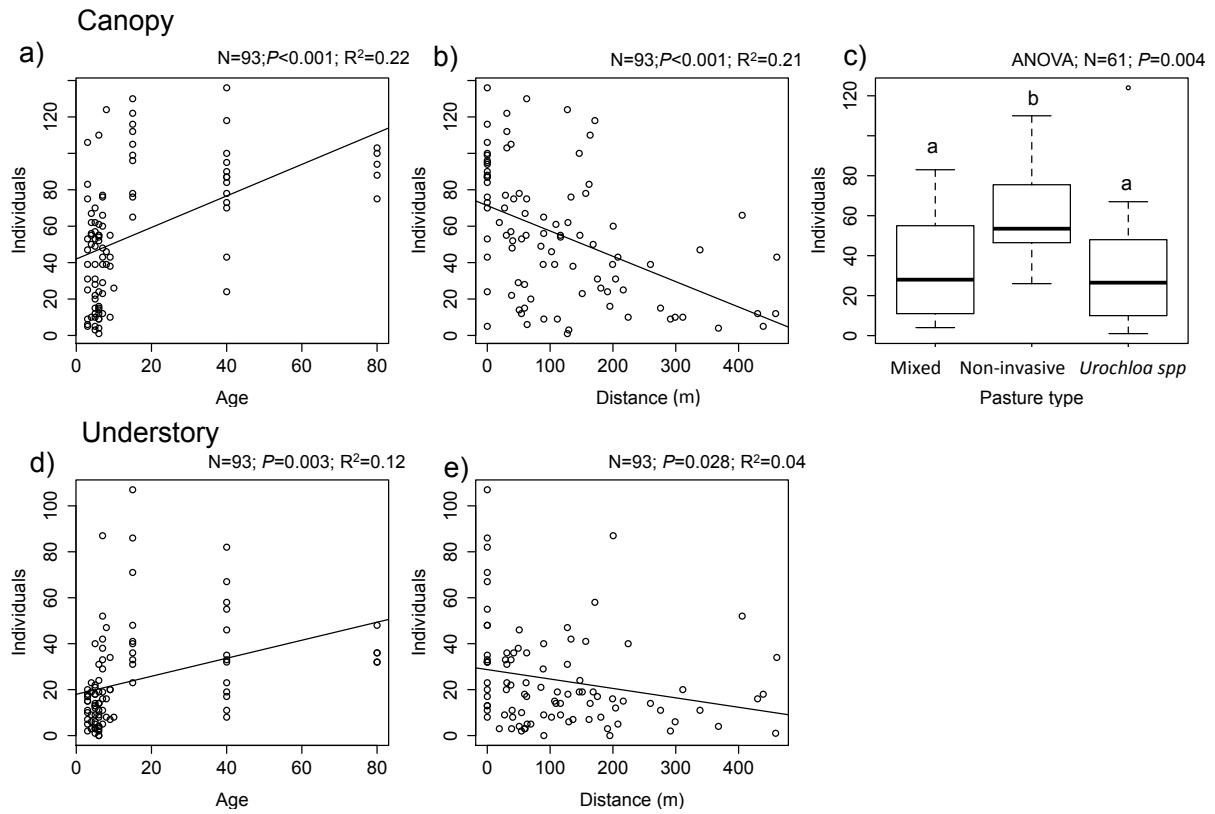


Figure 2. Effects of explanatory variables (a: restoration age, b: nearest-neighbor distance and c: pasture type, on the canopy and d: restoration age and e: nearest-neighbor distance on the understory) on the abundance of areas undergoing restoration, Atlantic Forest region, southern Brazil.

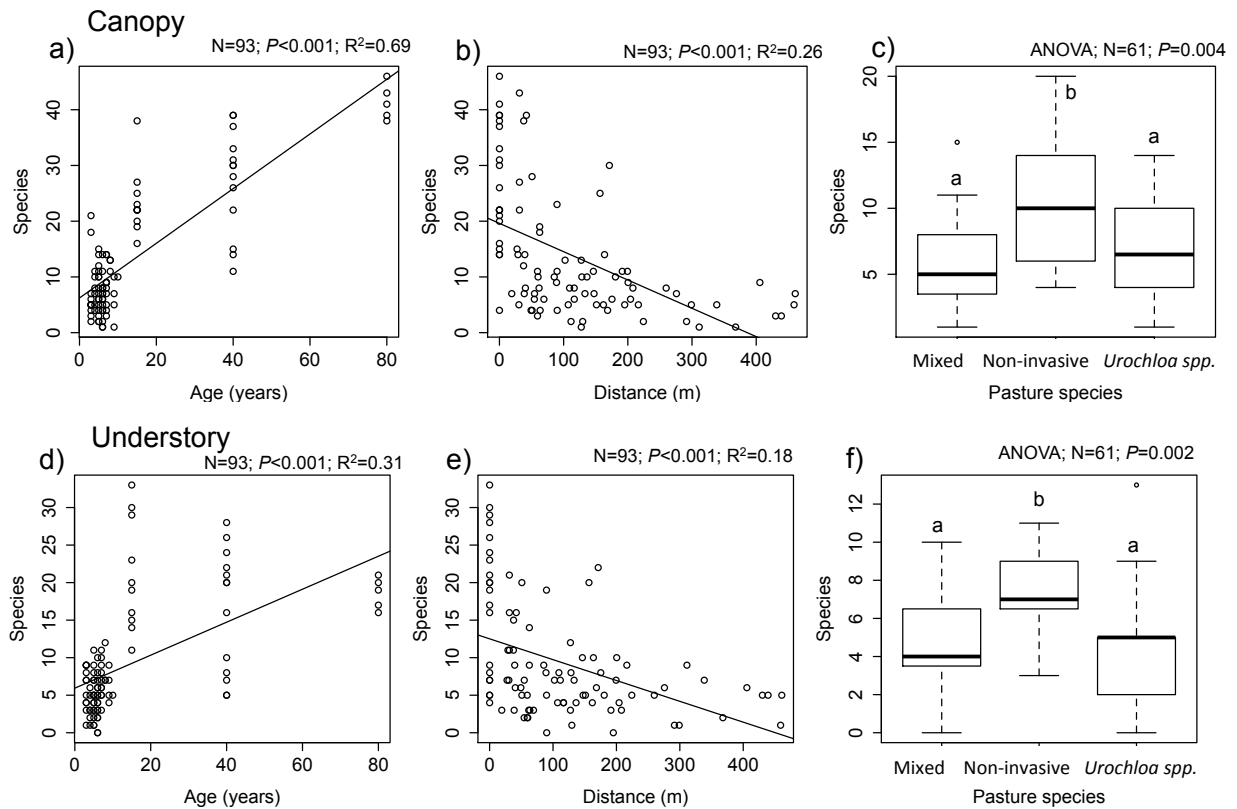


Figure 3. Effects of explanatory variables (a,d: restoration age; b,e: nearest-neighbor distance, and c,f: pasture type), on the species richness, in areas undergoing restoration in the Atlantic Forest region, southern Brazil.

Table 2: Results of the model selection showing the best model selected to explain abundance, species richness, basal area and height of **93 plots** and **61 plots** of Atlantic Forest undergoing restoration in Southern Brazil. Explanatory variables **93 plots:** terrain relief, restoration age, distance from the nearest neighbor, area of the nearest neighbor, Gleysol, Fluvisol, Cambisol, Acrisol. Variables **61 plots:** the same eight variables as above, plus restoration strategy, root removal, presence of remnant trees and pasture type. AIC= Akaike Information Criteria; AIC w_i = Akaike weight.

Response variables		Explanatory variables	R ²	AIC	AIC w_i
Canopy					
Abundance	93 plots	age, distance	0.32	899.25	0.087
	61 plots	restoration strategy, pasture	0.24	552.9	0.021
Richness	93 plots	relief, age, distance, Acrisol	0.78	593.17	0.194
	61 plots	pasture, distance	0.26	329,55	0.025
Basal Area	93 plots	relief, age, distance, Acrisol	0.67	604.45	0.076
	61 plots	restoration strategy, pasture, distance	0.24	342.72	0.018
Height	93 plots	relief, age, distance	0.48	354.66	0.093
	61 plots	restoration strategy, pasture	0.14	200.65	0.01
Understory					
Abundance	93 plots	age, distance, area, Fluvisol	0.21	822.23	0.042
	61 plots	relief, age, Gleysol	0.19	487.14	0.024
Richness	93 plots	age, distance	0.38	609.87	0.09
	61 plots	age, pasture type	0.22	289.82	0.024
Basal Area	93 plots	age, distance	0.07	390.63	0.04
	61 plots	root removal, age, distance	0.20	258.48	0.022
Height	93 plots	age	0.05	218.63	0.056
	61 plots	Gleysol	0.03	160.1	0.014

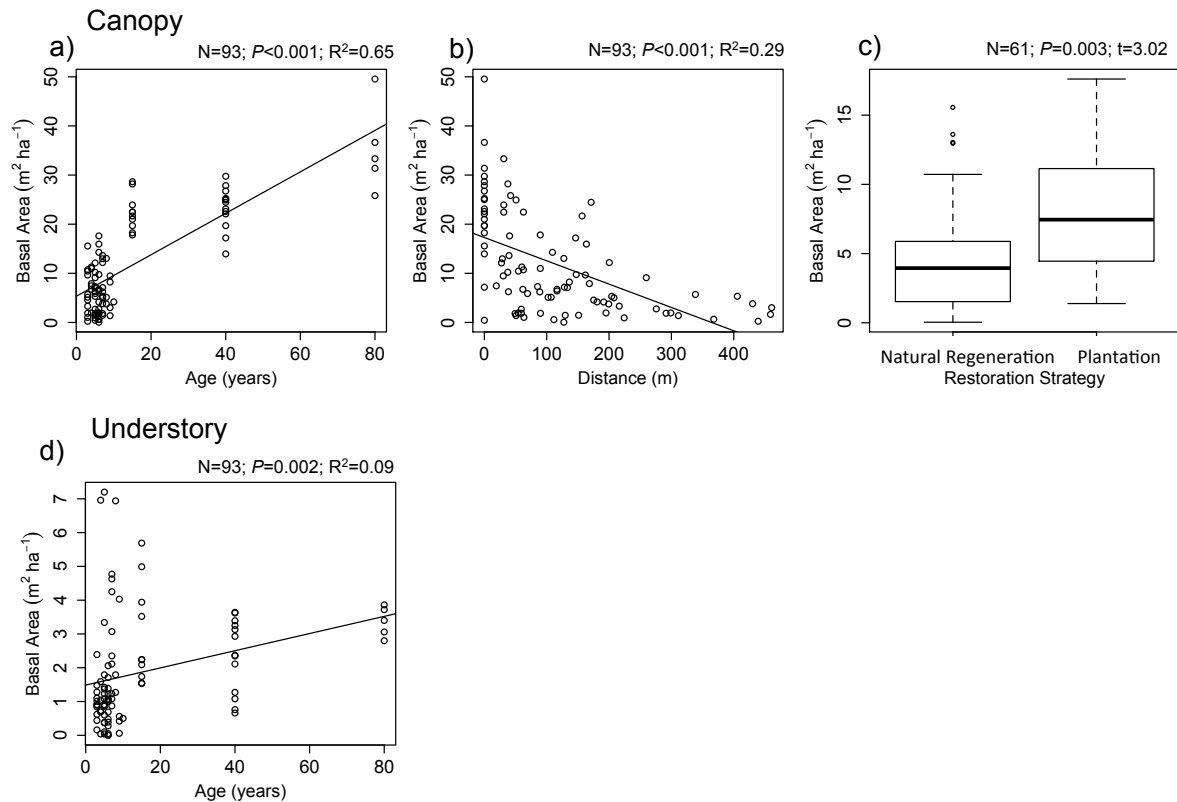


Figure 4. Effects of explanatory variables (a: restoration age, b: nearest-neighbor distance, and c: restoration strategy in the canopy, and variable d: restoration age in the understory) on the basal area in areas undergoing restoration in the Atlantic Forest region, southern Brazil.

The best models selected for explaining **mean height** had the same variables as the ones with basal area, except for the variable Acrisol. Likewise, tree mean height was higher in older plots (Fig. 5a), with shorter distances from the nearest forest (Fig. 5b). Plots with mixed pasture species, containing the invasive grass *Urochloa* spp. and the *Paspalum* had lower mean height (Fig. 5c). In the understory, only variables age and Gleysol composed the models. Older plots also had higher mean height than younger plots (Fig. 5d) and mean height did not differ between soils, although Gleysol was the only variable selected for the model for the 61 younger areas (Table 2).

Considering the model averaging procedure (which shows the importance value for each variable) (Fig. 6), we found out that in the 93-plots dataset, restoration age was the most important (importance value > 0.7) explanatory variable affecting abundance, species richness, basal area and mean height in restoration areas in all the possible models (considering canopy and understory) (Fig. 6). It was followed by nearest-neighbor distance (importance value > 0.5 in six of the eight possible models) and by terrain relief and Gleysol (importance values ranging between 0.27 and 0.92) (Fig. 6). However, when we used the 61-plot subset, which includes only the young restoration areas, restoration age explained understory abundance, species richness and basal area (importance values > 0.62), but was not so important to these variables in the canopy (importance values very low, around 0.25). For this subset, the variable pasture species was the main variable to affect restoration in the canopy (importance values ranged between 0.62 to 0.93), followed by restoration strategy (importance values ~ 0.7 in the canopy, except for species richness, that had comparatively low importance value: 0.24). Soil type contributed in some cases with importance value above 0.6, for example, in canopy species richness (Acrisol) and in understory abundance (Gleysol). The variable root removal was important in understory basal area (importance value=0.75) (Fig. 6). High importance values do not necessarily mean that variables have a good predictive power, but combining this result with the AIC models (Table 2), the cited variables stand out as important factors to the restoration success.

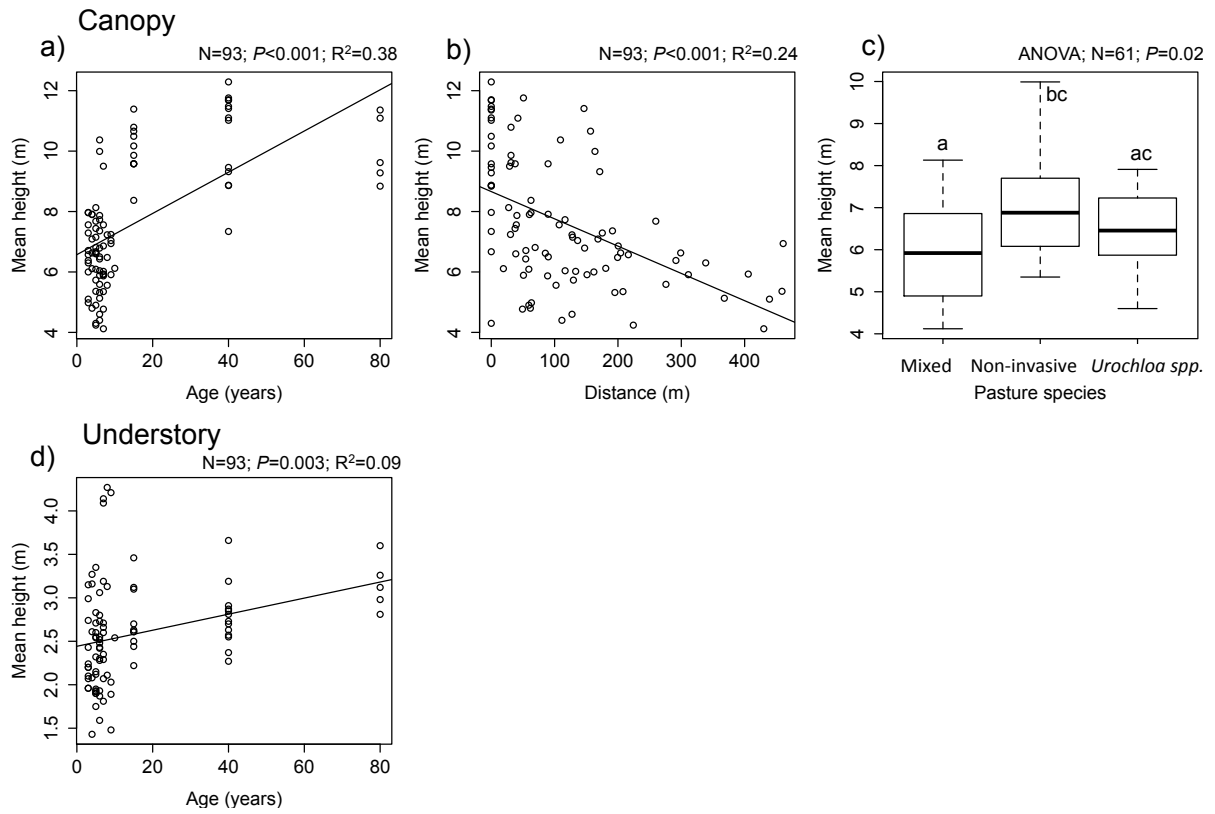


Figure 5. Effects of explanatory variables (a: restoration age, b: nearest-neighbor distance and c: pasture species, on the canopy and variable d: restoration age), on the plant height in areas undergoing restoration in the Atlantic forest region, southern Brazil.

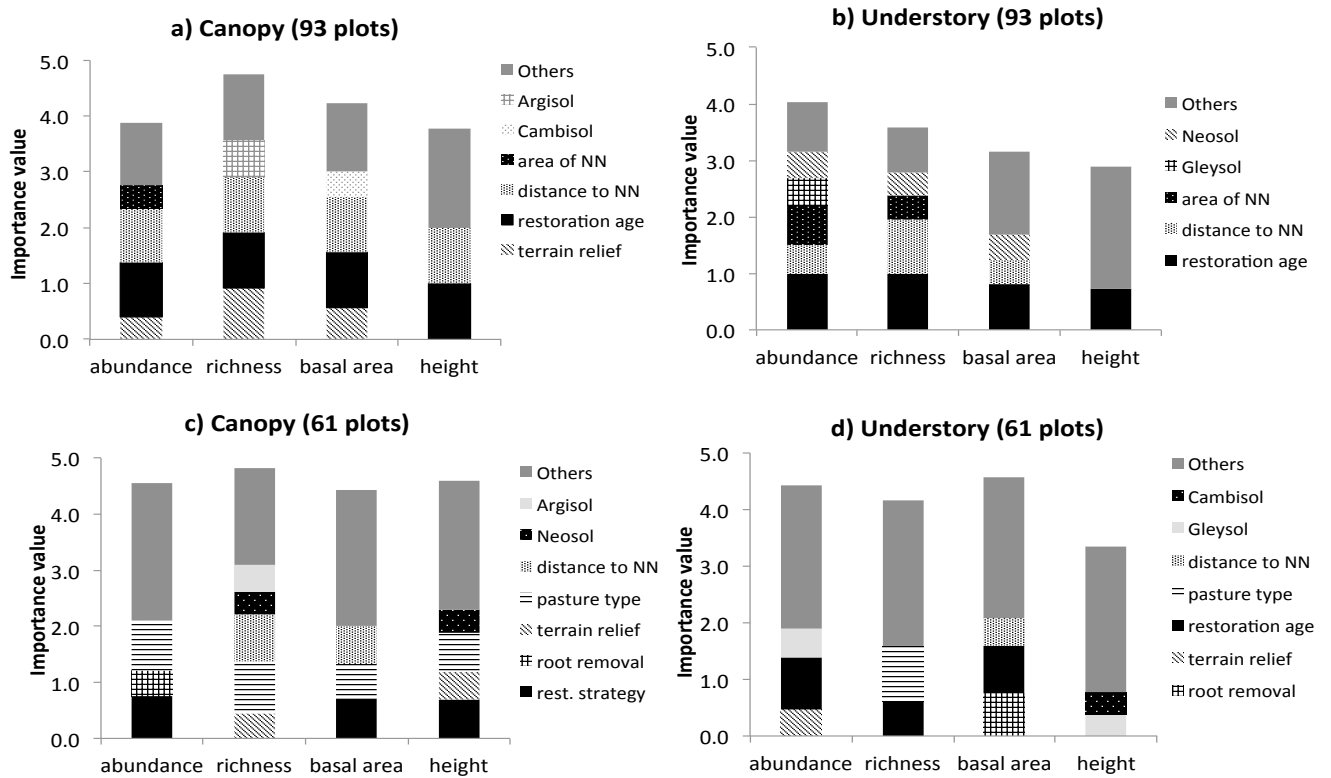


Figure 6. Diagram of the importance value of each explanatory variable in the canopy and understory in restoration areas in Southern Brazil. Importance values lower than 0.4 were placed together in the category “others”.

