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Fragmentação e mudanças nas comunidades arbóreas em distintas formações florestais no sul do Brasil

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Tese apresentada ao Programa de Pós-Graduação em Botânica, Instituto de Biociências, da Universidade Federal do Rio Grande do Sul, como parte dos requisitos necessários para a obtenção do título de Doutor em Botânica.

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Eliete Brunassi e Carlos Lozano Leonel

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SUMÁRIO

RESUMO - A conversão generalizada de florestas maduras em pequenos fragmentos florestais nos trópicos, aliada a crescente pressão para aumento da produção de alimentos, nas próximas décadas, é esperado que ocorra a conversão de 1 bilhão de hectares de habitats naturais em áreas agrícolas. Deste modo, os ecólogos deparam-se com o desafio de examinarem as respostas dos organismos aos distúrbios antrópicos e o papel de paisagens antropizadas como repositórios de biodiversidade. Nesta tese, nós examinamos o efeito da fragmentação florestal na estrutura e composição de comunidades arbóreas em três formações florestais, sazonais e não-sazonais no sul do Brasil (Floresta Ombrófila Densa - FOD, Floresta Ombrófila Mista - FOM e Floresta Estacional Decidual - FED). Para este fim, utilizamos dois conjuntos de dados. No primeiro, amostramos as comunidades arbóreas em 10 parcelas de 0,1 ha em florestas contínuas (na unidade de conservação de maior extensão de floresta contínua presente em cada formação florestal, no sul do Brasil) e em 10 fragmentos florestais adjacentes na região. Enquanto no segundo, as comunidades arbóreas foram amostradas em 389 parcelas de 0,4 ha cada, de variados tamanhos (entre 26° e 29° S e 48° e 53° O; dados Inventário Florístico Florestal de Santa Catarina). Neste conjunto de dados também examinamos a influência das métricas da paisagem (área florestal, forma e isolamento) e de variáveis climáticas (precipitação, temperatura e sazonalidade) na estrutura e composição das comunidades arbóreas. Em ambas as amostragens, todas as árvores com DAP $\geq$ 10 cm em cada parcela foram medidas, identificadas ao nível de espécies e caracterizadas em categorias funcionais descrevendo sua estratégia de regeneração, estratificação vertical, modo de dispersão de sementes, tamanho das sementes e densidade de madeira. As parcelas de FOD apresentaram a maior riqueza de espécies, seguida pela FOM e FED. A maioria dos atributos das comunidades apresentou diferenças significativas entre os tipos florestais, as principais diferenças compreenderam: riqueza de espécies, densidade de troncos, proporção de espécies e troncos de pioneiras, proporção de espécies de sub-bosque e espécies dispersas por vertebrados. As formações florestais apresentaram marcadas diferenças nas respostas às variáveis da paisagem e do fragmento. Devido ao fato de possuírem uma flora mais diversificada de espécies tolerantes ao estresse e de demandantes de luz, com uma reduzida riqueza/abundância de espécies de floresta madura tolerantes à sombra, ambas, FED e FOM, são intrinsecamente mais resilientes a distúrbios antrópicos contemporâneos, incluindo efeitos de borda induzidos pela fragmentação, em termos de erosão de espécies e mudanças funcionais. Nós sugerimos que essas diferenças intrínsecas nas respostas às mudanças na estrutura da paisagem entre as formações florestais deveriam guiar distintas estratégias de conservação.

Palavras-chave: Araucária; Floresta Atlântica; efeitos de borda; atributos funcionais; fragmentação de habitat; floresta sazonal.

ABSTRACT - The widespread conversion of old-growth tropical forests into small forest fragments, and mounting pressure to increase food production in the next decades is expected to expand natural habitat replacement with farmland by perhaps 1 billion ha; challenging applied ecologists to examine organismal response to human disturbance and the role played by anthropogenic landscapes as biodiversity repositories. At the present study, we examined the effects of forest fragmentation on the structure and composition of tree assemblages within three seasonal and aseasonal forest types of southern Brazil, including evergreen, Araucaria and deciduous forests. We used two datasets, in the first, we sampled tree assemblages in each forest type within 10 plots of 0.1 ha in both continuous forests (in the largest continuous protected forest areas within each forest type) and 10 adjacent forest fragments. While in the second dataset, trees assemblages were sampled in 389 plots of 0.4 ha forest fragments off all sizes (between 26° and 29° S and 48° and 53° W; data of Floristic and Forest Inventory of Santa Catarina). Using this second dataset, we also examined the influences of landscape metrics (forest area, shape and isolation) and climatic variables (precipitation, temperature and seasonality) on the structure and composition of tree assemblages. In both datasets, all trees with DBH $\geq$ 10 cm within each plot were measured, identified to species level, and assigned to trait categories describing their regeneration strategy, vertical stratification, seed-dispersal mode, seed size and wood density. Evergreen forest plots exhibited the highest species richness, followed by Araucaria and deciduous forests. Most tree assemblages attributes showed significant differences among forest types, the major differences comprised: species richness, stem density, the proportion of pioneer species and stems, and the proportion of understorey and vertebrate-dispersed species. The forest types demonstrate markedly divergent responses to patch and landscape variables. By supporting a more diversified light-demanding and stress-tolerant flora with reduced richness/abundance of shade-tolerant, old-growth species, both deciduous and Araucaria forests, the tree assemblages are more intrinsically resilient to contemporary human-disturbances, including fragmentation-induced edge effects, in terms of species erosion and functional shifts. We suggest that these intrinsic differences in responses to changes in landscape structure between forest types should guide conservation strategies.

Key-words: Araucaria; Atlantic Forest; edge effects; functional attributes; habitat fragmentation; seasonal forest.

1 INTRODUÇÃO GERAL

1.1 O desafio agrícola

A população mundial de humanos é esperada que aumente dos atuais 7 bilhões para 9 bilhões em 2040, mantidas as taxas de crescimento atual (Godfray et al. 2010). Além do aumento do número de habitantes, as demandas de produção agrícola serão pressionadas por mais dois fatores centrais, o aumento do consumo de proteínas e laticínios e pelo aumento do poder de consumo da população global, além da crescente demanda por biocombustíveis (Pigali 2006; Godfray et al. 2010; Tilman et al. 2011; Foley et al. 2011). Estimativas apontam que a agricultura ocupa hoje cerca de 40% da superfície terrestre, e pode ser considerado o maior *driver* da perda de biodiversidade em escala global. Em termos da promoção de alterações no planeta, rivaliza com as mudanças climáticas, e ambas estão acontecendo ao mesmo tempo (Foley et al. 2005). Estimativas apontam que a produção agrícola deveria aumentar de 60 a 110% até 2050 para atender à crescente demanda (Tilman et al. 2011). Para prover esses aumentos, por mais que aumentemos a produtividade das lavouras, é praticamente certo que será necessário aumentar a área cultivada no planeta (Ray et al. 2013). Este aumento de área se dará também pelo avanço sobre áreas naturais, incluindo florestas tropicais. Desse modo, os processos de desmatamentos e fragmentação florestal, que ocorrem, atualmente, em escalas alarmantes, é provável que ainda se intensifiquem nas próximas décadas (Laurance et al. 2014).

Por todos esses fatores o cenário para a biologia da conservação é altamente desafiador. É provável que num futuro próximo teremos uma quantidade ainda maior do que a atual de paisagens altamente fragmentadas, com fragmentos florestais dispersos nas paisagens antropizadas. Fragmentos com uma grande amplitude de tamanhos, mas a maior ncentração de menor tamanho, como é o cenário predominante na Mata Atlântica, onde 32-40% da área remanescente fragmentos apresentam menos de 100 hectares (Ribeiro et al. 2009).

A transformação de florestas contínuas em fragmentos florestais imersos em uma matriz não florestal é um processo generalizado nos trópicos (Skole e Tucker 1993). Taxas atuais e passadas de conversão de florestas indicam claramente que a maioria das florestas maduras irão eventualmente desaparecer e deixar para trás um complexo mosaico de áreas agrícolas e fragmentos florestais sob diferentes níveis de sucessão (Quesada et al. 2009). Este tipo de mosaico agro-florestal altamente fragmentado pelo homem já é a paisagem predominante em muitas regiões previamente florestadas. Contudo a intensidades dos impactos dessas mudanças sobre diferentes conjuntos de espécies e sobre o funcionamento dos ecossistemas permanece incerto (Foley et al. 2005, Stokstad 2005).