Discussion

The study of factors that may affect the restoration areas in the southern Atlantic Forest indicated that some factors together are mutually responsible for the outcome of restored forests. Some factors such as restoration age and distance from the nearest forest remnant were fundamental in most of the models constructed here. However, when we analyzed the beginning of succession separately (61 plot-subset), restoration age expressively decreased in importance. Restoration age was already described as primary factor determining forest structural parameters described in many other studies (Chazdon 2003, Howorth &

Pendry 2006), but the initial steps of restoration had been not been analyzed in this manner before. The strong relation with the distance of the nearest mature forest fragment shows that the presence of forests nearby is a key factor when planning restoration actions (Kauano *et al.* 2013).

Effects of soil and landscape features

All the response variables studied here showed a significant negative relationship with nearest neighbor distance. Considering that this study was conducted in an area with a forest matrix and where fragment distances vary from only 0 to 460m, we assume that even very small distances (under 500m) can have a strong influence in forest structural parameters as the ones studied here (abundance, richness, basal area and height). The presence of nearby forests and corridors are, thus, crucial for the recovery of Atlantic Forest areas. Small distances affecting succession were also reported in another study in the region (Zwiener *et al.* 2014), which found out that species composition of seeds and seedlings differed between areas distant 10m and 300m from the forest edge. In a study of natural regeneration in Puerto Rican tropical forest, distance to mature forests at the time of abandonment was a substantial predictor of species richness and diversity, along with site age, emphasizing the importance of seed dispersal for colonization (China 2002). Although the area of the nearest forest in our plots varied substantially, distance from these forests revealed to be more critical influencing succession in this area.

Terrain relief was not a central factor affecting the structural parameters plant abundance, basal area and height in our study. However, it had a high importance value in the models constructed for species richness. Species richness in slope areas is likely to be higher than lowland areas due to the contrasting land-use in rugged terrains, where the

difficult access has safeguarded mature forests in slopes and close to them, enriching the remaining species pool. Conversely, since the slope soils are usually coarser and have a more extreme microclimate, they are less easy to colonize and can therefore slowdown the spatial spread of species (Temperton *et al.* 2004). These two hypotheses, acting together, may have mitigated the effects of slope in this study. In addition, it is difficult to isolate the effect of the slope on the vegetation in our study. This is a constant bias of successional and restoration studies (Pascarella *et al.* 2000, Chazdon 2003), and should be considered carefully in future interpretations.

The variable soil type had weaker explanatory power than others, such as plot age and nearest neighbor distance. Acrisol explained canopy richness and Gleysol explained understory abundance. Gleysols tend to be more saturated with water, what may affect plant abundance, since many species do not tolerate flood. We did not measure the water table levels in this study, but a previous research in the same area indicated that Gleysols can be saturated with water during a long time of the year (Cardoso *et al.* 2012). Likewise, soil conditions were the primary factors affecting growth and survival of native tree seedlings in the same region (Sobanski & Marques 2014). Low levels of soil nutrients as well as soil physical characteristics (compaction, low levels of organic matter) also limit the establishment of the seedlings (Fernandes & Sanford 1995). Further studies on the effect of soil on restoration areas are necessary, considering soil-related effects more closely and trying to isolate them from other important variables, such as plot age.

Effects of pasture species and management

The variable pasture type was present in all the four best models for the canopy community and one model of the understory community. It was evident that the abandoned

areas previously colonized by any of the two *Urochloa* species had a significant negative effect on plant abundance and species richness than the areas that had only the non-invasive *Paspalum* sp. For basal area and height, although the difference between the three pasture types was not significant, the variable was selected in both models and the pastures with *Paspalum* sp. showed a tendency of having higher basal area and mean height than the ones with *Urochloa* spp. Nevertheless, in the understory, the presence of pasture type in the models was not so conspicuous. Pasture type only had a high importance value for understory species richness. For the other explanatory variables, there were other factors in this stratum that were even more important than pasture type, especially plot age, nearest-neighbor distance and soil type. One possible explanation for this result is that when the understory is actually present, it means that the first generation of plants (that are now adult trees) had already grown and transposed the barrier of the exotic grasses, producing shade and leaving it clear for the next generation, which is the current in the understory. Grass competition significantly decreased seedling growth in abandoned lands in Panama (Hooper *et al.* 2005). However, in a tropical forest in Puerto Rico, researchers have found that competition with grasses was a barrier to seedling establishment only for some species, and that species responded differently to pasture removal treatments (Zimmerman *et al.* 2000).

Effects of the restoration strategies and age

Restoration age was certainly a fundamental factor influencing most response variables in this study, except when the first years of succession were analyzed separately. In many other studies on Neotropical forests, structural patterns and species richness (Liebsch *et al.* 2008 and Zanini *et al.* 2014 in Atlantic Forest, Letcher & Chazdon 2009 in Costa Rica) also increased with forest age. In southern Brazil, results indicated that forest age overcame other

environmental and spatial variables on forest assembly patterns (Zanini *et al.* 2014). Aide *et al.* (2000) described vegetation recovery in a chronosequence of abandoned pastures and found that, after approximately 40 years of recovery, density, basal area, aboveground biomass, and species richness were similar to those of old growth forest sites.

The restoration strategy explained part of the variability in canopy abundance, basal area and mean height. Plots under active restoration by means of seedling plantation had more individuals, higher basal area and higher mean height, what is expected since there was an external input of individuals in the area. On the other hand, the plantation of these individuals was not important for species richness (importance value < 0.3), probably because few species were used in the restoration program. Plots of natural regeneration and plantation did not differ in number of species, suggesting that although plantation carries more individuals to the area, it does not necessarily lead to higher species richness. Our active restoration plots in this study are still young (maximum 11 years). Studies on the outcome of plantations after longer periods in different areas are needed to infer about the necessity of managing restoration areas. However, in areas with no restraints on seed dispersal and minor competition with exotic grasses, natural regeneration may be the best cost-benefit for restoration. In small abandoned pastures in Puerto Rico, adjacent to forested areas, results indicated that it is possible to make passive restoration, just letting trees naturally invade (Zimmerman *et al.* 2000).

The presence of remnant trees was not selected in any of the models and its importance value was generally low (<0.4) in this study. The proximity of the plots to remnant forests probably turned the remnant trees a secondary factor in attracting fauna and bringing propagules. Zwiener *et al.* (2014) found that isolated remnant trees received fewer seeds in the second year of their study in the same area. Over the course of succession, shrubs

and trees establish and thus, forest regeneration areas have more options of perching structures, decreasing the demand of the use of remnant trees as perches.

Most of our plots suffered root removal when forests were converted into pastures. Even though root removal was selected for the model for basal area in the understory, we might have not had a satisfactory number of plots without the root removal procedure to make this pattern more robust for the other variables.

In this study we concluded that abandoned pasture lands in the Atlantic forest in this kind of landscape have more favorable results when they are older (> 15 years old), closer to forest remnants, in the hillsides and without interference of the invasive grass species *Urochloa*. They also have differential development between different soil types and different restoration strategies. We conclude that there are important biotic and abiotic factors that interact strongly with the main factor (age since area abandonment) to influence successional processes. This study can provide insights into how to accelerate the regeneration process in tropical forests by determining its major barriers. The understanding of these limiting factors will also contribute to the knowledge of successional theory and mechanisms (Pickett *et al.* 1987) and to practical restoration actions. In the study region, for example, areas that are close to forest remnants, without invasive fodder grasses can be successfully restored with passive restoration techniques (natural regeneration). On the other hand, larger distances to forest remnants and the presence of *Urochloa* grasses may require active restoration strategies.

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Supplementary Material

Soil analysis

A preliminary soil sampling in order to find out main variations in chemical and physical soil compositions in the four soil types was carried out in 23 random plots (Cambisol: 10; Gleysol: 7, Acrisol: 3, Gleysol: 3). Samples were collected at a depth of 0–10 cm, at four equidistant points approximately 4m from the center of the plot and also one point in the center. Soil samples collected at the five points were then pooled in a container in order to make one composite sample per plot. Samples were then taken to the laboratory, air-dried and sifted. Standard chemical analyses were performed for pH, P, Al, Ca, Mg, K, Al and C (Embrapa 1997). Sum of basic cations (SB), base saturation levels (V%), cation exchange capacity (CEC) and Aluminum saturation (m%) were calculated. Soil textural analysis for the determination of clay, silt and sand content was performed using the densitometer method (Embrapa 1997) (Table S1). Other comparison between Cambisol and Gleysol soil parameters in the same study area can also be found at Cardoso *et al.* 2012.

Table. S1. Means (\pm SE) of the chemical and physical characteristics (depth= 0-10cm) of four soil types in Atlantic Forest areas, Southern Brazil.

	Fluvisol	Acrisol	Cambisol	Gleysol
pH CaCl ₂	4.03 \pm 0.11	3.85 \pm 0.14	3.78 \pm 0.06	3.96 \pm 0.04
Al (cmol _c .dm ⁻³)	1.13 \pm 0.36	1.35 \pm 0.43	2.36 \pm 0.21	2.14 \pm 0.28
Ca (cmol _c .dm ⁻³)	0.96 \pm 0.51	0.30 \pm 0.63	0.41 \pm 0.27	0.50 \pm 0.18
Mg (cmol _c .dm ⁻³)	0.58 \pm 0.17	0.30 \pm 0.21	0.31 \pm 0.09	0.43 \pm 0.09
K (cmol _c .dm ⁻³)	0.10 \pm 0.02	0.11 \pm 0.02	0.15 \pm 0.01	0.14 \pm 0.02
P _{Mehlich} (mg.dm ⁻³)	6.47 \pm 1.57	4.00 \pm 1.9	4.64 \pm 1.03	3.79 \pm 0.48
C (g.dm ⁻³)	34.5 \pm 5.5	40.3 \pm 6.7	4.47 \pm 0.25	7.72 \pm 0.43
Clay (g.kg ⁻¹)	179.7 \pm 48.9	263 \pm 59.9	390.7 \pm 37.59	225.14 \pm 47.99
Silt (g.kg ⁻¹)	283.7 \pm 88.7	181.5 \pm 108.7	143.23 \pm 50.47	318.91 \pm 51.87
Sand (g.kg ⁻¹)	537.7 \pm 124.0	556.5 \pm 151.91	463.48 \pm 51.19	456.23 \pm 94.24

**CARACTERÍSTICAS DO SOLO DETERMINAM DIFERENTES
TRAJETÓRIAS SUCESSIONAIS EM FLORESTAS TROPICAIS**

Soil characteristics determine different successional trajectories in tropical forests

Abstract

The forest structure and diversity of tropical forests recovering after a disturbance is determined by several factors. In areas previously occupied by pasturelands they include the impact of grass species, the distance and size of fragments, among others. We hypothesized that soil characteristics are an important factor to determine the successional trajectory in tropical forests. To test for this hypothesis we investigated the abundance, diversity, species composition and species specialization to soil types in the understory and canopy of successional forests occurring in two different soil types contrasting in water availability, namely, Gleysol (periodically flooded) and Cambisol (well drained) in the southern Atlantic Forest in Brazil. We sampled 45 circular plots (615.7m² each plot, 2.8ha total) of forests undergoing restoration (natural regeneration), 25 of them in Cambisol areas with age of abandonment varying from 2 to 80 years and 20 in Gleysol areas with age from 2 to 50 years. In all plots we sampled all trees with DBH \geq 5.0cm. In a concentric plot with smaller area (50.3m²) we also sampled all understory individuals (shrubs and saplings) with DBH \leq 5.0 and height \geq 1.3m. We sampled a total of 4389 individuals (3032 in the canopy and 1357 in the understory) distributed in 215 species of trees in the canopy and 181 species in the understory, including sapling and shrubs. We found a clear gradient of the plant communities' species richness, abundance, basal area and tree height along succession. Cambisol plots presented canopies with higher abundance, accumulated species, and diversity than Gleysol. In the understory, only a difference in abundance was found between soils, with Gleysol with more individuals in the younger plots and Cambisol with more individuals in the older plots. Despite these structural differences, species composition was similar. We found some species that were specialist to one or another soil types. We concluded that soil characteristics play an important role in determining the successional trajectories in tropical forests, and it should be taken into consideration when planning forest management.

Key words: natural regeneration; succession; soil type; Atlantic Forest

Introduction

The interest in tropical secondary forests dynamics and successional processes increased substantially in the past decades, when researchers have identified many of the factors that could affect them and their patterns of species diversity, biomass, structure and species composition (Hughes *et al.* 1999, Steininger 2000, De Jong *et al.* 2001, Guariguata & Ostertag 2001, Kennard 2002, Chazdon 2003, Letcher & Chazdon 2009). There are a variety of factors that influence regeneration of a forest, determining its capacity to recover and how fast this is going to happen (Uhl 1987, Aide & Cavelier 1994; Rodrigues *et al.* 2009). The vegetation that establishes after a disturbance or in newly abandoned areas is well varied and depends on such factors, like type and intensity of the disturbance, time since the area has been abandoned, size of the area and propagule availability (Swaine & Whitmore 1988; Gunderson 2000; Moran *et al.* 2000, Myster 2004, Chapter 1). While these factors allow us to understand the general successional pattern, they do not explain divergence between communities sharing the same landscape conditions. Other fine adjustments in micro-scale factors, such as soil characteristics may also be important in the plant community regeneration and succession. Soil texture, for example, is one of the most important characteristics of the soil, influencing directly and indirectly a cascade of relations between organic matter, ions and soil drainage (Silver *et al.* 2000, Castilho *et al.* 2006). Among many factors influencing species diversity, for example, soils are perhaps the most important and the least understood of them (Dubbin *et al.* 2006).

Species of tropical trees are differentially distributed with respect to habitat variables at both local and regional scales (Harms *et al.* 2001), and some of these variables can be related to edaphic conditions. It is known that soil characteristics may affect forest structure and dynamics (Quesada *et al.* 2009) and many other aspects of plant communities in tropical

forests, *e.g.* plant growth and phenology, individual density, biomass accumulation and species distribution (Laurance *et al.* 1999, de Toledo *et al.* 2011, Cardoso *et al.* 2012). Total stem density in neotropical lowland tropical forests, for example, tended to be lower in less fertile soils (DeWalt & Chave 2004). In addition, trees growing in a well drained soil, with more nutrients, showed higher diameter increment than the ones growing in a nutrient-poor and flooded soil in the Atlantic Forest (Cardoso *et al.* 2012). Laurance *et al.* (1999) found that soil-fertility parameters accounted for a third of the variation in aboveground biomass in Amazonia *terra-firme* forests while Zarin *et al.* (2001) found that soil texture influenced aboveground biomass accumulation in an Amazonian second-growth forest. In addition, Castilho *et al.* (2006) found a relationship between soil and topography with tree and palm biomass in central Amazonian Forest, with a tendency of increase in tree biomass in clay-rich soils. In a lowland tropical forest in Borneo, basal area and biomass growth had a strong positive relationship with soil nutrients, especially phosphorus (Paoli & Curran 2007). Regardless of all these findings, studies have not focused in comparing successional trajectories in contrasting soil conditions and determining how these trajectories can be influenced by soil during tropical forest succession.

The Atlantic Forest is one of the most threatened biomes on the planet, since it is extremely fragmented, with only 5 % of its original cover. Due to its high species richness and endemism, it is currently one of the hotspots for biodiversity conservation (Myers *et al.* 2000). Since the beginning of the 20th century, the Atlantic Forest in southern Brazil had its landscape greatly changed due to colonization and mining activity, and more recently due to the cultivation of banana, manioc, palm trees and buffalo farming (Borsatto *et al.* 2007). Along the remnants of the Atlantic Forest, there are areas with different levels of interference, often mingled with abandoned pastures that are now under regeneration process

and in different successional stages. The environmental mosaic formed by the combination of these areas in different ages creates a perfect scenario for studying succession and the factors that affect it. For these kind of studies, some researchers have used the chronosequence approach, which, although unrealistic in some cases (Chazdon 2008), is sometimes the only viable alternative for investigating temporal change in forest succession.

Previous studies in the area have already pointed that the presence of a forested landscape favors seed arrival (Leitão *et al.* 2010, Kauano *et al.* 2013, Zwiener *et al.* 2014), quickly resulting in structured forests (Liebsch *et al.* 2007, Cheung *et al.* 2010). However, the tree growth is limited by soil characteristics (Sobanski & Marques 2014, Cardoso *et al.* 2012) in some specific areas, which could potentially delay the successional trajectory.

We investigated how the succession trajectory differs in two different soil types contrasting in water and physical composition, namely, Gleysol (periodically flooded) and Cambisol (well drained). More specifically, we addressed the following questions: (1) Do abundance, species richness; basal area and tree height differ between Cambisol and Gleysol along the successional gradient? (2) Does species composition differ between soil types along the successional gradient? (3) Are there species that are specialists to a particular soil type?

Methods

Study site

This study was carried out in the Atlantic Forest of Paraná state, southern coast of Brazil, in the municipality of Antonina (25°19'15"S and 48°42'24"W). The study areas are within the Guaraqueçaba Environmental Protection Area, a large region (more than 300,000 ha) that includes forests, estuaries, bays, islands, mangroves and lowlands, and is part of one of the most important remaining areas of Atlantic Forest in Brazil (Ferretti & Brites 2006a).

We collected data in two reserves within these areas, *Rio Cachoeira Nature Reserve* and *Morro da Mina Nature Reserve*; both are property of the non-governmental organization *Society of Research in Wildlife and Environmental Education* (SPVS) and together, comprise nearly 10,000 ha (Fig. S1).

The climate in the region is humid subtropical (Cfa), according to Köppen's classification (Ferretti & Britez 2006b), with annual precipitation of 3106 mm and mean temperature of 21.2°C over the last 25 years (Cardoso *et al.* 2012). Altitude varies from sea level to 900m a.s.l.

Four soil types occur in the reserve: Acrisol, Fluvisol, Gleysol, and Cambisol (Ferretti & Britez 2006b). We focused this study in Gleysols and Cambisols. Gleysols are hydromorphic, mineral, with variable fertility and are permanently or periodically saturated with water. Cambisols comprise non-hydromorphic, mineral soils, with variable fertility and incipient B horizon, frequently found in slopes (Embrapa 2006).

Unlike other Atlantic Forest areas in Brazil that are surrounded within an anthropogenic matrix, the study area is located on a landscape that comprises 68% of forest remnants, including 9% of second growth forests that are mingled with buffalo grazing and agricultural areas (Kauano *et al.* 2012). With the increasing establishment of conservation areas in the region, some of these intensive use sites were abandoned and are now in a process of natural regeneration (Ferretti & Britez 2006a), resulting in areas with vegetation in different successional stages. Old growth forests present in the region are an important source of seeds (Leitão *et al.* 2010) and shelter for animals (Zwiener *et al.* 2012), which increases the speed of recovery.

The Atlantic Forest in the region is characterized by its high tree species richness, organized in defined strata and associated to other diverse biological forms (Roderjan &

Kuniyoshi 1988). Plant endemism levels in the Atlantic Forest can reach up to 40% (Thomas *et al.* 1998), which translates to a density of 8.7 endemic species for each 100 km² (Myers *et al.* 2000). In the study area, there are different forest typologies, resulting from a combination of varying altitudes and latitudes (Veloso *et al.* 1991). The sub-formations include Submontane, Lowland, Alluvial Forests and also pioneer areas with fluvial influence.

Part of the reserves suffered clear-cutting and later use for agriculture of banana, manioc, coffee and sugar cane, followed by pastures for buffalo breeding. Other areas suffered selective logging of native commercial species, such as the native palm tree *Euterpe edulis* (Ferreti & Britez 2006a, Bruel *et al.* 2010, Borgo 2010).