1.2 Fragmentação florestal, perda de hábitat e os efeitos de borda

A fragmentação florestal expõe os organismos que permanecem nos fragmentos às condições de um diferente ecossistema circundante e, consequentemente, ao que têm sido denominado “efeitos de borda” (Murcia 1995). As bordas podem afetar os organismos em um fragmento florestal por causarem mudanças nas condições bióticas e abióticas (Turner 1996, Laurance et al. 2000, Laurance et al. 2002). As mudanças microclimáticas próximas às bordas como redução na umidade, aumento da incidência luminosa e aumento na amplitude da variação térmica podem alcançar 100 m para dentro dos fragmentos (Laurance et al. 2006). Se a exposição à borda modificar as características do ambiente florestal além da sua amplitude natural de variação intrínseca, então a porção do fragmento sob a influência do efeito de borda pode passar a ser inadequada para a maioria das espécies do ecossistema original adaptadas às condições úmidas e sombreadas do interior da floresta, e para fins de conservação, a área do fragmento será efetivamente reduzida (Murcia 1995; Ewers & Banks-Leite 2013).

A fragmentação e a perda de hábitat podem alterar drasticamente a composição e estrutura de comunidades arbóreas tropicais (Laurance et al. 2006, Barlow et al. 2007). Estudos recentes demonstram que as bordas das florestas e até as porções centrais de fragmentos pequenos, devido aos efeitos de borda, apresentam comunidades arbóreas com menor abundância e riqueza de espécies emergentes (Laurance et al. 2000, Santos et al. 2008), de crescimento lento (Oliveira et al. 2008), com grandes sementes dispersas por vertebrados (Melo et al. 2007, Stoner et al. 2007, Santo-Silva et al. 2013) e tolerantes à sombra e sensíveis à dessecação (Laurance 2001) quando comparados as áreas internas de florestas maduras. Em contraste, espécies arbóreas pioneiras, em geral espécies de crescimento rápido, que produzem numerosas sementes pequenas e que precisam de alta intensidade luminosa quando plântulas para se estabelecerem (Whitmore 1989), parecem ser amplamente favorecidas em paisagens vastamente fragmentadas (Tabarelli et al. 1999, Oliveira et al. 2008, Santos et al. 2008). Conseqüentemente, tem se sugerido que paisagens largamente fragmentadas, reduzidas a arquipélagos de fragmentos isolados, provavelmente sejam capazes de manter apenas uma pequena parcela, não-aleatória, de espécies da flora original (Tabarelli & Gascon 2005, Santos et al. 2008).

Laurance et al. (2006), na Amazônia, encontraram um aumento drástico na abundância de espécies arbóreas pioneiras nas bordas e mesmo no interior de pequenos fragmentos isolados há apenas 14 a 17 anos. E apesar de não terem encontrado mudanças significativas na composição das comunidades das áreas centrais de fragmentos maiores (10-100 ha), eles advertem que essas mudanças, que podem ser conseqüência de declínios relacionados à área nas populações de dispersores e polinizadores (Silva e Tabarelli 2000, Girão et al. 2007), ou de mudanças associadas às áreas limitadas dos fragmentos, como o colapso de populações isoladas de árvores devido a eventos demográficos aleatórios ou por endogamia, podem requerer mais de duas décadas para serem notadas.

Santos et al. (2008), na floresta atlântica nordestina, em uma paisagem de fragmentos florestais formados há no mínimo 60 anos, encontraram que as comunidades arbóreas de pequenos fragmentos são bem mais similares às das bordas das florestas do que com as das áreas interiores de um grande fragmento contínuo (3500 ha). Eles também encontraram que nas regiões próximas às bordas dos fragmentos e mesmo na porção central de pequenos fragmentos retém apenas metade da riqueza total de espécies arbóreas, e menos de um terço das espécies arbóreas tolerantes à sombra, emergentes e com sementes grandes quando comparadas às comunidades do interior de florestas maduras. Inversamente encontraram um aumento de, pelo menos, quatro vezes no número de indivíduos e espécies de pioneiras nas bordas e nos pequenos fragmentos. Eles concluem que isto implicaria, caso esta tendência seja confirmada, que os arquipélagos encontrados em regiões de desmatamento antigo que são dominadas por uma paisagem de pequenas manchas de floresta poderão reter apenas subconjuntos empobrecidos não aleatórios de espécies da flora original, como postulado por Patterson (1987). E deste modo, diretrizes de planejamentos de conservação como a criação e/ou manutenção de corredores de biodiversidade irão, na verdade, fracassar em proteger as regiões florestais amplamente fragmentadas da perda acentuada de espécies, se os remanescentes de floresta consistirem principalmente de áreas sob influência do efeito de borda.