Experimental design

The study is based on a comparative analysis of the forest successional trajectory in areas with two soil types (Cambisol and Gleysol). Areas of the two soil types were chosen based on soil maps of the reserves. We established a total of 45 plots in areas of different ages after the abandonment: 2-6; 7-12; 15-25; 30-50 and > 80 years-old. Five plots were selected in each of these age groups, except for the last age (>80y), where only Cambisol plots could be found, due to the higher deforestation of the areas where Gleysols are predominant. The old-growth plots were given the arbitrary age of more than 80 years, considering the analysis of historical aerial photos and interviews with the locals. The areas up to 50 years old were previously used for cattle pasture (for approximately 30 years) and then abandoned. The older areas (>80 years old) have not suffered clear-cutting, but they were likely used for selective logging for local use in the past century.

Soil analysis

Soil characterization was carried out by sampling 17 random plots (Cambisol: 10; Gleysol: 7) for soil physical and chemical analysis. Samples were collected at a depth of 0–10 cm, at four equidistant points at 4m from the center of the plot and also one point in the center. Soil samples collected at the five points were then pooled in a container in order to make one composite sample per plot. Samples were then taken to the laboratory, air-dried and sifted (2mm). Standard chemical analyses were performed for pH (CaCl₂), P, Al³⁺, Ca²⁺, Mg²⁺, K⁺ (Mehlich) and C (Embrapa 1997). Soil texture analysis for the determination of clay, silt and sand content were performed using the densitometer method (Embrapa 1997).

Vegetation survey

All plots (total: 25 in Cambisol and 20 in Gleysol) were circular (radius of 14m; area of 615.7m² each), resulting in a total sampled area of 2.77ha (1.54ha in Cambisol and 1.23ha in Gleysol). Plots were distributed in the reserves and were selected in a way to account successional areas of lowland and mountain slope areas (Lowland and Submontane Atlantic Forest) (Fig. S1).

We recorded diameter at breast height (DBH, at 1.30m), total height (measured with a telescopic pole), and species identification for all tree individuals with DBH \geq 5.0cm within the 14m-radius circular plot, referred hereafter as canopy. Individuals with multiple basal stems were included when at least one of the stems had DBH \geq 5.0cm. In a smaller concentric radius (4m, area=50.3 m²), we measured all individuals (saplings and shrubs, referred hereafter as “understory”) with DBH < 5.0cm (or stem base diameter, for shrubs) and height \geq 1.30m. We calculated total tree abundance, species richness, basal area and mean height for each plot, for the 14m radius representing the canopy community; and total tree

abundance and species richness for the 4m radius, representing the understory community. Basal area and height were not calculated for the understory community because only individuals < 5.0cm of DBH were included, hence, these variables are limited in this stratum.

Data analysis

Analyses for differences in textural and chemical characteristics of two soil types were performed with *t*-test (C, pH, Al, K, clay) or Wilcoxon test (Ca, Mg, P, sand, silt). Wilcoxon test was used for the variables that were not distributed normally by the Shapiro-Wilk test (Zar 1999).

The data of canopy and understory were organized to test for effects of soil and forest age (used as co-factors) on the structural characteristics (species richness, abundance, basal area and tree height) of forests undergoing regeneration (explanatory variables). We performed an analysis of covariance (ANCOVA, Zar 1999) to test for differences in the slopes of the two soil types in relation to the age gradient. For this analysis we used the exact age of the plots up to 15 years; and for the other age-groups, which we do not know the exact age, we used the mean of the age interval between them, for example, the 15-25 year-old plots were given 20 years; the 30-50 years-old plots were given 40 years and finally, the plots with 80 years or more were given the approximate age of 80 years.

The number of species between soil types was also compared using rarefaction curves, so we could standardize the accumulation of species per number of individuals sampled. Rarefaction curves are indicated for species richness comparisons in cases where there may be differences in the mean number of individuals per sample (Gotelli & Colwell 2001), which is the case of many succession studies (Aide *et al.* 2000, Kennard 2002, Piotto *et al.* 2009, Zanini *et al.* 2014). For this analysis, the five plots representing the old-growth forest in the

Cambisol (>80 years) were not considered, so that the number of plots and ages is even between soils.

Species composition was evaluated comparatively between soil types and forest ages with a NMDS analysis (using Chao dissimilarity index, Chao *et al.* 2005). Chao is an abundance-based index that takes into account the number of unseen species pairs. In tropical forests, where rare species are frequent and the sampling is incomplete, this index is less biased by sample size and is, therefore, more appropriate than other similarity indices commonly used (Norden *et al.* 2009). In order to understand species affinities with the two soil types, species were categorized using the multinomial classification model proposed by Chazdon *et al.* (2011) that classifies the species in Generalists, Group 1 (Cambisol) specialists, Group 2 (Gleysol) specialists and rare (too rare to classify). The model uses species abundances in two distinguishable habitat types (Gleysol and Cambisol in this case) to estimate relative abundances, corrects for the fact that sampling tends to overestimate common species and underestimate rare species, and minimizes bias due to uneven sampling intensities (Chazdon *et al.* 2011).

The six more abundant species in the plots were also evaluated individually in order to detect patterns from their occurrence in the two soil types along successional ages. For these, proportions of the species in each age and each soil type were calculated individually based on the total abundance (n) of the species in the plots between 2 and 50 years old. Species present in the 80 year-old plots, although shown in the figures, were not used in the calculations, since we had uneven number of plots representing this age.

Results

Soil characteristics

Cambisol and Gleysol did not differ in nutrients, but differed for pH and texture (clay and silt) (Table 1). Cambisol samples were more acidic, had higher clay content and lower silt content than Gleysol ones. In addition to these differences, groundwater level in Cambisol is lower (deeper) during most of the year when compared to Gleysol, varying from 45 cm to 130 cm in Cambisol and from 20 cm to 90 cm in Gleysol (Supplementary Material, Fig. S2).

Table. 1. Means (\pm SE) of the nutritional and physical characteristics of two soil types in Atlantic Forest areas, Southern Brazil. ns= non significant

Soil parameter	Cambisol	Gleysol	<i>t</i> or <i>Z</i> test
pH (CaCl ₂)	3.78 \pm 0.06	3.96 \pm 0.04	<i>t</i> =2.24; <i>P</i> =0.04
Al (cmol _c .dm ⁻³)	2.36 \pm 0.21	2.14 \pm 0.28	ns
Ca (cmol _c .dm ⁻³)	0.41 \pm 0.27	0.50 \pm 0.18	ns
Mg (cmol _c .dm ⁻³)	0.31 \pm 0.09	0.43 \pm 0.09	ns
K (cmol _c .dm ⁻³)	0.15 \pm 0.01	0.14 \pm 0.02	ns
P (mg.dm ⁻³)	4.64 \pm 1.03	3.79 \pm 0.48	ns
C (g.dm ⁻³)	4.47 \pm 0.25	7.72 \pm 0.43	ns
Clay (g.kg ⁻¹)	390.7 \pm 37.59	225.14 \pm 47.99	<i>t</i> =2.5; <i>P</i> =0.03
Silt (g.kg ⁻¹)	143.23 \pm 50.47	318.91 \pm 51.87	<i>Z</i> =2.64; <i>P</i> =0.008
Sand (g.kg ⁻¹)	463.48 \pm 51.19	456.23 \pm 94.24	ns

Species richness and individual abundances

We sampled a total of 4389 individuals in 45 plots, where 3031 were canopy trees and 1358 were understory individuals, including saplings and shrubs (Table S1). A total of

215 species of canopy trees (Cambisol: 185 species; Gleysol: 113 species) and 182 species of understory (Cambisol: 134 species; Gleysol: 116 species) were recorded. General characteristics of the plots showed successional changes along the chronosequence, with mean number of individuals and species, species diversity, basal area and mean height increasing with age in both soil types (Table 2).

Rarefaction curves showed the increase of species richness as individuals were added. For canopy trees, this increase was faster in the Cambisol plots when compared to Gleysol (Fig. 1a). For example, when the same number of individuals was considered, Cambisol presented more species than Gleysol. In contrast, this was not the pattern for the understory (saplings and shrubs), in which no clear difference was detected in the rarefaction curves of Gleysol and Cambisol (Fig 1b).

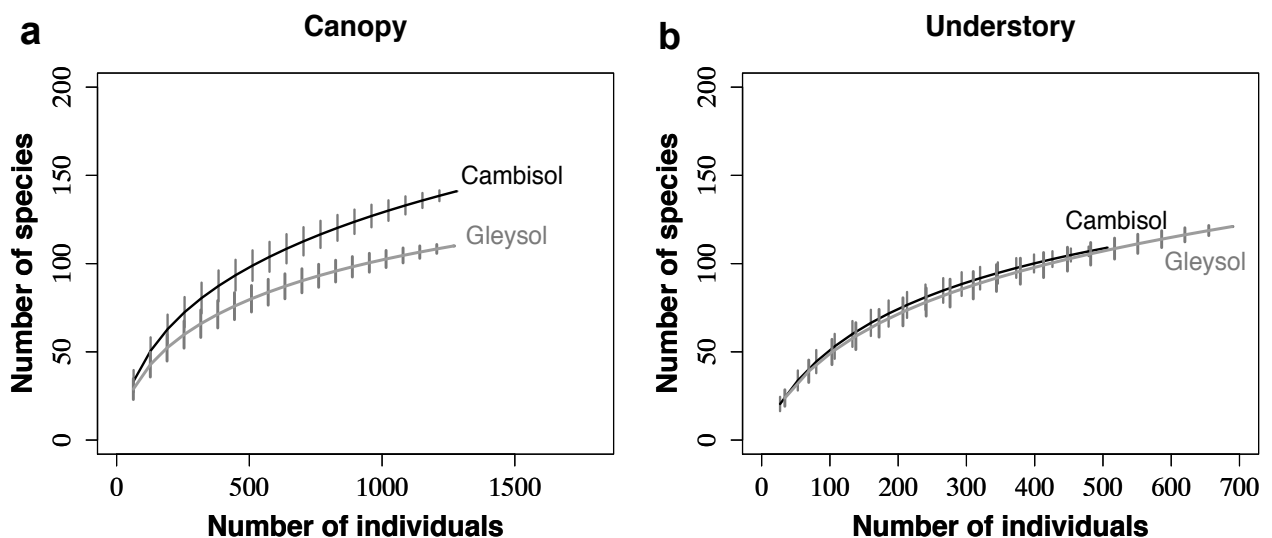


Figure 1. Individual-based rarefaction curves comparing two soil types (Cambisol and Gleysol) for canopy (a) and understory (b) along the successional trajectory of the Atlantic Forest in southern Brazil. Error bars indicate 95% confidence intervals for the number of species. N=20 in Cambisol and N=20 in Gleysol.

Comparison of forest structure along forest ages and soil types

In the canopy, the covariance analysis showed a significant effect of age on all four measured variables. Plant abundance in the canopy also had a significant interaction between

age and soil, with Gleysol plots reaching higher abundances earlier in the succession (Fig. 2a). Soil type was not a significant factor for the other variables (richness, basal area and height), where only an effect of the age gradient was found (Fig. 2c, 2e and 2g). In the understory abundance, the interaction was not significant as it was in the canopy, but, in addition to age, there was also an effect of the variable soil type (Fig. 2b). Species richness also had an effect of age, but not soil (Fig. 2d).

Species composition

The NMDS scatterplot (Stress= 0.159) showed some floristic patterns along succession (Fig. 3). The axis 1 separated plots according to forest age, and younger plots (in the two first age classes) were positioned in the right and older plots (> 40 years of age) in the left of the axis. The axis 2 did not show clear patterns for strata (canopy and understory) and soil types (Cambisol and Gleysol) (Fig. 3).

Soil specialization

We found that some species are specialists to one or another soil type, or are generalists (abundant in both soil types) (Table S1). For the canopy, 24 species were classified as generalists, 24 as Cambisol specialists, 13 Gleysol specialists and the remaining species (154) were considered too rare to classify (Table S1). For the understory, generalists accounted for 13 species, Cambisol specialists included 15 species, Gleysol specialists 12 and the remaining species (142) were considered too rare to classify (Table S1).

Considering the six more abundant species, *Tibouchina trichopoda* was the most abundant species sampled in the study (311 individuals) and it was considered a Gleysol specialist. We noticed a higher proportion of this species in the Gleysol plots along all ages,

reaching 45% of all individuals present in the Gleysol 7-11 year-old plots, compared to approximately 35% in the Cambisol plots of the same age. The occurrence of this species fell drastically in the 15-25 year-old and 30-50 year-old plots in both soil types (Fig. 4a). *Myrsine coriacea*, a generalist, was the second most abundant species, and its occurrence was considerably different between soils and along succession. In the younger ages of succession it was more frequent in the Gleysol plots and as succession proceeded, it became more frequent in the Cambisol plots. Its frequency reduced to zero in the 30-50 year-old plots in both soil types (Fig. 4b). *Tibouchina pulchra* and *Pera glabrata* were both Gleysol specialists for the canopy, but *T. pulchra* was too rare to classify in the understory while *P. glabrata* was a Cambisol specialist in the understory. They had similar pattern and also had distinct distributions between soils, both reaching higher proportions (35 to 50%) in Gleysol plots (Fig. 4c, 4d). *Casearia obliqua*, a Cambisol specialist, was remarkably more abundant in Cambisol plots along succession (Fig. 4e). *Miconia cinerascens* had its occurrence varying along age, but not as much between soils. It was a generalist in the canopy and a Gleysol specialist in the understory (Fig. 4f).

Table 2. Means (\pm SE) of abundance, species richness, tree height and Shannon-Weiner Diversity Index (H') and basal area (total) of canopy and understory communities, in two soil types (Cambisol and Gleysol) along the successional trajectory of the Atlantic Forest in southern Brazil.

	Forest age and soil type									
	2-6y		7-11y		15-25y		30-50y		>80y	
	Cambisol	Gleysol	Cambisol	Gleysol	Cambisol	Gleysol	Cambisol	Gleysol	Cambisol	
Canopy										
Individuals	35.0 \pm 18.4	21.8 \pm 5	34.4 \pm 10.5	45.5 \pm 8.4	106.6 \pm 7.8	98.0 \pm 10.3	83.0 \pm 3.1	90.2 \pm 17.0	92.0 \pm 5.0	
Species	7.8 \pm 3.1	5.2 \pm 1.0	7.2 \pm 2.1	8.4 \pm 0.7	26.2 \pm 3.1	19.4 \pm 2.9	34.2 \pm 2.4	28.0 \pm 2.3	42.6 \pm 2.5	
Basal area (m ² .ha ⁻¹)	28.8	16.8	21.7	21.1	117.0	103.6	130.0	105.8	175.2	
Height (m)	6.3 \pm 0.7	6.1 \pm 0.5	5.7 \pm 0.5	6.2 \pm 0.3	10.3 \pm 0.2	10.1 \pm 0.6	11.8 \pm 0.1	9.2 \pm 0.6	10.1 \pm 0.5	
H'	1.18 \pm 0.3	1.02 \pm 0.3	1.17 \pm 0.4	1.28 \pm 0.2	2.49 \pm 0.2	2.14 \pm 0.4	3.21 \pm 0.1	2.79 \pm 0.1	3.40 \pm 0.1	
Understory										
Abundance	9.8 \pm 3.8	17.2 \pm 5.9	20.6 \pm 8.2	21 \pm 7.2	35.2 \pm 4.2	50.4 \pm 12.2	32.6 \pm 4.6	47.6 \pm 13.8	37.0 \pm 2.8	
Species richness	3.8 \pm 1.6	5.4 \pm 1.0	6.2 \pm 0.9	5.4 \pm 0.7	17.2 \pm 2.2	21.2 \pm 4.4	17 \pm 2.4	17 \pm 4.6	19.6 \pm 0.9	
Basal area (m ² .ha ⁻¹)	3.4	12.5	18.8	17.8	11.8	15.3	12.0	13.8	16.8	
Height (m)	1.8 \pm 0.5	2.4 \pm 0.1	2.8 \pm 0.5	3.1 \pm 0.4	2.8 \pm 0.1	2.9 \pm 0.3	2.8 \pm 0.1	2.6 \pm 0.1	3.2 \pm 0.1	
H'	0.96 \pm 0.4	1.18 \pm 0.3	1.39 \pm 0.2	1.34 \pm 0.2	2.51 \pm 0.1	2.65 \pm 0.2	2.5 \pm 0.2	2.28 \pm 0.3	2.72 \pm 0.1	

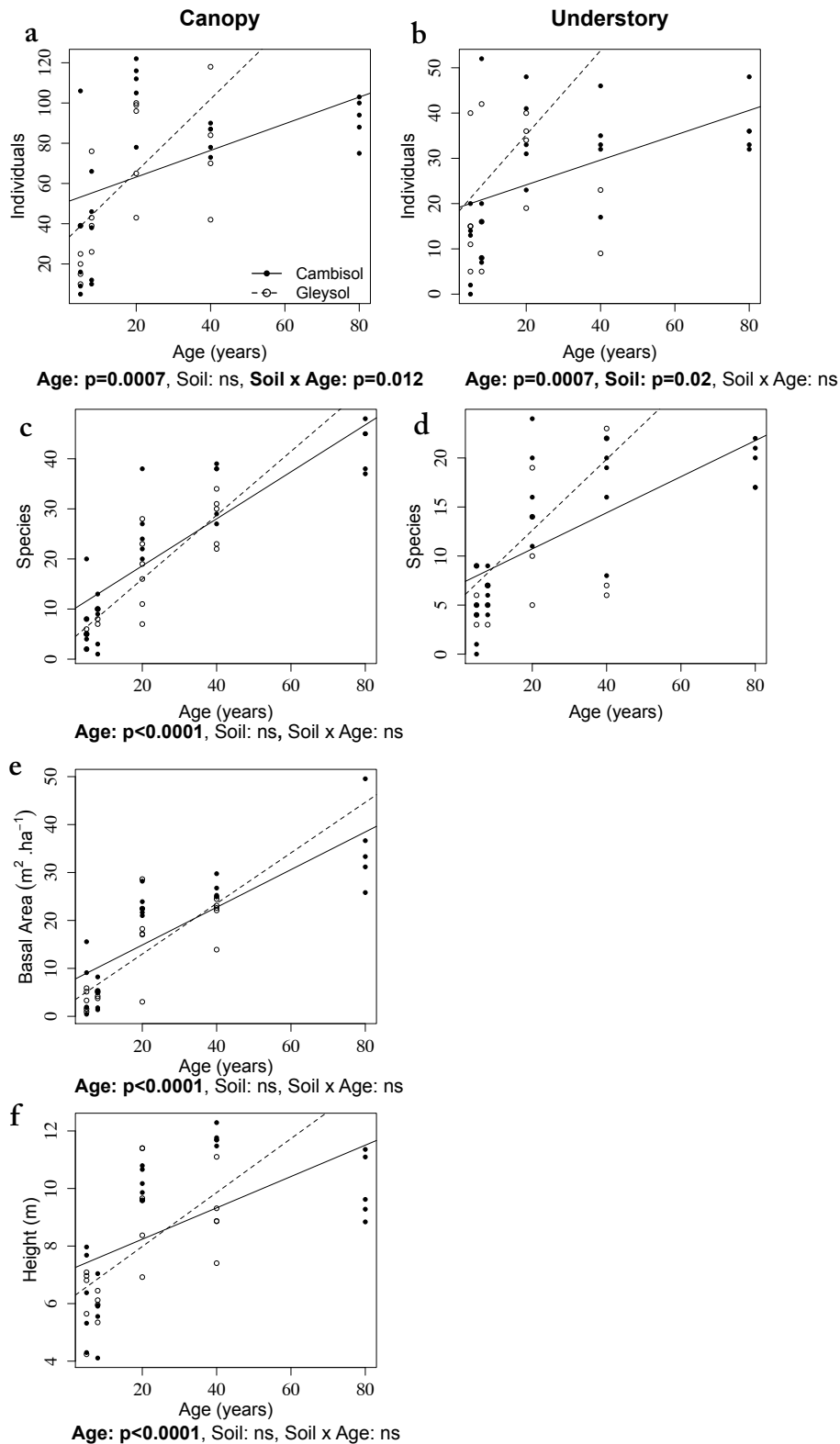


Figure 2. Number of individuals (a, b), species richness (c, d) of the canopy and understory communities and basal area (e) and mean height (f) of canopy the community in two soil types (Cambisol and Gleysol) along the successional trajectory of the Atlantic Forest in southern Brazil. Gleysol (n=20) and Cambisol (n=25). ANCOVA results are over each figure; ns=non-significant.

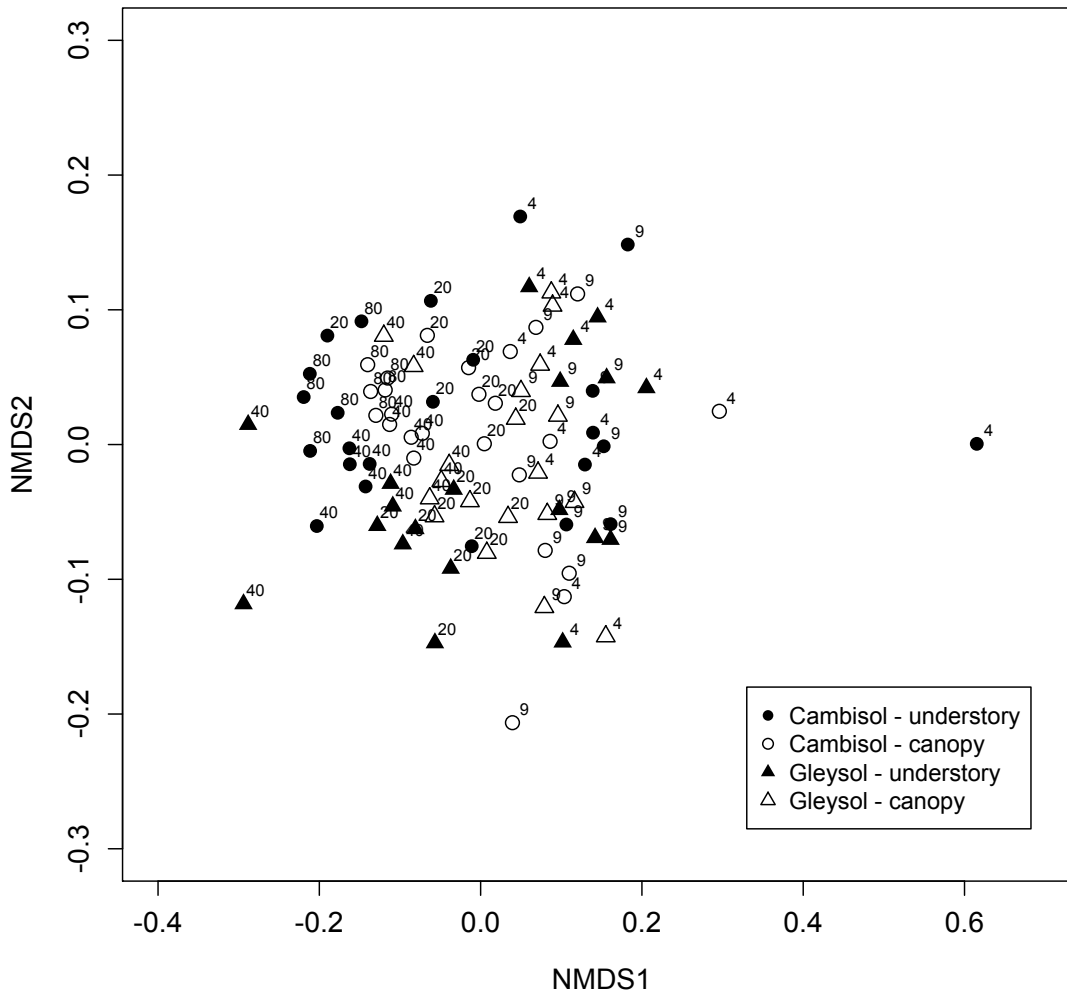


Figure 3. Scatterplot of the non-metric multidimensional scaling (NMDS) for canopy and understory plant communities in two soil types (Cambisol and Gleysol) along the successional trajectory of the Atlantic Forest in southern Brazil. Numbers refer to the mean age of plots (4: 2-6 years, 9: 7-15 years, 20: 15-25 years, 40:30-50 years and 80:> 80 years).

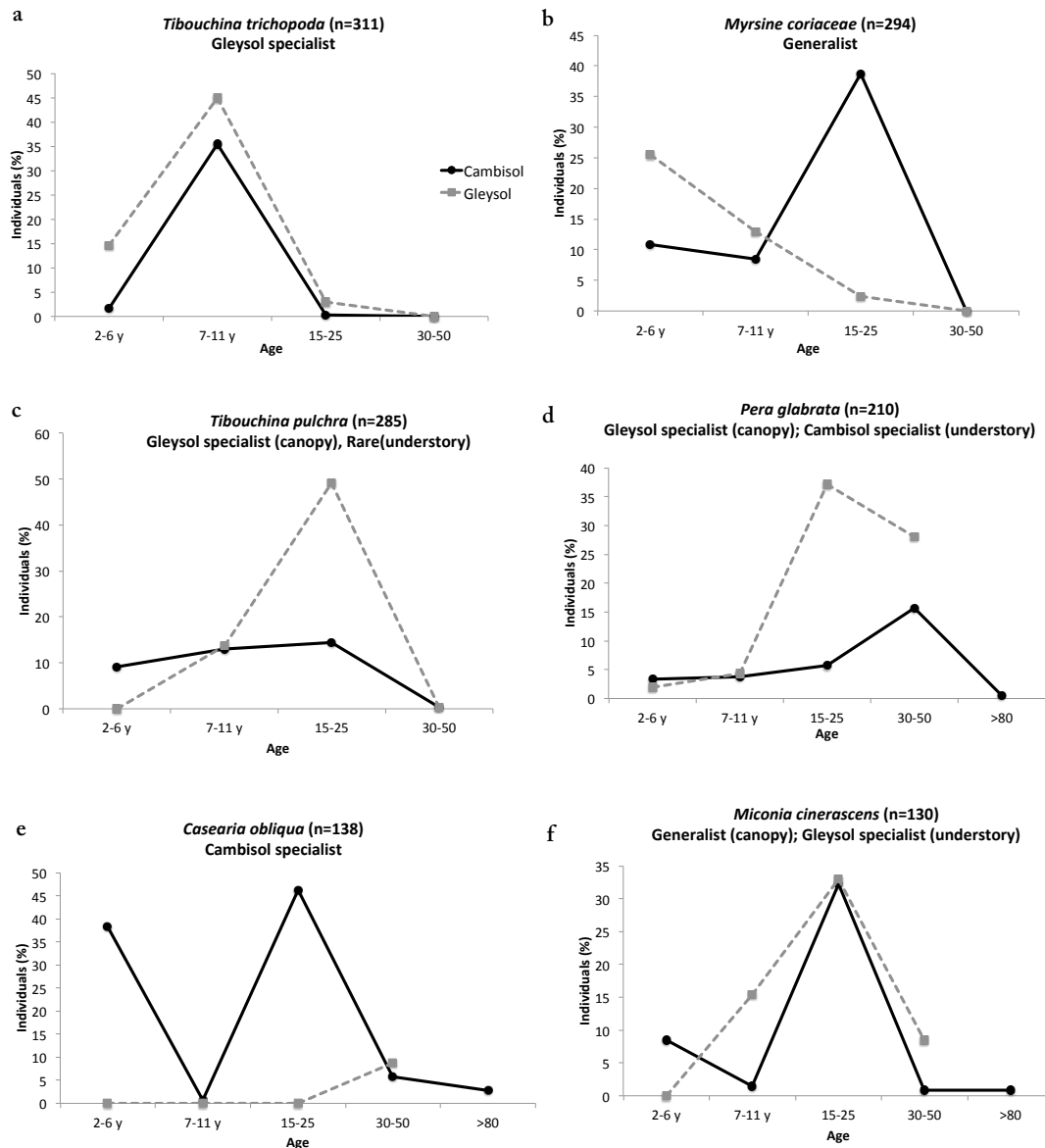


Figure 4. Proportion of the six most abundant species occurring in two soil types (Cambisol and Gleysol) along the successional trajectory of the Atlantic Forest in southern Brazil. Individuals occurring in the >80 year-old plots are represented in the figures, although they were not used in the calculations.

Discussion

Our study comparing the chronosequence of second growth forests in two different soil types suggests differences in successional trajectories according to soil characteristics. Soil differences were related to higher individual density and faster species accumulation in Cambisol compared to Gleysol, which is apparently associated to a specialization of some species to one or another soil type. These results suggest that soil is an important factor explaining successional changes in tropical forests. Other studies in neotropical lowland forests also showed some effects of soil characteristics on the general forest structure (DeWalt & Chave 2004, Martins 2012).

We found some differences in the pH and in the physical characteristics of the two soil types, but not a difference in the nutrient composition. Since both soils had relatively low nutrient availability, fertility might not be a factor that distinguishes them. In fact, the soil water conditions are probably what contribute more to the differences between the two soil types. Previous analysis in the same region indicated that the water level is more superficial in Gleysols compared to Cambisols (Cardoso *et al.* 2012). High moisture levels in the soil may result in weak aeration, with most of the pore space filled with water (Korning *et al.* 1994). Given that Gleysols can be periodically saturated with water, this can reduce the amount of air and dissolved oxygen in the soil, affecting metabolic activities, plant growth and causing tree mortality (Pimenta *et al.* 1996; Gale & Barford 1999), once very few species can cope with anoxic conditions (Quesada *et al.* 2009). Cambisol, on the other hand, with better water drainage may offer fewer limitations to seedling development.

Richness and diversity across soil types and forest ages

In the canopy community, the rarefaction curves showed that the species accumulation rate was faster in Cambisol compared to Gleysol, but for the understory, this distinct pattern between soils was not observed. Cambisol may offer better conditions for the establishment of a wider range of canopy species, while Gleysol excess of water may act as a filter in which less species are able to transpire. The differences between the understory and canopy may be due to the depth in which plants from each stratum reach the soil. Understory plants (juveniles and shrubs) have shorter roots that acquire water and nutrients in the upper layer of the soil, while canopy individuals, with their longer roots, will reach for resources deeper in the soil, where the differences between the two studied soils may be sharper.

Diversity (as measured with the H') also tended to increase with age in all community levels (understory and canopy), which was also reported in other studies (Ruiz *et al.* 2005, Borgo 2010). We also found some small distinctions of diversity between soil types in the canopy community. Except for the 2-6 year-old plots, all other ages (7-11y, 5-25y and 30-50y) had approximately 10% higher H' in Cambisol compared to Gleysol.

The ANCOVA revealed a steep increase in species richness along succession, as also reported in other studies in the Atlantic Forest (Zanini *et al.* 2014, Liebsch *et al.* 2008). However, this increase in species richness was similar between soil types, indicating that despite the contrasting species richness and diversity explained above, the rate of change in the number of species during the successional trajectory is the same. Likewise, in successional forests in Malaysia, although poor soils sustain forests with high diversity, no relationship between soil and species richness were found

(Proctor *et al.* 1983). At the beginning of succession the species richness in these communities are limited by invasive grass species used in the pastures (Chapter 1). Studies have suggested that the presence of grasses is the leading limiting factor affecting the survival and growth of tree seedlings (Holl *et al.* 2000; Sun & Dickinson 1996). Hence, it is possible that in the beginning of succession (~10 first years), the effects of the competition with grasses exceed the soil limitations for seedling establishment. As succession continues, most of the invasive grasses disappear and that is when soil may become a more important factor influencing species richness. In fact, it is the interaction of soil and grass in the first years of succession in abandoned pastures that may potentially be more limiting to species establishment. For example, the invasive grass *Urochloa humidicola*, is better adapted to the water saturated soils (Miles *et al.* 1996), so, it grows more and might also have a longer life span in this type of soil, influencing the seedling establishment for an extended period in studied Gleysol areas.

Abundance, basal area and height

The number of individuals in the canopy communities was positively affected by forest age and the relationship differed among soil types; however, in the understory there was an independent positive effect of forest age and of soil type. In a chronosequence study in a tropical forest in Colombia, they found that tree abundance reached its peak between 30 and 50 years of age (Ruiz & Fandiño 2005), while in our study abundance values reached its peak a little earlier (around 15-25 years). With the increase of abundance, we also expected a differential increase in basal area between soils, but both soils seem to increase basal area similarly along successional age. Although it has been reported in the same study area that trees growing in Cambisol

had increased diameter growth than the ones growing in Gleysol (Cardoso *et al.* 2012), this did not correspond to basal area in our study. Likewise, Clark *et al.* (1998, 1999) showed that many species had significant associations with soil type in a tropical forest in Costa Rica, although they did not find relation of soil and diameter growth. One factor that may hide possible differences in the basal area between soils is that the abundance of individuals was higher in Gleysol while mean DBH was higher in Cambisol. It is possible that the individuals with higher DBH in Cambisol did not compensate for total basal area in the Gleysol areas.

Canopy trees height increased with age, but it did not differ between soils. In situations where soils contrasts are more pronounced, tree height growth rate can be limited by soil fertility (Moran *et al.* 2000). However, for the study region, fertility differences between Cambisols and Gleysols probably were not sufficient for causing tree height growth limitations. In a tropical forest in southeastern Brazil, canopy species also had higher and more variable growth rates (height and diameter) than understory species, attributed to greater access to light at the canopy level (van den Berg *et al.* 2012).

The similarity in the basal area and in the mean height between soils in our study may also be attributed to the scale of the study. Some studies have found interaction between soil fertility and above ground biomass in Amazonia (Laurance *et al.* 1999, Roggy *et al.* 1999), but many other studies have found no relationship of biomass with soil fertility (Proctor *et al.* 1983, Chave *et al.* 2001, DeWalt & Chave 2004). These are mostly large-scale studies and climate was considered a strong factor affecting aboveground biomass. In a local scale and in successional forests, such as our

study area, the community biomass production might also be controlled only by forest age (Shimamoto *et al.* 2014).

Species composition and specialization

Although differences in species composition were not very clear between soils and between strata, we could find some tendencies of site groupings. In addition, we also found a clear age gradient in species composition. In other tropical forests, such as one studied in Belize, soil was described as the main determinant of forest composition, more specifically water holding capacity and nutrient availability (Dubbin *et al.* 2006). It is likely that species composition could be indirectly affected by soil physical conditions, since adverse soil conditions could favor the dominance of pioneer species with short lifetimes (Quesada *et al.* 2009). The extremely high number of rare species in the samples, many of them sampled only once or twice, could be a reason why the analyses could not separate the species pool of the two soil types more clearly.

Although most of the species in our study were considered too rare to classify, there were some that had a much higher abundance (or even exclusivity) in one of the soil types. This suggests that species respond differently to edaphic conditions and some are probably more sensitive to soil than others. Gleysol specialists, for example must tolerate poor nutrient conditions and excess of water, while Cambisol specialists might need a deeper and better drained soils. Species-specific differences between different climate, microclimate and soil characteristics were also detected in the growth of tropical species (Worbes 1999; Yáñez- Espinosa *et al.* 2006; Couralet *et al.* 2010). In a study of nine tropical species in Costa Rica, the majority of them also showed highly significant associations with different soil types, such as old alluvial soils, residual soils

and stream valley soils (Clark *et al.* 1998). In the same two soils studied here (Cambisol and Gleysol), two species presented contrasting response to soil type, one of them noticeably differing in diameter growth between soils while the other showed equivalent growth rates between soils (Cardoso *et al.* 2012). Species associations with soil types were also reported in the landscape scale, where 33 species showed non-random spatial distribution in relation to edaphic factors in Costa Rica (Clark *et al.* 1999).

The importance of secondary forests is increasing substantially in the past decades (Chazdon 2014), and also is the need of accurate ecological bases to manage and maintain them. Considering the dynamism and diversity of tropical forests, the understanding of all the factors that govern their ecological processes is a difficult, but important task. Although age is the main driver to determine structure and diversity of secondary forests (Zanini *et al.* 2014), we found that soil characteristics is an additional factor determining successional trajectory of tropical forests, and should also be taken into consideration when analyzing and implementing ecological restoration plans. The influence of soil type is a novelty that will contribute with the knowledge of succession in tropical forests, explaining part of the stochasticity of the process.

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Supplementary material

Methods

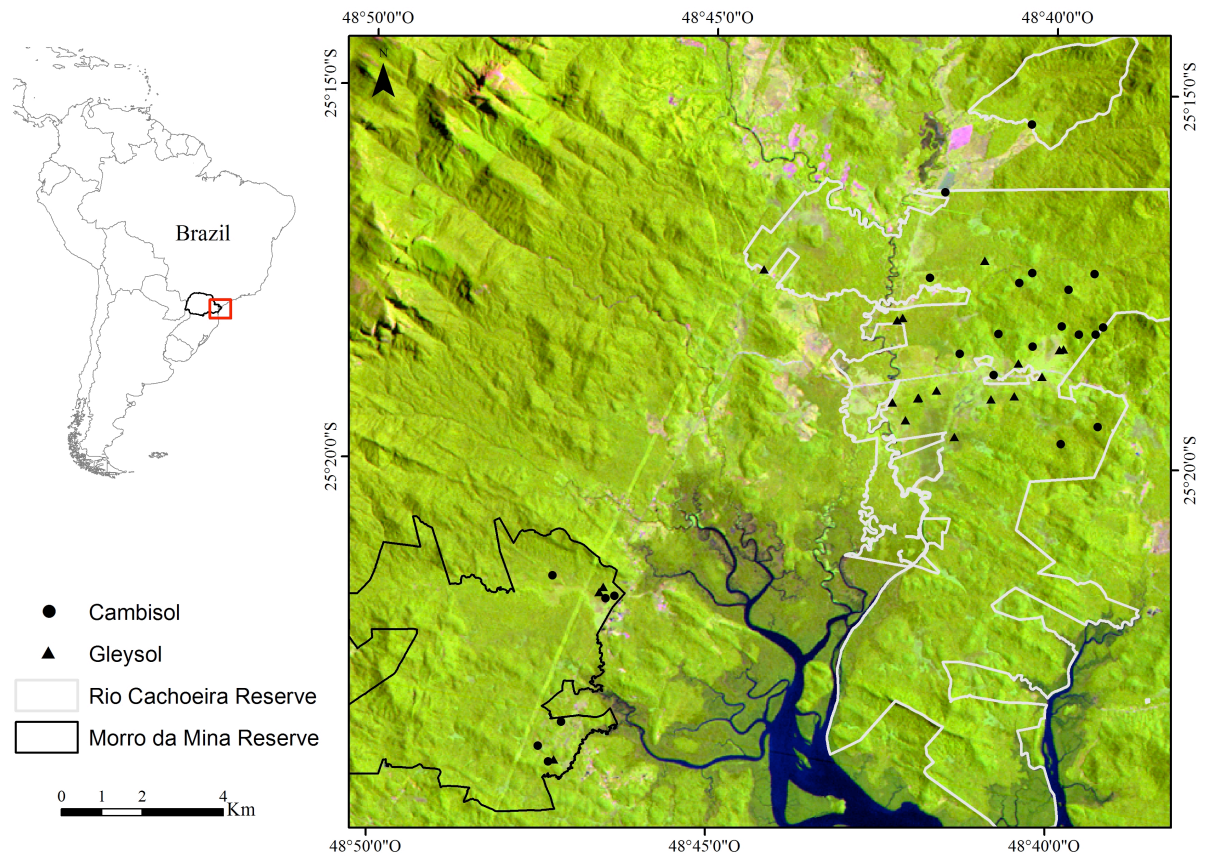


Figure S1. Location of the study area in the state of Paraná, southern Brazil and of the 45 studied plots (20 Gleysol and 25 Cambisol plots).

Groundwater level

In order to assess the groundwater available in both soil types, 12 piezometers were placed in Gleysol areas and 17 in Cambisol areas. Piezometers were made of perforated PVC pipes, 10 cm in diameter, and were installed as much as 100 to 150 cm below ground level (Walthall and Ingram 1984). Variation in groundwater level along the year was similar in the two sites; however, groundwater level in Cambisol was lower in most of the year in relation to Gleysol (Fig. S2). Groundwater was deeper (less water

available to plants) in July and September (months with lower precipitation), when water was more than 130 cm deep in Cambisol and approximately 90 cm deep in Gleysol. The lower depth (water closer to surface) occurred in March (end of the wettest period) when it was only around 50 cm below surface in Cambisol and around 20 cm in Gleysol.