Contudo a extensão em que a fragmentação reduz as populações, altera as comunidades vegetais, e como as distintas formações florestais diferem no grau de sensibilidade à fragmentação permanecem pouco compreendidas. A compreensão da sucessão, no contexto de diferentes formações florestais e dimensões dos impactos causados pelo homem, representa um dos desafios chave para a promoção e desenvolvimentos de programas efetivos de conservação para estas paisagens no futuro (Gardner et al. 2009, Quesada et al. 2009).

1.3 Considerações ecofisiológicas

Plantas tolerantes à sombra, de estádios sucessionais mais tardios, são geralmente mais sensíveis a níveis decrescentes de umidades do solo do que plantas de estádios sucessionais iniciais (Bazzaz 2000). Apesar da presença de mecanismos que ajustam a fotossíntese em resposta ao grau de exposição das folhas a diferentes níveis de intensidade luminosa, a taxa de resposta das folhas geralmente se mantém inalterada se as folhas de plantas pioneiras são expostas a níveis acima do seu ponto de saturação. Isto é, não se espera que elas apresentem “fotoinibição”. É provável que estas plantas tenham desenvolvido mecanismos bioquímicos para dissipar o excesso de energia, e deste modo, não sofrer danos significativos sob altas intensidades luminosas. Diversas plântulas e juvenis de indivíduos de estádios sucessionais mais tardios, em contraste, podem apresentar atividade fotossintética muito reduzida, ou mesmo mortandade quando expostas a altas intensidades luminosas devido ao excessivo calor nas folhas e fotoinibição (Bazzaz 2000).

Diferentes sensibilidades à seca moldam as distribuições das plantas em florestas tropicais, tanto em nível local quanto regional (Engelbrecht et al. 2007). A diferenciação de nichos em relação a disponibilidade hídrica é um determinante direto da distribuição de espécies tropicais. Mudanças na disponibilidade da umidade no solo causadas pela fragmentação florestal são, deste modo, prováveis a alterarem a distribuição das espécies, composição das comunidades e diversidade (Engelbrecht et al. 2007).

A variabilidade na disponibilidade hídrica – especialmente durante períodos secos – mediada através da precipitação, caracteristicas do solo ou topografia, é, deste modo, um importante candidato para a partição de nichos de espécies florestais (Engelbrecht et al.

2007). As diferenças entre as espécies, quando plântulas, na sensibilidade à seca, está relacionada às diferenças na efetividade dos mecanismos fisiológicos de tolerância à seca (isto é, nas diferentes habilidades de sobreviver apesar de baixos potenciais hídricos das folhas).

Sazonalidade

A sazonalidade e a fisionomia das florestas tropicais são determinadas pela quantidade de precipitação anual e sua distribuição sazonal (Borchert 1998). A variabilidade na precipitação anual, na intensidade e nos momentos em que ocorrem os períodos úmidos e secos, é geralmente considerável em áreas tropicais. Enquanto o coeficiente de variação da precipitação anual em regiões temperadas é próximo de 15%, em áreas tropicais é mais comum encontrá-lo na faixa dos 30% (Murphy e Lugo 1986). Esta variabilidade é significativa para ecossistemas que são compostos por numerosas espécies animais e vegetais que vivem próximos dos seus limites de tolerâncias em relação à umidade (Murphy e Lugo 1986).

O número de espécies lenhosas, assim como a densidade de árvores, tende a crescer com o aumento da precipitação e com o decréscimo da sazonalidade em florestas maduras tropicais (Wright 1992, Phillips et al. 1994, Givnish 1999, Davidar et al. 2005), entretanto a relação entre estas variáveis não é bem compreendida (Davidar et al. 2005). A variação estacional na disponibilidade hídrica parece ser o principal determinante da distribuição das espécies arbóreas, em florestas tropicais mais secas e sazonais (Borchert 1994ª; Engelbrecht et al. 2007). Os altos níveis de estresse hídrico que ocorrem durante os períodos secos, uma causa comum da mortalidade de árvores (Donley 1981; Engelbrecht et al. 2010), sugerem que os anos extremos, ao invés dos anos situados na média, devem ser os mais significativos em moldar a estrutura, composição e propriedades funcionais dos ecossistemas florestais mais secos e estacionais (Murphy e Lugo 1986; Engelbrecht et al. 2007, 2010).