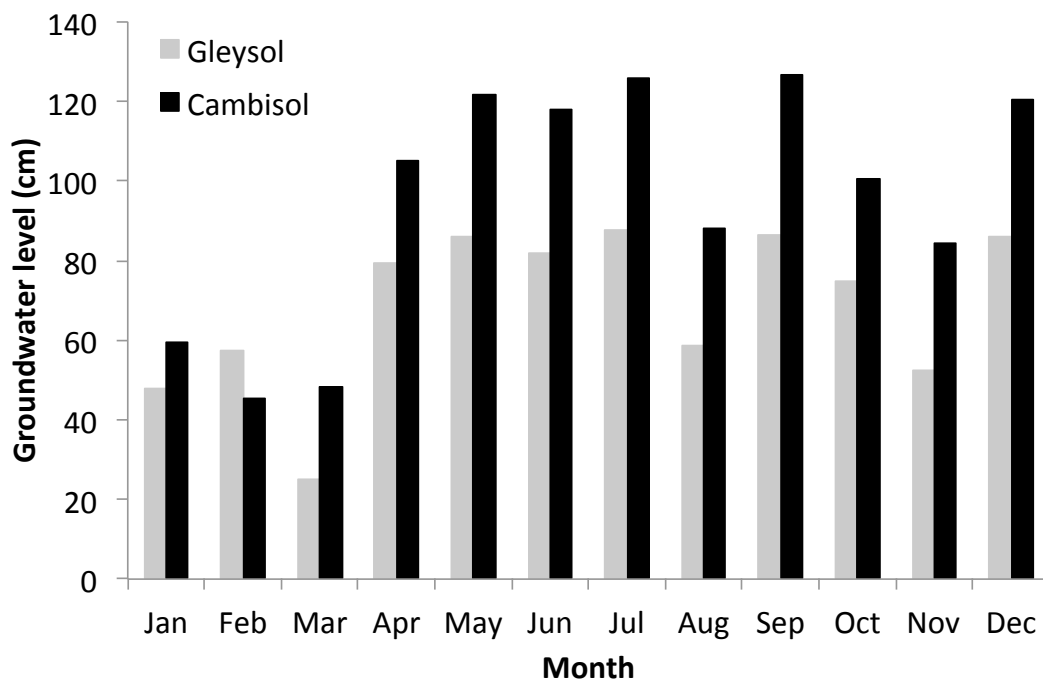


Figure S2. Mean groundwater level throughout the year measured with 17 piezometers in Cambisol areas and 13 in Gleysol areas, in the Atlantic Forest, Southern Brazil

Table S1: Canopy and understory species and their abundances by soil type in 45 plots in the Atlantic Forest, Southern Brazil. CAM=Cambisol; GLE=Gleysol ¹: Families according APG III; ²: species names and authors according to *Specieslink* (www.splink.cria.org.br/). cat.=category of soil specialization: gen=generalist, cam=Cambisol specialist, gle=Gleysol specialist, r=rare

FAMILY/ Species	Canopy			Understory		
	CAM	GLE	cat.	CAM	GLE	cat.
ANACARDIACEAE						
<i>Tapirira guianensis</i> Aubl.	5	8	gen	1	4	r
ANNONACEAE						
<i>Annona neosericea</i> H.Rainer	1	-	r	-	-	r
<i>Rollinia sericea</i> (R.E. Fries) R.E. Fries	14	5	cam	1	2	r
<i>Rollinia</i> sp1	-	1	r	-	-	r
<i>Rollinia sylvatica</i> (A. St.-Hil.) Mart.	4	2	r	-	2	r
<i>Xylopia brasiliensis</i> Spreng.	1	1	r	-	-	r
APOCYNACEAE						
<i>Malouetia cestroides</i> (Nees ex Mart.) Müll. Arg.	1	-	r	-	-	r
<i>Tabernaemontana catharinensis</i> A. DC.	-	1	r	-	-	r
AQUIFOLIACEAE						
<i>Ilex dumosa</i> Reissek	4	3	r	1	-	r
<i>Ilex integerrima</i> Reissek	6	21	gle	5	12	gen
<i>Ilex</i> sp	-	-	r	-	1	r
ARALIACEAE						
<i>Dendropanax australis</i> Fiaschi & Jung-Mend.	-	-	r	-	6	r
<i>Schefflera angustissima</i> (Marchal) Frodin	-	1	r	-	-	r
<i>Schefflera</i> sp	1	-	r	-	-	r
ARECACEAE						
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	8	-	r	-	-	r
<i>Attalea dubia</i> (Mart.) Burret	2	-	r	3	1	r
<i>Bactris setosa</i> Mart.	-	2	r	3	6	r
<i>Euterpe edulis</i> Mart.	40	32	gen	5	16	gle
<i>Geonoma schottiana</i> Mart.	1	-	r	1	-	r
<i>Geonoma</i> sp	-	-	r	17	-	cam
<i>Syagrus romanzoffiana</i> Cham.	1	12	gle	-	-	r
ASTERACEAE						
Asteraceae sp1	-	-	r	2	-	r

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Eupatorium</i> sp1	1	-	r	1	3	r
<i>Eupatorium</i> sp2	-	1	r	-	-	r
<i>Vernonanthura beyrichii</i> (Less.) H.Rob.	-	-	r	11	18	gen
<i>Vernonanthura puberula</i> (Less.) H. Rob.	1	2	r	1	-	r
<i>Vernonia</i> sp1	-	2	r	-	3	r
APOCYNACEAE						
<i>Cybistax antisiphilitica</i> (Mart.) Mart.	-	3	r	-	1	r
<i>Jacaranda puberula</i> Cham.	8	59	gle	9	30	gle
<i>Tabebuia serratifolia</i> (Vahl) G. Nicholson	2	2	r	-	-	r
<i>Tabebuia umbellata</i> (Sond.) Sandwich	-	-	r	-	1	r
BORAGINACEAE						
<i>Cordia sellowiana</i> Cham.	-	2	r	-	2	r
<i>Cordia silvestris</i> Fresen.	3	2	r	-	-	r
BURSERACEAE						
<i>Protium kleinii</i> Cuatr.	4	1	r	-	-	r
CANELACEAE						
<i>Cinnamodendron dinisii</i> Schwacke	1	-	r	-	-	r
CANNABACEAE						
<i>Trema micrantha</i> (L.) Blume	1	-	r	-	-	r
CELASTRACEAE						
<i>Maytenus alaternoides</i> Reissek	-	-	r	1	-	cam
<i>Maytenus schumanniana</i> Loes.	4	-	r	10	1	r
CHYSOBALANACEAE						
<i>Hirtella hebeclada</i> Moric. ex A.P. DC.	6	-	r	1	-	r
CLETHRACEAE						
<i>Clethra scabra</i> Pers.	-	6	r	-	3	r
CLUSIACEAE						
<i>Calophyllum brasiliense</i> Cambess.	-	-	r	-	2	r
<i>Clusia criouva</i> Cambess.	1	-	r	-	-	r
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	10	-	cam	8	-	cam
COMBRETACEAE						
<i>Buchenavia kleinii</i> Exell	-	-	r	1	-	r
CYATHEACEAE						
<i>Cyathea atrovirens</i> (Langsd. & Fisch.) Domin	4	1	r	-	-	r
<i>Cyathea corcovadensis</i> (Raddi) Domin	3	-	r	-	-	r
<i>Cyathea</i> sp1	3	7	gen	-	-	r
<i>Cyathea</i> sp2	2	1	r	-	-	r

	CAM	GLE	cat.	CAM	GLE	cat.
ELAEOCARPACEAE						
<i>Sloanea guianensis</i> (Aubl.) Benth.	32	30	gen	5	7	gen
ERYTHROXYLACEAE						
<i>Erythroxylum</i> sp1	-	-	r	1	1	r
<i>Erythroxylum</i> sp2	-	-	r	1	-	r
EUPHORBIACEAE						
<i>Actinostemon concolor</i> (Spreng.) Müll.Arg.	3	-	r	4	-	r
<i>Alchornea glandulosa</i> Poepp.	42	6	cam	8	3	gen
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	17	5	cam	2	-	r
<i>Maprounea brasiliensis</i> A. St.-Hil.	1	-	r	-	-	r
<i>Pachystroma longifolium</i> I.M. Johnst.	4	-	r	1	-	r
<i>Pausandra morisiana</i> (Casar.) Radlk.	8	-	r	2	-	r
<i>Pera glabrata</i> (Schott) Baill.	51	141	gle	10	9	gen
<i>Sapium glandulatum</i> (Vell.) Pax	15	7	gen	1	2	r
<i>Tetrorchidium rubrivenium</i> Poepp. & Endl.	4	7	gen	-	-	r
FABACEAE						
<i>Andira anthelmia</i> (Vell.) J.F.Macbr.	10	50	gle	3	3	r
<i>Bauhinia forficata</i> Link.	-	3	r	-	-	r
<i>Copaifera trapezifolia</i> Hayne	-	-	r	1	-	r
<i>Dahlstedtia pentaphylla</i> (Taub.) Burkart	1	-	r	-	-	r
<i>Dalbergia brasiliensis</i> Vogel	-	1	r	-	-	r
<i>Dalbergia frutescens</i> (Vell.) Britton	-	-	r	1	-	r
<i>Inga edulis</i> Mart.	4	34	gle	1	8	gle
<i>Inga marginata</i> Willd.	-	1	r	-	-	r
<i>Inga sellowiana</i> Benth.	1	-	r	-	-	r
<i>Inga sessilis</i> DC.	3	1	r	3	1	r
<i>Inga striata</i> Benth.	1	-	r	-	-	r
<i>Luetzelburgia guaissara</i> Toledo	1	-	r	-	-	r
<i>Machaerium hatschbachii</i> Rudd	2	1	r	-	-	r
<i>Machaerium nyctitans</i> (Vell.) Benth.	2	-	r	-	-	r
<i>Mimosa bimucronata</i> (DC.) Kuntze	9	1	cam	3	-	r
<i>Myrocarpus frondosus</i> Allemafio	1	-	r	-	-	r
<i>Piptadenia paniculata</i> Benth.	2	-	r	-	-	r
<i>Platymiscium floribundum</i> Vogel	-	2	r	-	-	r
<i>Pseudopiptadenia warmingii</i> Benth.	4	-	r	-	-	r
<i>Pterocarpus violaceus</i> Vogel	2	2	r	1	1	r
<i>Schizolobium parahyba</i> (Vell.) S.F.Blake	3	2	r	-	-	r

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Senna multijuga</i> (L.C.Richard)H.S. Irwin & Barneby	7	19	gle	-	1	r
<i>Senna</i> sp	1	-	r	-	-	r
<i>Senna sylvestris</i> (Vell.) H.S.Irwin & Barneby	-	1	r	-	-	r
<i>Zollernia latifolia</i> Smith	-	-	r	-	1	r
SALICACEAE						
<i>Casearia decandra</i> Jacq.	11	2	cam	1	-	r
<i>Casearia obliqua</i> Spreng.	119	12	cam	11	-	cam
<i>Casearia sylvestris</i> Sw.	63	10	cam	7	-	r
LAMIACEAE						
<i>Aegiphila sellowiana</i> Cham.	1	-	r	-	-	r
<i>Vitex polygama</i> Cham.	1	-	r	-	-	r
LAURACEAE						
<i>Aniba firmula</i> (Nees) Mez	-	-	r	-	1	r
<i>Cryptocarya mandioccana</i> Meisn.	4	-	r	1	-	r
<i>Endlicheria paniculata</i> (Spreng.) Macbr.	3	-	r	3	2	r
<i>Nectandra leucantha</i> Nees	4	3	r	-	1	r
<i>Nectandra megapotamica</i> (Spreng.) Mez	2	-	r	-	-	r
<i>Nectandra membranacea</i> Griseb.	19	6	cam	3	3	r
<i>Nectandra oppositifolia</i> Nees	9	11	gen	1	5	r
<i>Ocotea</i> sp	1	-	r	-	-	r
MYRISTICACEAE						
<i>Virola bicuhyba</i> (Schott ex Spreng.) Warb.	18	2	cam	3	1	r
<i>Ocotea catharinensis</i> Mez	5	-	r	-	-	r
<i>Ocotea dispersa</i> (Nees & Mart.) Mez	-	1	r	-	1	r
<i>Ocotea nunesiana</i> (Vattimo-Gil) Baitello	2	-	r	-	-	r
<i>Ocotea odorifera</i> (Vell.) Howher	-	3	r	-	1	r
<i>Ocotea puberula</i> Nees	1	-	r	-	-	r
<i>Ocotea pulchella</i> (Nees & Mart.) Mez	3	1	r	-	1	r
<i>Ocotea teleiandra</i> (Meisn.) Mez	3	16	gle	2	6	r
LECYTHIDACEAE						
<i>Cariniana estrellensis</i> (Raddi) Kuntze	8	3	gen	1	1	r
LEGUMINOSAE						
<i>Albizia edwallii</i> (Hoehne) Barneby & J.W.Grimes	-	1	r	-	-	r
<i>Erythrina speciosa</i> Andrews	1	-	r	-	3	r
MAGNOLIACEAE						
<i>Magnolia ovata</i> P.Parm.	3	-	r	-	-	r
MALPIGHIACEAE						

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Bunchosia pallescens</i> Skottsbo.	-	-	r	-	1	r
MALVACEAE						
Malvaceae sp1	-	-	r	1	-	r
Malvaceae sp2	-	-	r	-	2	r
<i>Pseudobombax grandiflorum</i> (Cav.) A.Robyns	4	-	r	-	-	r
<i>Triumfetta semitriloba</i> Jacq.	-	-	r	4	1	r
MELASTOMATACEAE						
<i>Clidemia biserrata</i> DC.	-	-	r	14	-	cam
<i>Clidemia hirta</i> (L.) D. Don	-	-	r	3	-	r
<i>Clidemia urceolata</i> DC.	-	-	r	1	11	gle
<i>Leandra melastomoides</i> Raddi	-	-	r	2	8	r
<i>Miconia cabucu</i> Hoehne	12	11	gen	2	-	r
<i>Miconia cinerascens</i> Miq.	39	35	gen	18	40	gle
<i>Miconia cinnamomifolia</i> (DC.) Naud.	14	-	cam	-	-	r
<i>Miconia cubatanensis</i> Hoehne	-	-	r	-	1	r
<i>Miconia latecrenata</i> (DC.) Naudin	-	-	r	4	3	r
<i>Miconia tristis</i> Spring	-	-	r	2	1	r
<i>Ossaea amygdaloides</i> Triana	-	-	r	2	2	r
<i>Tibouchina pulchra</i> (Cham.) Cogn.	100	177	gle	5	3	r
<i>Tibouchina trichopoda</i> Baill.	60	107	gle	56	88	gle
MELIACEAE						
<i>Cabralea canjerana</i> (Vell.) Mart.	6	4	gen	4	-	r
<i>Cedrela fissilis</i> Vell.	9	-	cam	-	-	r
<i>Guarea macrophylla</i> Vahl	6	8	gen	8	10	gen
<i>Trichilia lepidota</i> Mart.	12	-	cam	2	-	r
<i>Trichilia pallens</i> C.DC.	3	-	r	1	-	r
MONIMIACEAE						
<i>Mollinedia schottiana</i> Perkins	30	4	cam	24	10	cam
<i>Mollinedia uleana</i> Perkins	-	1	r	-	1	r
MORACEAE						
<i>Brosimum lactescens</i> (S. Moore) C.C. Berg	9	-	cam	1	-	r
<i>Ficus adhatodifolia</i> Schott ex Spreng.	1	-	r	-	-	r
<i>Ficus insipida</i> Willd.	2	-	r	-	-	r
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanj. & Boer	2	-	r	2	-	r
MYRTACEAE						
<i>Calycorectes australis</i> D.Legrand	2	1	r	-	1	r
<i>Calypttranthes grandifolia</i> O.Berg	32	18	gen	7	14	gen

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Calyptranthes lucida</i> Mart.ex DC.	5	1	r	4	-	r
<i>Calyptranthes strigipes</i> O.Berg	29	-	cam	8	-	cam
<i>Campomanesia neriifolia</i> (O.Berg) Nied.	1	3	r	-	-	r
<i>Campomanesia</i> sp	6	1	r	2	-	r
<i>Eugenia beaurepairiana</i> (Kiaersk.) D.Legrand	2	-	r	-	-	r
<i>Eugenia brevistyla</i> D.Legrand	4	-	r	-	-	r
<i>Eugenia brunneopubescens</i> Mazine	-	-	r	-	1	r
<i>Eugenia burkartiana</i> (D.Legrand) D.Legrand	18	-	cam	4	1	r
<i>Eugenia candolleana</i> DC.	2	-	r	-	-	r
<i>Eugenia cerasiflora</i> Miq.	3	-	r	-	-	r
<i>Eugenia cereja</i> D.Legrand	1	-	r	2	-	r
<i>Eugenia magnibracteolata</i> Mattos & D. Legrand	-	-	r	1	-	r
<i>Eugenia melanogyna</i> D.Legrand) Sobral	-	-	r	1	-	r
<i>Eugenia mosenii</i> (Kausel) Sobral	2	-	r	-	-	r
<i>Eugenia multicostata</i> D.Legrand	4	-	r	-	-	r
<i>Eugenia neoglomerata</i> Sobral	-	-	r	1	-	r
<i>Eugenia obovata</i> O.Berg	-	-	r	3	-	r
<i>Eugenia platysema</i> O.Berg	-	1	r	-	3	r
<i>Eugenia</i> sp1	12	-	r	-	-	r
<i>Eugenia stigmata</i> DC.	5	-	r	1	4	r
<i>Eugenia subavenia</i> O.Berg	1	-	r	-	-	r
<i>Eugenia uniflora</i> L.	1	-	r	-	-	r
<i>Eugenia verticillata</i> (Vell.) Angely	2	2	r	-	-	r
<i>Gomidesia flagellaris</i> D.Legrand	5	-	r	12	-	cam
<i>Gomidesia schaueriana</i> O.Berg	3	-	r	-	-	r
<i>Gomidesia</i> sp1	-	-	r	-	3	r
<i>Gomidesia spectabilis</i> (DC.) O.Berg	14	12	gen	8	1	cam
Myrtaceae sp1	1	-	r	6	1	r
Myrtaceae sp2	-	7	gle	-	-	r
Myrtaceae sp3	-	4	r	-	-	r
Myrtaceae sp4	-	1	r	-	-	r
Myrtaceae sp5	-	3	r	-	-	r
<i>Marlierea obscura</i> O.Berg	19	15	gen	5	28	gle
<i>Marlierea sylvatica</i> (O.Berg) Kiaersk.	5	5	gen	-	2	r
<i>Marlierea tomentosa</i> Cambess.	13	17	gen	6	9	gen
<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg	-	-	r	-	1	r
<i>Myrcia bicarinata</i> (O.Berg) D.Legrand	2	-	r	-	-	r

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Myrcia glabra</i> (O.Berg) D.Legrand	-	-	r	-	7	r
<i>Myrcia multiflora</i> (Lam.) DC.	-	-	r	1	2	r
<i>Myrcia pubipetala</i> Miq.	17	21	gen	2	10	gle
<i>Myrcia racemosa</i> (O.Berg) Kiaersk.	-	2	r	-	9	gle
<i>Myrcia richardiana</i> (O.Berg) Kiaersk.	-	-	r	1	-	r
<i>Myrcia splendens</i> (Sw.) DC.	3	3	r	2	7	r
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	2	-	r	2	-	r
<i>Neomitranthes glomerata</i> (D. Legrand) D. Legrand	2	-	r	-	-	r
<i>Plinia edulis</i> (Vell.) Sobral	1	-	r	-	-	r
<i>Plinia trunciflora</i> (O.Berg) Kausel	1	-	r	-	-	r
<i>Psidium cattleianum</i> Sabine	1	5	r	1	6	r
<i>Psidium guajava</i> L.	15	18	gen	1	4	r
<i>Syzygium jambos</i> (L.) Alston	-	-	r	-	1	r
NYCTAGINACEAE						
<i>Guapira asperula</i> (Standl.) Lundell	-	-	r	-	3	r
<i>Guapira opposita</i> (Vell.) Reitz	21	2	cam	12	13	gen
<i>Pisonia ambigua</i> Heimerl	1	-	r	-	-	r
OCHNACEAE						
<i>Ouratea parviflora</i> (DC.) Baill.	5	1	r	22	9	cam
<i>Heisteria silvianii</i> Schwacke	6	-	r	3	-	r
<i>Tetrastylidium grandifolium</i> (Baill.) Sleum.	6	1	r	6	1	r
<i>Hieronyma alchorneoides</i> Allemaffio	57	25	gen	2	5	r
<i>Margaritaria nobilis</i> L.f.	-	1	r	-	-	r
<i>Gallesia integrifolia</i> (Spreng.) Harms	1	-	r	-	-	r
<i>Phytolacca dioica</i> L.	1	-	r	-	-	r
PIPERACEAE						
<i>Piper arboreum</i> Aubl.	-	-	r	10	-	cam
<i>Piper cernuum</i> Vell.	-	-	r	4	-	r
<i>Piper dilatatum</i> Rich.	-	-	r	6	2	r
<i>Piper gaudichanianum</i> Kunth	-	-	r	6	15	gen
<i>Piper</i> sp1	-	-	r	-	2	r
<i>Piper</i> sp2	1	-	r	-	-	r
<i>Piper</i> sp3	-	-	r	-	1	r
<i>Coccoloba warmingii</i> Meisn.	1	-	r	-	-	r
PRIMULACEAE						
<i>Myrsine coriacea</i> R. Br.	157	99	gen	14	24	r