O desenvolvimento das árvores durante a estação seca varia consideravelmente entre as espécies e entre diferentes regimes hídricos. A maior capacidade interna de armazenamento de água diminui o impacto da seca sazonal e permite, inclusive, o florescimento e a emissão de novos ramos durante a estação seca para algumas espécies (Borchert 1994a). A densidade da madeira e capacidade de armazenamento de água, que estão altamente correlacionados com o grau de dessecação durante a seca, varia amplamente entre as espécies arbóreas (Borchert 1994b). Contudo estudos da distribuição destas características fisiológicas em relação às diferentes categorias sucessionais das espécies arbóreas são escassos.

Supomos que pelas espécies da floresta estacional decidual serem espécies adaptadas a uma condição de seca sazonal (mesmo que pretérita, nos centros de origens dos táxons) e periodicamente expostas à altas taxas de radiação solar, tanto pelo dossel naturalmente descontínuo (Inácio & Jarenkow 2008) quanto pela abertura do dossel, devido à queda das folhas em determinada época do ano, uma menor porcentagem das espécies presentes nesta formação seria sensível aos efeitos de borda quando comparadas ao conjunto de espécies de formação não sazonais como a floresta ombrófila densa.

1.4 Assimetria nos estudos sobre fragmentação florestal na América do Sul

Um significativo viés na distribuição das pesquisas realizadas nos biomas tropicias, ressalta uma das maiores dificuldades que os pesquisadores que trabalham com a biologia da conservação em ambientes pouco estudados enfrentam. Existe o risco real de apenas algumas poucas paisagens intensamente estudadas terem resultados e padrões demasiadamente propagados na literatura, sem as corretas ponderações sobre a generalidade dos padrões observados naquele ambiente, resultando potencialmente em uma transferência inapropriada de conhecimentos e no uso de paradigmas enganosos, que dessa maneira poderiam atrasar o desenvolvimento de estratégias de conservação realmente efetivas em outras partes menos estudadas do globo (Gardner et al. 2009). Deste modo considero importante, primeiro, ressaltar a potencial relevância do conjunto de dados que será debatido neste tese, sobre uma região relativamente ainda pouco estudada em termos de fragmentação florestal – os subtrópicos da América do Sul; e segundo, analisar em detalhes, as particularidades das fontes das informações mais frequentemente usadas e citadas nos estudos de conservação da América do Sul. Dentre as mais importantes podemos destacar:

Amazônia – PDBFF

O PDBFF (Projeto Dinâmica Biológica de Fragmentos Florestais) se intitula o maior estudo experimental sobre fragmentação de habitat, que vem sendo conduzido há mais tempo no mundo, assim como uma das investigações ecológicas mais altamente citadas já realizadas (Gardner et al. 2009, Peres et al. 2010). Basicamente, esse grande conjunto de publicações (mais de 600 artigos), foca a resposta de uma ampla gama de táxons vegetais e animais à fragmentação, assim também como estudos abordando florestas secundárias, mudanças globais e ecologia florestal básica.

Foram publicadas duas revisões (altamente citadas) sintetizando os principais resultados obtidos, o primeiro compilando os principais resultados dos primeiros 22 anos de estudos (Laurance et al. 2002) e o segundo dos 32 anos (Laurance et al. 2011). O PDBFF é localizado 80 km ao norte de Manaus e abrange aproximadamente 1000 km². A topografia é relativamente plana (80-160 m de elevação), cortadas por córregos. Os solos altamente lixiviados, pobres em nutrientes, da área de estudo são típicos de grandes extensões da bacia amazônica. As precipitações variam entre 1900 e 3500 mm, com uma estação moderadamente seca entre junho e outubro. O dossel da floresta é de 30-37 metros de altura, com emergentes que atingem 55 m. A riqueza de espécies de árvores (≥ 10 cm de diâmetro à altura do peito) normalmente ultrapassa 280 espécies ha^{-1}, com um alto grau de diversidade em também outros grupos animais e vegetais (Oliveira e Mori, 1999; Laurance et al. 2010).