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Myrsine gardneriana</i> A. DC.	3	1	r	-	2	r
<i>Rapanea hermogenesii</i> Jung-Mend. & L.C. Bernacci	-	-	r	1	-	r
PROTEACEAE						
<i>Roupala brasiliensis</i> Klotzsch	1	-	r	-	-	r
OCHNACEAE						
<i>Quiina glaziovii</i> Engl.	12	1	cam	1	-	r
RUBIACEAE						
<i>Amaioua guianensis</i> Aubl.	5	6	r	2	-	r
<i>Bathysa australis</i> (A. St.-Hil.) K. Schum.	20	-	cam	6	-	r
<i>Chomelia brasiliensis</i> A. Rich.	-	-	r	2	-	r
<i>Cordia concolor</i> (Cham.) Kuntze	6	-	r	-	-	r
<i>Coussarea contracta</i> Benth. & Hook f.	1	-	r	-	-	r
<i>Posoqueria latifolia</i> Roem. & Schult.	4	-	r	-	-	r
<i>Psychotria brachypoda</i> (Müll. Arg.) Britton	-	-	r	-	1	r
<i>Psychotria carthagenensis</i> Jacq.	-	-	r	5	-	r
<i>Psychotria dusenii</i> Standl	2	-	r	1	-	r
<i>Psychotria cf. hastisepala</i> Müll. Arg.	-	-	r	-	3	r
<i>Psychotria leiocarpa</i> Cham. & Schltldl.	-	-	r	1	2	r
<i>Psychotria mapourioides</i> DC.	22	-	cam	2	-	r
<i>Psychotria nuda</i> (Cham. & Schltldl.) Wawra	77	3	cam	51	26	cam
<i>Psychotria pubigera</i> Schltldl.	-	1	r	3	19	gle
<i>Psychotria stenocalix</i> Müll. Arg.	7	-	r	10	4	gen
<i>Psychotria suterella</i> Müll. Arg.	12	3	gen	18	2	cam
<i>Psychotria vellosiana</i> Benth.	-	-	r	-	2	r
Rubiaceae sp1	-	-	r	-	1	r
Rubiaceae sp2	-	-	r	1	4	r
Rubiaceae sp3	-	-	r	-	10	gle
Rubiaceae sp4	2	-	r	-	3	r
<i>Rudgea jasminioides</i> (Cham.) Müll. Arg.	14	-	cam	27	-	cam
<i>Rudgea recurva</i> Müll. Arg.	1	-	r	4	6	gen
RUTACEAE						
<i>Zanthoxylum rhoifolium</i> Lam.	2	1	r	-	-	r
SABIACEAE						
<i>Meliosma sellowii</i> Urb.	4	-	r	1	-	r
SAPINDACEAE						
<i>Allophylus edulis</i> Radlk. ex Warm.	-	-	r	2	1	r
<i>Allophylus petiolatus</i> Radlk. ex Wihl. Muller.	1	-	r	4	5	r

	CAM	GLE	cat.	CAM	GLE	cat.
<i>Cupania oblongifolia</i> Mart.	24	4	cam	7	-	r
<i>Matayba guianensis</i> Aubl.	10	10	gen	12	1	cam
<i>Matayba juglandifolia</i> Radlk.	6	-	r	1	2	r
SAPOTACEAE						
<i>Chrysophyllum inornatum</i> Mart.	4	4	r	7	-	r
<i>Manilkara subsericea</i> (Mart.) Dubard	1	-	r	-	-	r
<i>Pouteria venosa</i> (Mart.) Baehni	2	-	r	1	-	r
SOLANACEAE						
<i>Acnistus arborescens</i> (L.) Schldl.	3	-	r	-	-	r
<i>Cestrum amictum</i> Schldl.	1	-	r	-	1	r
<i>Solanum rufescens</i> Sendtn.	-	-	r	4	-	r
SYMPLOCACEAE						
<i>Symplocos celastrinea</i> Mart. ex Miq.	1	-	r	-	-	r
<i>Symplocos laxiflora</i> Benth.	6	1	r	2	6	r
THEACEAE						
<i>Gordonia fruticosa</i> (Schrad.) H.Keng	-	14	gle	-	4	r
THYMELAEACEAE						
<i>Daphnopsis fasciculata</i> (Meisn.) Nevlng	-	-	r	-	1	r
URTICACEAE						
<i>Cecropia glaziovii</i> Snethl.	8	2	gen	-	-	r
<i>Cecropia pachystachya</i> TreĬcul	3	5	r	-	-	r
<i>Coussapoa microcarpa</i> (Schott) Rizzini	3	3	r	1	-	r
<i>Pourouma guianensis</i> Aubl.	3	1	r	-	-	r
<i>Urera nitida</i> (Vell.) P.Brack	-	-	r	-	2	r
VERBENACEAE						
<i>Citharexylum myrianthum</i> Cham.	3	4	r	-	-	r
<i>Stachytarpheta maximiliani</i> Schauer	-	-	r	2	-	r
<i>Verbena lobata</i> Vell.	-	-	r	-	3	r
VOCHYSIACEAE						
<i>Vochysia bifalcata</i> Warm.	12	30	gle	4	19	gle
UNDETERMINED						
Undetermined 1	1	-	r	1	-	r
Undetermined 2	1	-	r	1	-	r
Undetermined 3	-	-	r	1	-	r
Undetermined 4	1	-	r	-	-	r
Undetermined 5	-	-	r	-	1	r
Undetermined 6	-	-	r	4	-	r

	CAM	GLE	cat.		CAM	GLE	cat.
Undetermined 7	3	-	r		-	-	r
Undetermined 8	-	1	r		-	-	r
Undetermined 9	1	-	r		-	-	r
Undetermined 10	-	-	r		1	-	r
Undetermined 11	-	-	r		-	1	r
Undetermined 12	-	1	r		-	-	r
Undetermined 13	1	-	r		-	-	r
Undetermined 14	-	-	r		-	1	r
Undetermined 15	1	-	r		-	-	r
Undetermined 16	1	-	r		-	-	r

PADRÕES FUNCIONAIS DAS COMUNIDADES VEGETAIS EM
DOIS TIPOS DE SOLO AO LONGO DA TRAJETÓRIA
SUCESSIONAL DE UMA FLORESTA TROPICAL

Plant functional patterns of plant communities in two different soil types along tropical forest succession

Abstract

Each species within a community has its own set of functional traits that will influence the way each of them respond to the environmental conditions. The abiotic factors, such as soil conditions, may play an important role in structuring communities and might direct them to functional convergence, due to the environmental filters. On the other hand, interspecific interactions, such as competition, may also explain community assembly, directing communities to functional divergence of traits. In this study we aimed to test if tropical forests undergoing the successional process are structured differently in two contrasting soil types. We considered a chronosequence of secondary forests, varying from 2 to 80 years in two soil types in southern Brazil: Gleysol (seasonally flooded soil) and Cambisol (well drained soil). In this age-soil gradient we established a total of 45 circular plots (2.8ha total) where canopy (trees with $DBH \geq 5$ cm) and understory (shrubs and saplings with $DBH < 5$ and height ≥ 1.3 m) were sampled. A dataset of plant functional traits was assembled by collecting them from literature and herbarium samples. We used a method of multiplication of matrices to analyze functional patterns of convergence and divergence in the community. We also calculated diversity indices (taxonomic and functional) and community-weighted means of each trait to evaluate how they change with time and soil type. We sampled a total of 4389 individuals (3032 in the canopy and 1357 in the understory) distributed in 215 plant species in the canopy and 181 species in the understory. We found both convergence and divergence patterns acting in the community assembly in our age-soil gradient, maximized by different sets of traits. The frequency of selected traits in the canopy (pollination by vertebrates, shade-tolerance and leaf compoundness) and in the understory (leaf slenderness and shade tolerance) increased in the successional gradient and was markedly more intense in areas of Gleysol. The frequency of other traits (leaf area, leaf margin, pollination by bees, maximum DBH and maximum height) was either affected only by forest age or did not significantly change in the age-soil gradient. All metrics of taxonomic and functional diversity increased with age in both strata. In the canopy, Shannon diversity, functional richness and Rao quadratic entropy also varied with soil type. In the understory, all variables, except for Rao quadratic entropy had influence of soil type. We conclude that both abiotic filters and biotic

interactions structure communities developing in the age-soil gradient. In addition, contrasting limitations imposed by soil characteristics lead communities to differences in functional patterns along succession, affecting ecosystem processes.

Key words: assembly patterns, succession, soil gradient, Atlantic Forest, forest regeneration

Introduction

One of the most important challenges in plant ecology is to understand what processes determine the distribution of species in tropical forests (Wright 2002). Each species within a community has its own particular set of traits that will influence the way each of them respond to the environmental conditions (Reich *et al.* 2003, Violle *et al.* 2007). The diversity of states of each functional trait present in a community will determine its functional diversity, an important feature of biological assemblages that enables prediction of the rate and reliability of ecosystem processes and that indicates ecosystem resource dynamics, stability and production (Mason *et al.* 2005, Tilman 2000, Díaz & Cabido 2001). The variation of functional traits, which allow the coexistence of plant species, may be explained by niche or neutral processes (McGill *et al.* 2006; Kraft *et al.* 2008; Hubbell 2001). The first considers that species have particular characteristics that determine their capacity to use certain resources (Hutchinson 1957) while the latter considers that all species have the same capacity of using resources, so that the occurrence of species in an area depends on stochastic processes (Hubbell 2001).

Plant traits evolve in response to environmental conditions and interactions with other species (Reich *et al.* 2003). Environmental filters may select species that will occur in a given place due to limiting conditions such as luminosity, temperature and humidity (Keddy 1992). Hence, only species that have attributes that give them ability

to withstand such conditions will be able to survive in a particular location (Cavender-Bares *et al.* 2009). These adaptations to the conditions of the environment should lead to a convergence of certain functional traits within the community. On the other hand, species that use a resource in a similar manner should not co-exist very often, since the one that is competitively superior will exclude the other when resources are limited in the environment (Weiher *et al.* 1998, Grime 2006). Thus, competition implies a limitation of similarity in the use of resources by co-occurring species (MacArthur & Levins 1967). As a result, a divergence in functional traits among species in a community is expected in environments with limiting resources.

Given the importance of community composition to ecosystem function, it is essential to understand how the ecological rules that govern species composition vary along forest succession. Patterns of trait convergence and divergence along environmental gradients may vary according to successional stage and perturbations (Ding *et al.* 2011; Helsen *et al.* 2012), since changes in forest structure and composition imply changes also on functional diversity and ecosystem functioning (Lohbeck *et al.* 2011). Young forest areas are known to be less structurally complex and to contain a lower proportion of animal dispersed, non-pioneer and understory species (Liebsch *et al.* 2008). Consequently, it also may contain different reproductive and vegetative trait states than mature forests, possibly altering functional diversity. Functional traits of seedlings, saplings and trees can be strong determinants of demographic rates during forest regeneration (Chazdon 2014).

Not only successional age may shift plant functional trait distribution in tropical forests. Plants communities establishing in contrasting edaphic conditions show differences in diversity, individual density and species composition (Chapter 2),

probably resulted from distinct soil water and nutrient availability among contrasting soil types. Thus, if soil does affect forest structure and species composition, it potentially changes the distribution of functional traits and thus, functional diversity. Disentangling the role of processes that lead to trait convergence and divergence in these emergent environments is fundamental to the understanding of how plant communities are structured.

In this work we compared forest chronosequences (second growth forests varying from 2 to 80 years after disturbance) occurring in two contrasting soil characteristics (Gleysol, seasonally flooded soil, and Cambisol, well drained soil), in areas of Atlantic Forest, southern Brazil. We aimed to test if tropical forests undergoing succession process are structured differently in two contrasting soil types. We asked if (1) there is trait convergence (related to environmental filters) or trait divergence (related to competition) along the age and soil gradient; (2) there are differences in taxonomic and functional diversities between soil types; (3) there are differences in changes of specific functional traits during the succession in the two soil types.

Methods

Study site

This study was carried out in the Atlantic Forest of Paraná state, southern coast of Brazil, in the municipality of Antonina (25°19'15"S and 48°42'24"W). The study areas are within the Guaraqueçaba Environmental Protection Area, a large region (more than 300,000 ha) that includes forests, estuaries, bays, islands, mangroves and lowlands, and is part of one of the most important remaining areas of Atlantic Forest in Brazil (Ferretti & Britez 2006a). We collected data in two reserves within these areas, *Rio*

Cachoeira Nature Reserve and *Morro da Mina Nature Reserve*, both are property of the non-governmental organization *Society of Research in Wildlife and Environmental Education* (SPVS) and together, they comprise nearly 10,000 ha.

The climate in the region is humid subtropical (Cfa), according to Köppen's classification (Ferretti & Britez 2006a), with annual precipitation of 3106 mm and mean temperature of 21.2°C over the last 25 years (Cardoso *et al.* 2012). Altitude varies from sea level to 900m a.s.l. Four soil types occur in the reserve: Acrisols, Fluvisols, Gleysols, and Cambisols (Ferretti & Britez 2006b), being the last two predominant in the area and the ones where the plots of this study are located. Gleysols are hydromorphic, mineral, sandy, with variable fertility and are periodically saturated with water. Cambisols comprise non-hydromorphic, mineral soils, with variable fertility and incipient B horizon, frequently found in slopes (Embrapa 2006).

The Atlantic Forest in the region is characterized by different typologies, including Submontane, Lowland, and Alluvial Forests. Regarding the landscape, 68% is comprised of forest remnants and 9% of secondary forest areas that are mingled with buffalo grazing and agricultural areas (Kauano *et al.* 2012). With the increasing establishment of conservation areas in the region, some of these intensive use sites were abandoned and are now in a process of restoration (natural regeneration or planted forest) (Ferretti & Britez 2006a), resulting in areas with vegetation in different successional stages.

Most areas suffered some degree of interference in the past, including clear-cutting and later use for agriculture (mainly plantations of manioc, sugar cane, banana and corn), pasture for buffalo farming, or selective logging of native commercial species, for example the native palm *Euterpe edulis* (Ferretti&Britez 2006b, Bruelet *al.* 2010, Borgo

et al. 2011). Old growth forests present in the region are an important source of seeds (Leitão *et al.* 2010) and shelter for animals (Zwiener *et al.* 2012).

Soil analysis

Soil characterization was carried out by sampling 17 random plots (Cambisol: 10; Gleysol: 7) for soil physical and chemical analysis. Samples were collected at a depth of 0–10 cm, at four equidistant points at 4m from the center of the plot and also one point in the center. Soil samples collected at the five points were then pooled in a container in order to make one single sample per plot. Samples were then taken to the laboratory, air-dried and sifted (2mm). Standard chemical analyses were performed for pH (CaCl₂), P, Al³⁺, Ca²⁺, Mg²⁺, K⁺ (Mehlich) and C (Embrapa 1997). Physical analysis (soil texture) for the determination of clay, silt and sand content were performed using the densitometer method (Embrapa 1997).

Survey and analysis of vegetation

The study is based on a comparative analysis of the successional trajectory in two soil types (Cambisol and Gleysol) in lowland and mountain slope areas (Atlantic Forest of Submontane and Lowland sub-formations). We established a total of 45 plots in forests in different successional stages, defined by the age after pasture abandonment: 2-6; 7-12; 15-25; 30-50 and > 80 years-old. Five plots were selected in each of these age groups, except for the last age (>80y), where only Cambisol plots could be found, due to the higher deforestation of the lowlands, where Gleysols are more frequent. All these areas were previously used for pasture and abandoned and were under natural regeneration, except area >80 years that passed for some selective logging in the past.

Plots were circular (radius of 14m; area of 615.7m² each), resulting in a total sampled area of 2.77ha. They were randomly distributed in the reserves. In each plot (14m in radius), we sampled all trees with diameter at breast height (DBH) \geq 5cm, to characterize the canopy. In a smaller concentric sub-plot (4m in radius, 50.3 m²), we measured all individuals (saplings and shrubs, which were referred hereafter as “understory”) with DBH $<$ 5.0cm and height \geq 1.30m. For all sampled individuals we determined the species and measured the DBH (or stem base diameter, for shrubs) and total height. Individuals that we were not able to identify on site were collected and identified in the laboratory using reference collections and consulting specialists.

Trait collection

We selected nine reproductive and vegetative traits related to plant competitive ability, reproductive success and photosynthesis, as suggested by Cornelissen *et al.* (2003), Weiher *et al.* (1999), Pérez-Harguindeguy *et al.* (2013) and Rosado *et al.* (2013) (Table 1). All the identified species in each plot, in the canopy and in the understory, had their traits collected from the field, herbarium material or references. Height and DBH were measured in the field for all individuals and the maximum height and maximum DBH for each species among all sampled individuals were used to characterize each species. Leaf traits were gathered from the literature (Reitz 1975; Carvalho 2003, 2006, 2008; Borgo *et al.* 2011) or collected from herbarium material. We used the formula of an ellipse to calculate leaf area; and ratio between length and width to calculate leaf slenderness. Pollination, dispersal modes and shade tolerance were gathered in the literature (Reitz 1975, Carvalho 2003, 2006, 2008; Borgo *et al.* 2011).

Table 1. Functional traits sampled and their functions that can possibly cause effects on the community, in the Atlantic Rainforest, southern Brazil. *traits transformed to dummy variables

Trait	State	Function
<i>Vegetative traits</i>		
Leaf area (cm ²)	-	thermal balance, light interception
Leaf slenderness	-	thermal balance, light interception
Leaf margin	entire (1) non-entire (0)	herbivore defense, light interception
Leaf compoundness	simple (1) compound (0)	leaf cooling, light interception
Maximum height (m)	-	competition for light
Maximum DBH (cm)	-	competitive ability, carbon storage
Shade tolerance	tolerant (1) intolerant (0)	competitive ability
<i>Reproductive traits</i>		
Pollination mode	bees* other insects* vertebrates* abiotic*	reproduction
Seed dispersal mode	animal abiotic	reproduction, dispersal distance

For the analysis, categorical attributes were expanded to dummy variables, that is, presence or absence of a certain characteristic (Legendre & Legendre 1998) (Table 1). For 27 species (15% of total) we did not complete the trait list, either because they are rare species and no information was found in literature or because they could not be

identified to species level. These species were not considered in the following functional analysis.

Data analysis

Analyses for differences in physical and chemical characteristics of two soil types were performed with *t*-test (C, pH, Al, K, clay) or Wilcoxon test (Ca, Mg, P, sand, silt). Wilcoxon test was used for the variables that were not distributed normally by the Shapiro-Wilk test (Zar 1999).

The analysis of functional patterns of the community, convergence and divergence of attributes was performed with the methodology described in Pillar *et al.* (2009). The method consists of analyses of multiplications and correlations between three different matrices (**W**, **B** and **E**), thus, scaling up the information of the traits in species level to the community level (Table S1). The first matrix (**W**) is composed by species abundances in each plot, where species are represented by lines and plots by columns. The second matrix (**B**) holds the traits and consists of species in the lines and mean trait values by species in the columns. The third matrix (**E**) is the environmental matrix and in this study, included plots in the lines and two environmental variables (forest age and soil type) in the columns. Convergence patterns are obtained by multiplying the matrix **B'** (**B**transposed) and **W**, resulting in the matrix **T** ($T = B'W$). The elements of **T** are the weighted mean values of the community, and allow the identification of convergence patterns (TCAP, trait-convergence assembly patterns). To obtain patterns of divergence, the **B** matrix is used to obtain species similarity based on the characterization of the species by traits in a 0 to 1 interval, resulting in a similarity matrix (matrix **U**), calculated with Gower distance (Legendre & Legendre 1998).

Matrix U' (U transposed) and W are then multiplied, resulting in matrix X ($X = U'W$), which represents the performance of species, weighted (fuzzy) by the traits in the studied communities. Subsequently, relationship of the matrices T and X is evaluated in relation to the environmental variables (matrix E). This evaluates in what extent the patterns observed in the matrices T and X are related to environmental variations considered in this study. For this, community distance matrices are calculated from T (D_T), X (D_X) and E (D_E) and matrix correlations (ρ) can then be estimated among the datasets [$\rho(T, E) = \rho(D_T; D_E)$, $\rho(X, E) = \rho(D_X; D_E)$], revealing the level of congruence between the variations between them. Thus, $\rho(T, E)$ measures the trait convergence assembly pattern (TCAP) along the ecological gradient. On the other hand, high values of $\rho(X, E)$ may indicate that both TCAP and trait divergence (TDAP, trait-divergence assembly patterns) (one or both of them) are related to the environmental gradient. Hence, it is necessary to remove the convergence component (TCAP) from the $\rho(X, E)$, resulting in $\rho(X, E.T)$, which finally represents the effect of TDAP on the $\rho(X, E)$, or its relationship along the environmental gradient. The method allows the selection of a subset of optimal attributes that maximize convergence (TCAP) and /or divergence (TDAP) along the studied gradient. The significance of the correlations is tested by permutation compared to a null model with 999 repetitions (Pillar *et al.* 2009).

We calculated two taxonomic measures (species richness and Shannon's diversity index, H') and five functional measures (Rao entropy and functional richness, redundancy, evenness and divergence) for each plot. The use of multiple functional diversity measures prevent loss of some ecological information of individual measures (Mouillot *et al.* 2005, Villéger *et al.* 2008). Rao quadratic entropy (Rao 1982) combines species relative abundance and functional differences between pairs of species (Zoltán

2005). Functional richness is independent of abundance and characterizes the volume of the functional space occupied by the community (Mason *et al.* 2005). Low functional richness indicates that some of the resources potentially available to the community are unused. Functional evenness is the regularity of the distribution of abundances in niche space; and functional divergence stands for the divergence in the distribution of abundance in the volume (Mason *et al.* 2005, Villéger *et al.* 2008). Functional redundancy is defined purely as the difference between species diversity and Rao's quadratic entropy based on their functional dissimilarity (Bello *et al.* 2007). We also calculated the community weighted mean for each trait, defined as the mean of values present in the community weighted by the relative abundance of taxa bearing each value (Lavorel *et al.* 2008). The analyses were performed using the packages SYNCSA (Debastiani & Pillar 2012) and FD (Laliberté & Shipley 2013) in R software (R Core Team 2012).

After that, we tested the relationship between each calculated variable (functional and taxonomic measures) with plot age, separately for the two soil types (Cambisol and Gleysol). An analysis of covariance (ANCOVA, Zar 1999) was performed in order to compare the slopes obtained for the two soil types. We followed the same procedure for comparing the community-weighted means of each trait between soil types. These analyses were carried with JMP (SAS Institute) and R softwares (R Core Team 2012).

Results

Soil characteristics

Cambisol and Gleysol did not differ in nutrients, but differed for pH and texture (clay and silt) (Table 2). Cambisol samples were more acidic, had higher clay percentage and lower silt percentage than Gleysol ones. In addition to these differences, groundwater level in Cambisol is lower (deeper) during most of the year when compared to Gleysol, varying from 45 cm to 130 cm in Cambisol and from 20 cm to 90 cm in Gleysol (Supplementary Material Chapter 2, Fig. S2).

Table. 2. Means (\pm SE) of the nutritional and physical characteristics of two soil types in Atlantic Forest areas, Southern Brazil.

Soil parameter	Cambisol	Gleysol	<i>t</i> / <i>Z</i> test
pH (CaCl ₂)	3.78 \pm 0.06	3.96 \pm 0.04	<i>t</i> =2.24, <i>P</i> =0.04
Al (cmol _c .dm ³)	2.36 \pm 0.21	2.14 \pm 0.28	ns
Ca (cmol _c /dm ³)	0.41 \pm 0.27	0.50 \pm 0.18	ns
Mg (cmol _c /dm ³)	0.31 \pm 0.09	0.43 \pm 0.09	ns
K (cmol _c /dm ³)	0.15 \pm 0.01	0.14 \pm 0.02	ns
P _{Mehlich} (mg.dm ⁻³)	4.64 \pm 1.03	3.79 \pm 0.48	ns
C (g/dm ³)	4.47 \pm 0.25	7.72 \pm 0.43	ns
Clay (g.kg ⁻¹)	390.7 \pm 37.59	225.14 \pm 47.99	<i>t</i> =2.5 <i>P</i> =0.03;
Silt (g.kg ⁻¹)	143.23 \pm 50.47	318.91 \pm 51.87	<i>Z</i> =2.64; <i>P</i> =0.008,
Sand (g.kg ⁻¹)	463.48 \pm 51.19	456.23 \pm 94.24	ns

Species richness and individual abundances

We sampled a total of 4389 individuals in 45 plots, where 3031 were canopy trees and 1358 were understory individuals, including saplings and shrubs. A total of

215 species of canopy trees (Cambisol: 185 species; Gleysol 113 species) and 182 species of understory (Cambisol: 134 species; Gleysol 116 species) were recorded (Table S1, Chapter 2).

Trait convergence and divergence

The traits that maximized trait convergence (TCAP) for the canopy community were leaf area, pollination by vertebrates, shade tolerance, and leaf slenderness. For the understory, the selected traits were shade tolerance, leaf area and leaf slenderness (Table 2). The traits maximizing divergence patterns (TDAP) for the canopy community were pollination by bees, abiotic pollination, shade tolerance, maximum DBH, leaf margin, maximum height, leaf compoundness and zoochoric seed dispersal. For the understory the traits that maximized TDAP were pollination by vertebrates, abiotic pollination, shade tolerance, maximum DBH, maximum height and leaf compoundness (Table 2). Most of the traits that maximized divergence appeared in both strata, except for pollination by bees, entire leaf margin and zoochoric seed dispersal, which were selected only in the canopy; and pollination by vertebrates, which was selected only in the understory (Table 2). Some traits maximized convergence in both strata (canopy and understory), such as shade tolerance and leaf slenderness, while the others were selected only in one stratum. Shade-tolerance maximized both convergence and divergence in both strata (canopy and understory). With the trait subset selected above, we found some significant assembly patterns ($P < 0.05$) associated with the environmental gradient assessed in this study (plot age and soil type) for both canopy and understory communities (Table 2). Trait convergence (TCAP) patterns were significant for the subset of traits that maximized convergence in the canopy and in the understory. For

the subset of traits that maximize divergence, we did find significant divergence assembly patterns (TDAP) in the canopy and in the understory (Table 2).

Table 3. Canopy and understory subset of traits that maximize convergence and divergence and significance of the assembly patterns (ρ and P) associated to the successional and edaphic gradient, in the Atlantic Forest in southern Brazil. Bold results indicate statistical significance ($P < 0.05$)

	Maximizing Convergence	Maximizing Divergence
Canopy	<i>Leaf area, pollination by vertebrates, shade tolerance, leaf slenderness</i>	<i>Pollination by bees, abiotic pollination, shade tolerance, maximum DBH, entire leaf margin, maximum height, compound leaves, zoochoric seed dispersal</i>
TCAP [ρ (TE)]	0.276 (0.016)	0.133 (0.17)
TDAP [ρ (XE.T)]	0.063 (0.059)	0.191 (0.012)
Understory	<i>Shade tolerance, leaf area, leaf slenderness</i>	<i>Pollination by vertebrates, abiotic pollination, shade tolerance, maximum height, maximum DBH, compound leaves</i>
TCAP [ρ (TE)]	0.257 (0.003)	0.095 (0.182)
TDAP [ρ (XE.T)]	0.068 (0.052)	0.253 (0.004)

Taxonomic and Functional Diversities

In general, taxonomic diversity (species richness and Shannon Diversity Index - H') and functional diversity (functional richness, functional redundancy and Rao quadratic entropy) measured in this study increased with forest age in the canopy and in the understory (Figs. 1 and 2). In the canopy, the covariance analysis revealed an

interaction of the variables age and soil type, that affected the variables H' , functional richness and functional diversity (as measured by the Rao quadratic entropy). On the other hand, species richness and functional redundancy only responded to plot age (and not to soil type) (Fig. 1). In the understory, four of five variables were influenced by an interaction of age and soil type: species richness, H' , functional richness and functional redundancy. The only exception was Rao quadratic entropy, which was only weakly influenced by age (Fig. 1).

Traits

Most of the selected traits in the canopy responded to the age gradient, in one or both of the soil types. For the traits that maximize convergence (TCAP), leaf area, pollination by vertebrates and leaf slenderness increased with forest age (Fig. 3). For traits that maximize divergence (TDAP), abiotic pollination decreased with forest age; and the means (community weighted means) of individuals with entire leaves, animal-dispersed and with compound leaves increased (Fig. 3). Shade-tolerance, that maximized both TCAP and TDAP also increased with forest age (Fig. 3d). Four traits responded not only to forest age, but also to soil type: seed dispersal by vertebrates, abiotic pollination, shade-tolerance, and leaf compoundness (Fig. 3). The community means of plants pollinated by vertebrates had a weak interaction with age and soil and; although Cambisol had a slighter higher proportion of vertebrate seed-dispersal, this pattern was not very clear (Fig. 3b). Abiotic pollination declined drastically with forest age for both soil types, but the decrease was steeper in Cambisol (Fig. 3c). The means of shade-tolerant species had its peak at around 40 years of age in both soils, and the rate of increase in shade-tolerance mean slowed down in the 80-year-old Cambisol plots (Fig. 3d). Finally, Gleysol plots seemed to have higher means of compound leaves

along succession compared to Cambisol plots (Fig. 3g).

In the understory, the traits had similar patterns to the ones in the canopy. However, only shade-tolerance had a significant interaction between age and soil type. The community means of shade-tolerant species increased with age in both soil types, but more sharply in the Gleysol (Fig. 4d). Leaf slenderness had a different pattern from all other traits, being affected only by soil type. The values were consistent along succession, but leaves in the Gleysol were more slender than the ones in Cambisol (Fig. 4e). Maximum height and maximum DBH were important in maximizing divergence in both strata, but the community means for these traits were not related to the age or soil, hence, they are not shown in the figures.

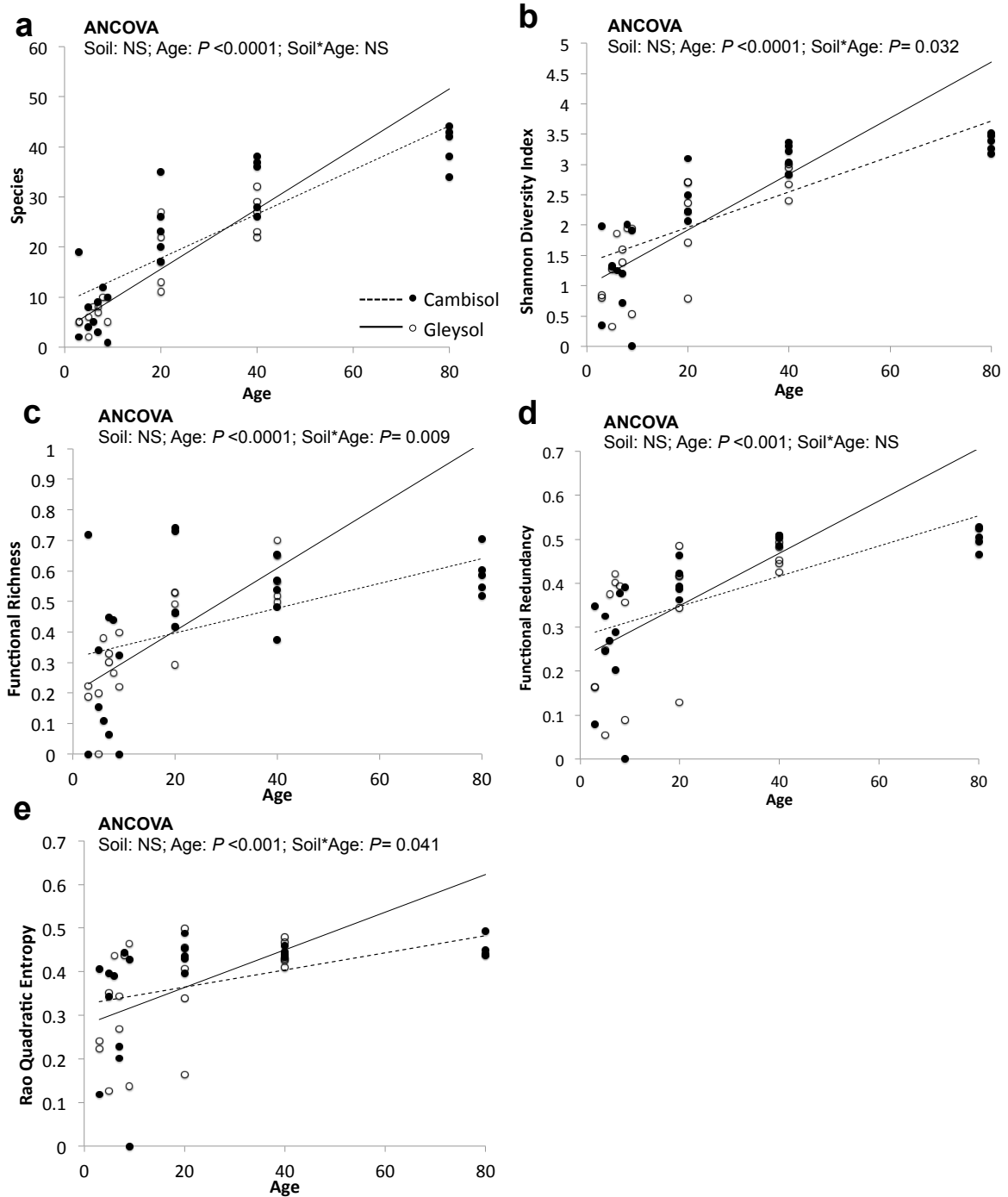


Figure 1. Species richness (a), Shannon’s Diversity Index (b), Functional Richness (c), Functional Redundancy (d) and Rao Quadratic Entropy (e) in the **canopy** community growing in two soil types in the Atlantic Forest, southern Brazil.

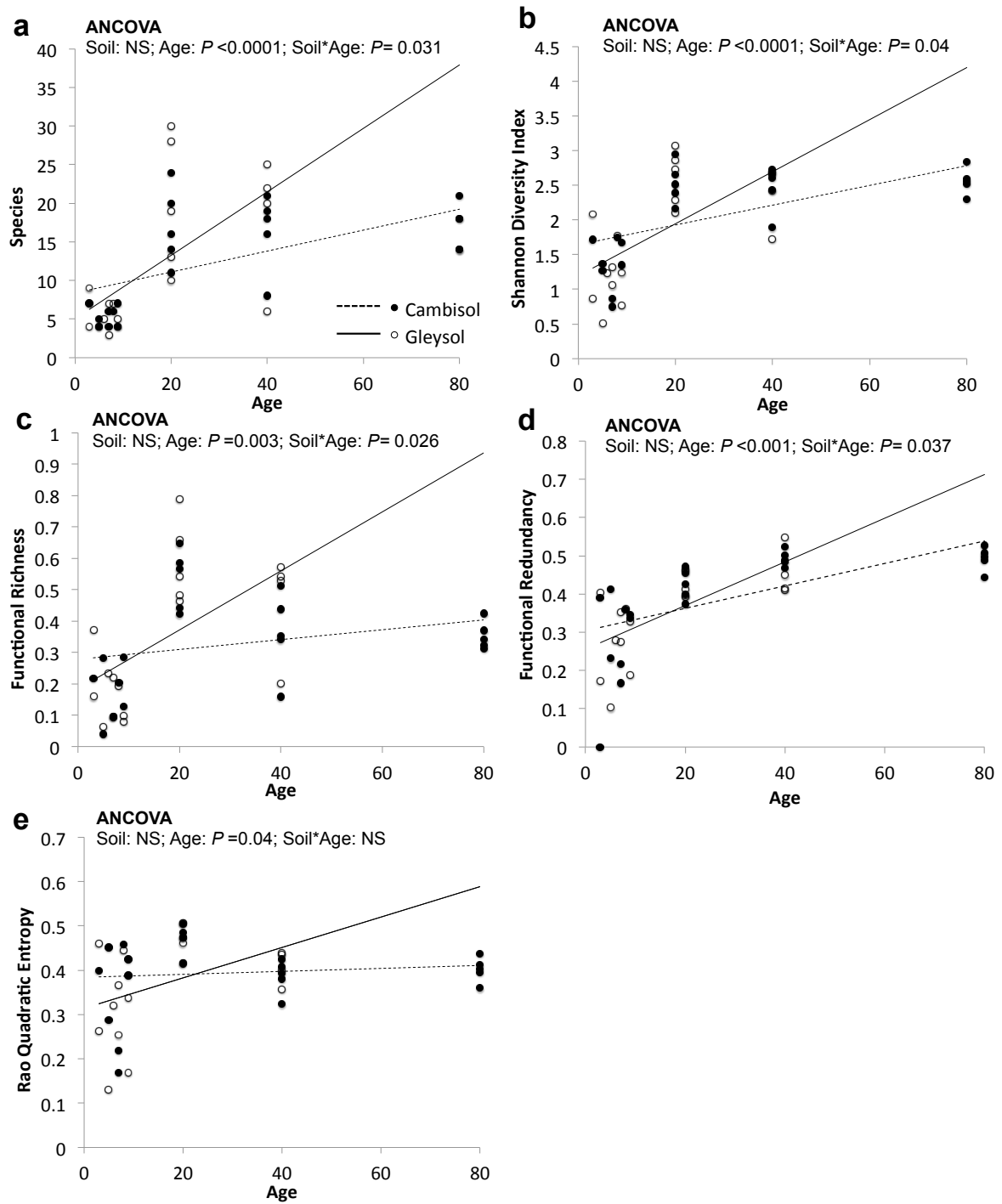


Figure 2. Species richness (a), Shannon Diversity Index (b), Functional Richness (c), Functional Redundancy (d) and Rao Quadratic Entropy (e) in the **understory** community growing in two soil types in the Atlantic Forest, southern Brazil.

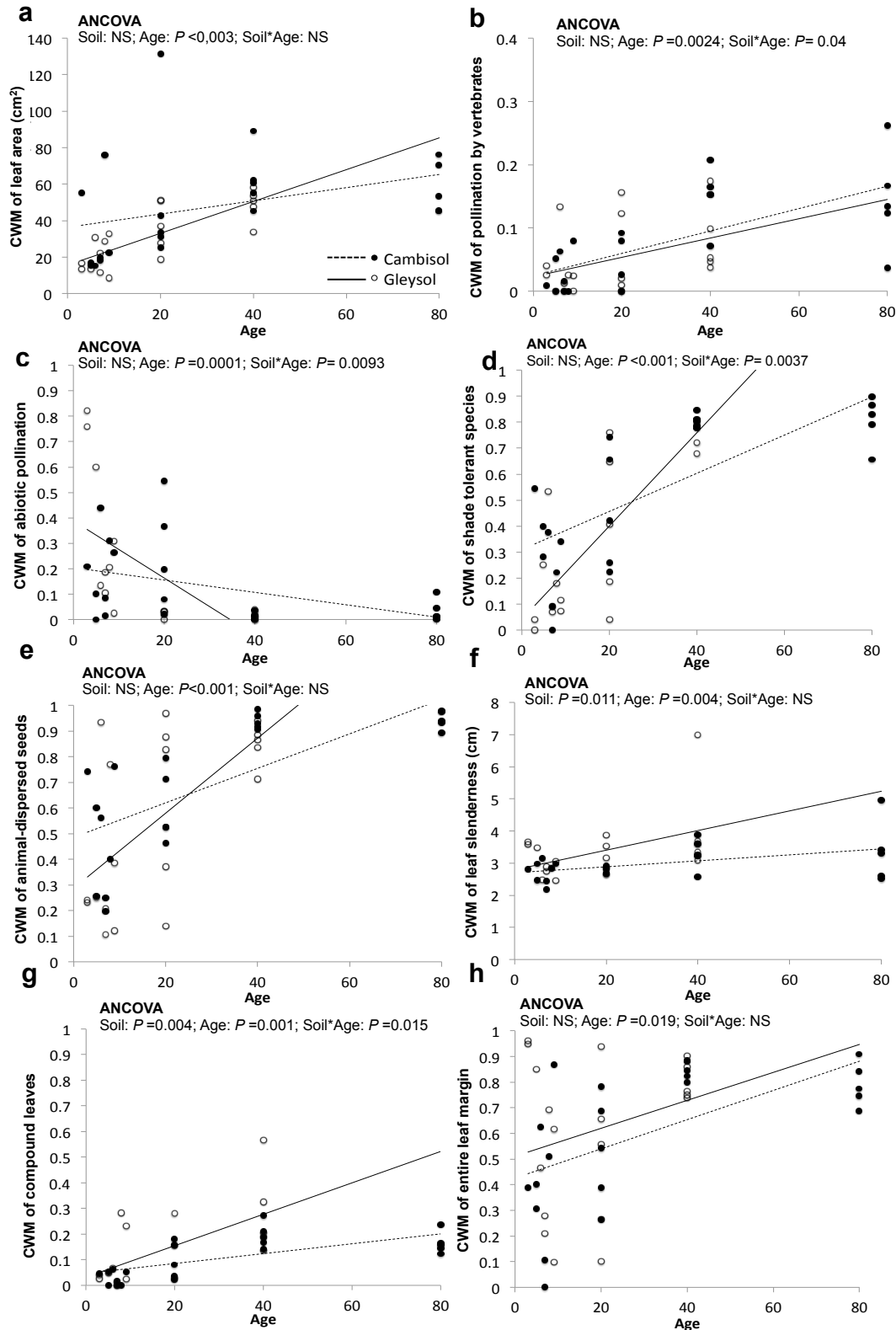


Figure 3. Community weighted means (CWM) of the traits: leaf area (a), pollination by vertebrates (b), abiotic pollination (c), shade-tolerance (d), zoochoric seed dispersal (e) leaf slenderness (f), leaf compoundness (g) and leaf margin (h) in the canopy community growing in two soil types in the Atlantic Forest, southern Brazil.

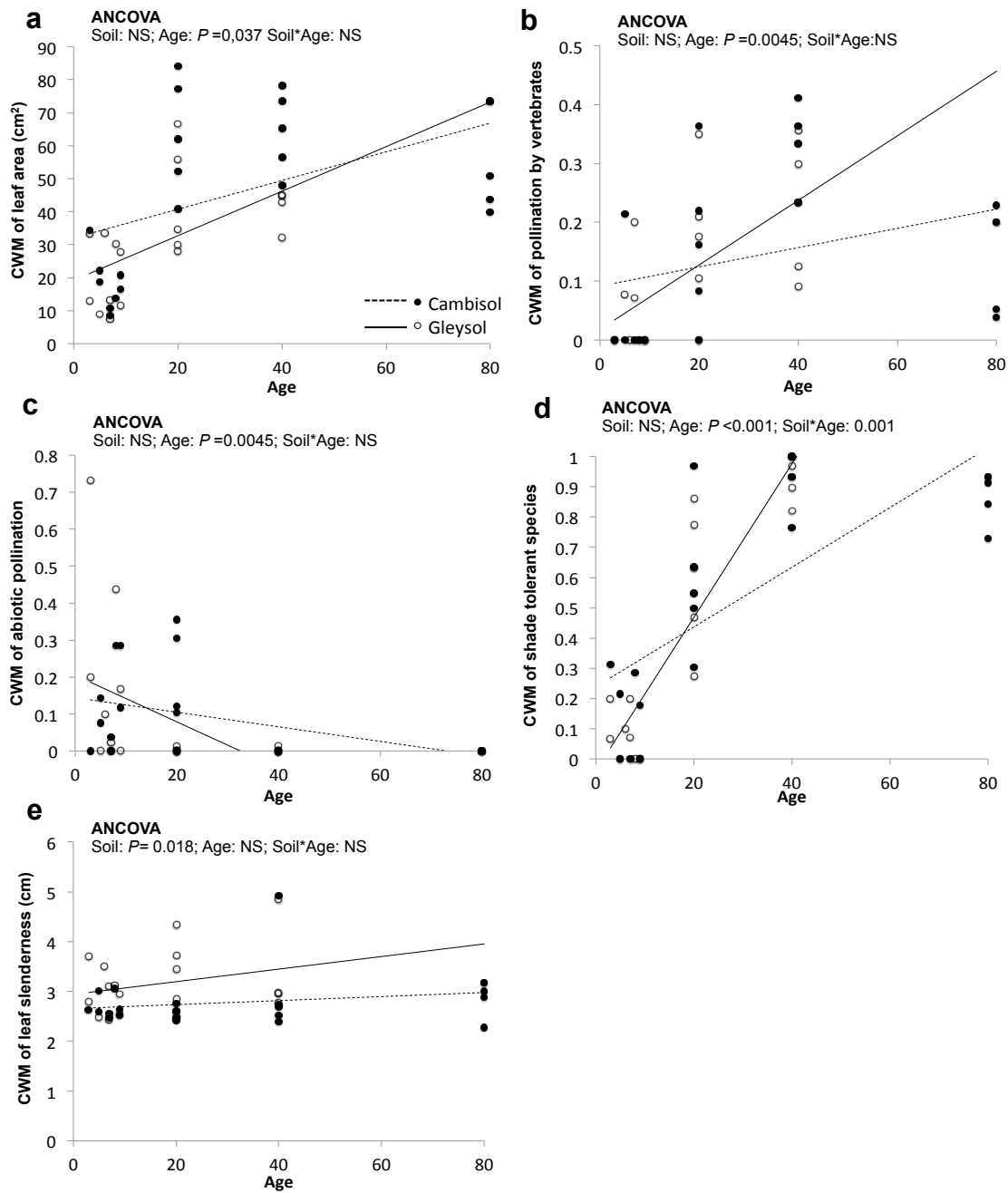


Figure 4. Community weighted means (CWM) of the traits: leaf area (a), pollination by vertebrates (b), abiotic pollination (c), shade-tolerance (d) and leaf slenderness (e), in the **understory** community growing in two soil types in the Atlantic Forest, southern Brazil.

Discussion

The dynamics of functional traits of canopy and understory species during succession of the Atlantic Forest in southern Brazil revealed some directional patterns of functional changes in communities over time and some distinctions of these patterns according to the type of soil in which the communities are growing.

With the finding of convergence and divergence patterns of functional traits in this study, we agree with the idea that functional similarities and differences are important in determining the coexistence patterns of species in communities in environmental gradients (Tilman & Pacala 1993). The expression of convergence patterns (TCAP) is usually related to environmental filters, which can lead species present in a same community to express a greater similarity of traits than what would be expected by chance (Keddy 1992, Weiher *et al.* 1998, Pillar & Duarte 2010). The expression of patterns of convergence in both strata (canopy and understory) suggests that both are subject to transposing environmental or biotic filters, resulting in ecological similarity along succession, with higher redundancy in the older stages. On the other hand, the expression of divergence patterns (TDAP) may indicate the limiting similarity among coexisting species (MacArthur & Levins 1967), due to competition for limiting resources. In general, patterns of convergence and divergence in the canopy and in the understory were associated with distinct traits, suggesting that the temporal gradient associated with successional changes results in different pressures for these two strata.

The two measures of taxonomic diversity (number of species and Shannon diversity index) increased with age in both soil types, as we expected. The number of species, however, had a similar increase in both soil types, reaching its maximum in

more advanced stages of succession, whereas the Shannon diversity index increased in a different rhythm in each soil type. The use of number of species alone may not be sufficient to indicate differences in soil types, since species in this study largely varied in their abundances. But when we used a measure that simultaneously considers species abundances (diversity indices) we could detect a difference between soil types.

All functional diversity measures calculated for the canopy increased with forest age, and two of them also had an influence of soil type: functional richness and Rao diversity. In both cases, they had lower values in the Gleysol in the very young stages of succession (0-15 years), reaching the same values as Cambisol around the 20-year-old plots. Species richness increased uniformly with plot age, while the three functional diversity measures seemed to have a steeper growth in the first years of succession and the increase rate declined later, with the middle-aged plots functionally more similar to the old-growth forests, although with less species. This is explained by functional redundancy, since there is a point in succession when functional diversity stabilizes, even with the increasing number of species. In the beginning of succession, as communities accumulate species, traits do not overlap with those of existing species, but as the forest gets more developed, their functional traits start overlapping and functional redundancy increases (Chazdon 2014). Similar to the canopy, all variables in the understory also increased with forest age and all of them, except for Rao diversity, also had an influence of the soil type, with the variables in the Gleysol plots increasing more steeply than in the Cambisol plots. In successional areas in the Araucaria Forest, Silva (2010) also found an increase in the Rao diversity with age and a decrease in the variability of this measure in the older plots for both the upper and lower strata.

Mean functional trait values of a plant community change along environmental

gradients (Temperton *et al.* 2004). All the four measured leaf traits were selected for maximizing either convergence or divergence of traits. Leaf traits, in general, are related to the fitness of the species and can provide competitive advantage for them (Cornelissen *et al.* 2003). Leaf area, for example, although selected for the set of traits maximizing convergence, was only significantly influenced by age in both strata. The leaf area increased during succession, which maximizes the leaf light capture in the shaded areas of late-successional areas. Leaf area was also reported to increase with age in other tropical forests (Kalascka *et al.* 2005, Sansevero 2013) and in tropical dry forests (Lebrija-Trejos *et al.* 2011), which had species with large leaves and long petioles that maximize light interception per leaf area in the advanced stages of succession. The increase in leaf area along succession may be due to the microclimate in the beginning of succession, since direct exposure to sunlight can considerably raise the temperature. Therefore, plants need to control thermal balance, resulting in smaller leaves in the beginning of succession.

Regarding the soil characteristics, it was reported that leaf economic traits related to resource acquisition, such as leaf area, were more correlated with soil nutrient content than other gradients, such as climate (Ordonez *et al.* 2009). In our study we did not find a significant relation of the community weighted means of leaf area with soil type. One of the reasons could be that even though we had two soils contrasting in water availability and physical characteristics, they did not differ in nutrient content, which seems to affect the leaf area more strongly. On the other hand, in a study in tropical forests in Panama, only two traits (leaf area and wood density) were related to the variation in soil nutrients, not supporting most of their predictions that trait variation would be explained by local-scale soil fertility and acidity gradients (Liu *et al.*

2012).

We found that leaf related traits can be very variable. In an analysis considering nine different leaf-traits in a global database, it was found that leaf traits were usually related to the species' life form, and the trees and shrubs leaf traits were the most variable ones, covering almost the entire observed range of each trait (Wright *et al.* 2004). Leaf compoundness increased with age in the canopy. The entire leaves were generally more frequent in the Gleysol compared to Cambisol. One of the 40-year old sites had more than 50% of entire leaves, while in the Cambisol the values were all low along all ages. Leaf slenderness had only a slight increase with forest age in both strata (canopy and understory), but the soil had an independent effect on it (independent of age). This difference between soils has probably emerged in the younger ages of succession (up to 20 years of age) where the leaves of the Gleysol sites seemed to be wider than the ones in the Cambisol sites. The last leaf-related trait was leaf margin. The community means of entire leaf margin increased with age, but this increase did not have any relation with soil. In the beginning of succession the variance on the leaf margin values was very high, with values in the wide range of 0 to 1. However, in the older phases (40 to 80 years), sites had clearly increased in the amount of species with entire leaf margin, with more than 70% of the community presenting this trait.

Shade tolerant species also had very similar community means between canopy and understory, a pattern also found for some other traits. Changes in functional characteristics in the forest understory, observed in early successional stages, predict subsequent changes in the canopy that occur decades later (Chazdon 2008). The community means of shade tolerant species reached high levels in both soil types already in the 40 years of forest age. In the 80-year-old Cambisol sites we had our highest

values, with more than 90% of the community being shade-tolerant. Similar to leaf margin and other traits the variance of shade tolerance among plots was also much higher in the first two decades of succession. This is explained by the stronger environmental filtering for pioneer species establishing in shaded areas than to non-pioneer species establishing early in the succession (Chazdon 2014).

Shifts in functional traits during succession reflect dramatic changes in resource availability and species interactions (Chazdon 2014), especially regarding the reproduction-related traits. Pollination by vertebrates increased along the successional gradient, but in the Gleysol this increase was slightly steeper than in the Cambisol. This may be a result of the presence of one of the older plots (>80y) in the Cambisol, which unexpectedly had much more species pollinated by bees and other insects than by vertebrates, pulling the slope down in the Cambisol. In the understory, a similar trend occurred for pollination by vertebrates in the Cambisol 80-year old plots, where two plots had considerably lower pollination by vertebrates probably caused by other local reasons rather than soil type. It is important to note that in the 40 year-old plots where both soils types were sampled, we had very high community weighted means of vertebrate pollination in the Cambisol. The other pollination mode that maximized divergence in both strata was abiotic pollination. This trait decreased drastically with age in both soil types. In the 40 year-old plots both soils had very low community means of abiotic pollination. When forest age achieved 80 years old, one of the plots had CWM marginally higher than 0.1, slightly changing the slope in Cambisol in relation to Gleysol. Two Gleysol sites had abiotic pollination 20% higher than the Cambisol sites of the same age (young areas). Similar trends occurred in the understory, with Gleysol showing a steeper decline in abiotic pollination means than Cambisol.

Zoochoric seed dispersal increased along succession and, around the 40 years of age, the means of zoochoric dispersal were already similar to the ones of 80-year old forests. Changes in dispersal mode are predictable in tropical forests, with abiotic dispersal mode prevailing in environments with higher levels of disturbance, thus, decreasing along succession (Opler *et al.* 1980, Tabarelli & Peres 2002, Piotto *et al.* 2009). However, there were no differences in the means of zoochoric dispersal between two soil types, which suggest this trait is not filtered by soil limitations.

With this study, we can gain insights into the ecological processes that drive community assembly during succession in environments with contrasting edaphic characteristics. The patterns of convergence and divergence of traits in the Atlantic forest allow species to coexist and to colonize areas with different age and soil characteristics. Canopy and understory communities are subject to abiotic filters and to biotic interactions, which are revealed by different traits. Trait composition in the plant communities may have different trajectories depending on the characteristics of the soils in which they are growing. Plants with different attributes, in turn, will develop communities with varied structures, hence, they are expected to play different roles in the ecosystems and strongly influence ecosystem functions.

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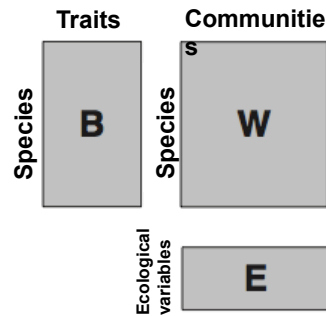
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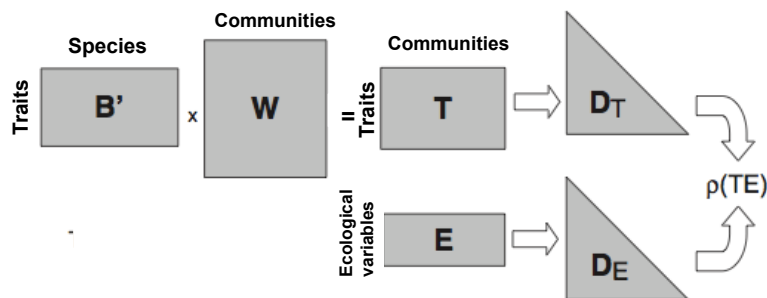
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Supplementary material

(a) Data entrance matrices



(b) Trait convergence



(c) Trait convergence and divergence

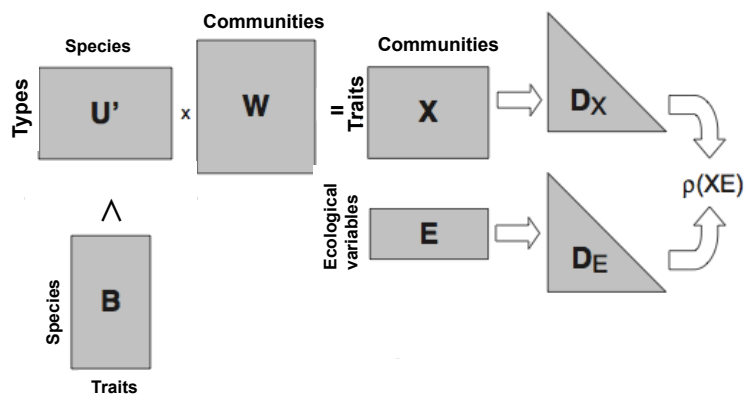


Figure S1 – Scaling up of trait-based data to the community level to reveal trait-convergence and trait-divergence assembly patterns related to ecological gradients. The three data matrices needed for the analysis are in (a), where **B** describes species by traits, **W** the communities by abundances, and **E** the community sites by ecological variables. The procedure in (b) finds trait-convergence assembly patterns (TCAP) related to **E**, via the computation of $\rho(TE)$, the matrix correlation between dissimilarity matrices **D_T** and **D_E** computed after **T** and **E**, where $T=B'W$. The procedure in (c) finds trait-divergence and trait-convergence assembly patterns related to **E**, via the computation of $\rho(XE)$, the matrix correlation between **D_X** and **D_E** computed after **X** and **E**, where $X=U'W$. Adapted from Pillar *et al.* (2009).

CONSIDERAÇÕES FINAIS

O presente trabalho contribuiu com o entendimento dos mecanismos que estruturam as comunidades vegetais durante a sucessão, o que poderá subsidiar futuros projetos de restauração e otimizar o manejo de florestas tropicais secundárias, especialmente na região da Floresta Atlântica.

Antigas áreas de pastagem em processo de sucessão na Floresta Atlântica, por meio de regeneração natural ou plantio de mudas de espécies nativas, são gradualmente estruturadas após o abandono das áreas. Após aproximadamente 50 anos, a abundância e a diversidade taxonômica das comunidades vegetais atingem valores semelhantes aos encontrados em comunidades estabelecidas há mais tempo (>80 anos). Um fator que contribuiu positivamente para o sucesso das ações de restauração na região é a proximidade das florestas maduras adjacentes de onde chegam propágulos, aumentando a riqueza de espécies nas áreas em restauração. As áreas com a presença da gramínea invasora *Urochloa* spp., utilizada para alimentação do gado nas antigas pastagens, limitam a riqueza de espécies e densidade de indivíduos nos primeiros anos de implantação da restauração. Outros fatores estudados (tipo de solo, técnicas de manejo, área da floresta madura mais próxima, relevo) tiveram efeitos menos importantes nas comunidades, embora possam ser relevantes em outras escalas temporais e espaciais não tratadas no presente estudo.

As diferenças entre os tipos de solos predominantes na região de estudo (Cambissolo e Gleissolo), mostraram que características do solo podem ocasionar diferenças estruturais, florísticas e funcionais em áreas florestais em sucessão. Desta forma, características do solo devem ser levadas em consideração na implementação de

planos de restauração, auxiliando na escolha de métodos de restauração e espécies para plantios. As diferenças no solo também determinam estruturas distintas das comunidades no gradiente solo-idade. Aparentemente, não apenas filtros abióticos (determinados, por exemplo, pelas diferentes limitações impostas por Gleissolo e Cambissolo), mas também por interações bióticas, que promovem a convergência e divergência de conjuntos de atributos. De maneira geral, os atributos vegetativos relacionados às folhas (área foliar, divisão da lâmina foliar e esbelteza da folha), tolerância à sombra e atributos reprodutivos (síndromes de polinização e dispersão) diferiram de maneira significativa entre os tipos de solo ao longo do gradiente de idade. As relações da idade com a estrutura e diversidade da floresta e com os atributos corroboraram outros estudos já realizados sobre o tema e ajudaram a confirmar tendências. No entanto, as diferenças estruturais e funcionais aqui demonstradas em solos com características contrastantes são novidades em estudos sucessionais o que poderá trazer contribuições teóricas e práticas para a sucessão e restauração.