A área de estudo ainda inclui três grandes áreas de pastagem (aproximadamente 5000 ha cada) contendo 11 fragmentos florestais (cinco de um hectare, quadro de 10 ha, e dois de 100 ha), além de florestas contínuas ao redor que funcionam como controle do experimento. No início da década de 1980, os fragmentos foram isolados das florestas intactas contínuas ao redor por distâncias de 80-650 metros através do corte raso e queima desses trechos da floresta. O principal ponto que diferencia estes estudos de todos os demais é que foram conduzidos censos para muitos grupos animais e vegetais, dessa maneira, permitindo acessar as alterações de longo prazo nesses grupos de maneira mais confiável do que na maioria de outros estudos sobre fragmentação florestal.

Devido os solos pobres e a baixa produtividade, as pastagens ao redor dos fragmentos do PDBFF, foram largamente abandonados. Florestas secundárias (inicialmente dominadas por *Vismia* spp. em áreas que foram desmatadas e queimadas, ou por *Cecropia* spp., em áreas que foram desmatadas e não foram queimadas) proliferaram em muitas áreas previamente desmatadas (Mesquita et al. 2001). Algumas das áreas que regeneraram inicialmente dominadas por *Cecropia* ssp. se desenvolveram em relativamente maduras (> 20 m de altura), florestas secundárias ricas em espécies. Florestas em regeneração dominadas por *Vismia*, por outro lado, são relativamente pobres em espécies, e a sua composição se altera em uma lentamente (Norden et al. 2010). Para auxiliar a manter o isolamento dos fragmentos experimentais, faixas de 100 metros de largura da regeneração foram cortadas e queimadas ao redor de cada fragmento em 3-4 ocasiões, mais recentemente entre 1999 e 2001. Além disso, distúrbios humanos que são deletérios em várias paisagens fragmentadas na Amazônia, como grandes incêndios e corte seletivo foram em larga escala prevenidos no PDBFF. A pressão de caça também foi bastante limitada. Descrições detalhadas da área de estudo e do delineamento podem ser obtidas em Laurance e Bierregaard (1997) e Bierregaard et al. (2001). O PDBFF já gerou mais de 600 publicações ao longo de três décadas de estudos e tem um grande impacto sobre o conhecimento atual, sendo a maior fonte de dados sobre perda de hábitat e fragmentação em florestas tropicais. Contudo como explicitado as condições prevalentes na área de abrangência dos estudos difere marcadamente das condições e ambientes que imperam nos domínios da Mata Atlântica, por exemplo (onde os artigos do PDBFF são largamente citados), contudo essas distinções nem sempre são adequadamente explicitadas na literatura.

Nordeste do Brasil – Serra Grande

Outra paisagem no Brasil que também foi amplamente estudada no Brasil, é a área da Usina de Serra Grande, uma grande companhia privada, localizada no estado de Alagoas, no nordeste do Brasil. Estas áreas renderam dezenas de estudos, que são amplamente citados, coordenados principalmente pelo Dr. Marcelo Tabarelli. Esta grande propriedade abriga 9000 hectares de florestas de uma origem biogeogeográfica particular da floresta Atlântica, o centro de endemismo de Pernambuco (Santos et al. 2007). Esta paisagem abriga um grande fragmento florestal contínuo de 3500 hectares, um dos maiores localizados na Mata Atlântica ao norte do Rio São Francisco, e aproximadamente 108 outros fragmentos que possuem os mais variados tamanhos (desde 1,67 ha ao grande fragmento de 3500 ha). Todos esses fragmentos são rodeados por uma matriz única, a monocultura de cana-de-açúcar. A precipitação média anual é ao redor de 2000 mm, com uma estação seca que dura aproximadamente 3 meses (<60 mm/mês) de novembro a janeiro. O uso agrícola de Serra Grande data do século 19, o que proporciona uma condições, sob um ponto de vista ecológico, marcadamente distintas daquelas observadas nas áreas do PDBFF, enquanto este último apresenta um processo de desmatamento e fragmentação florestal relativamente recente, esta região em Alagoas apresenta um desmatamento ocorrido hpa mais de 100 anos, tendo restado na região apenas 9,2% da cobertura florestal original (Santos et al. 2008), tendo os grandes mamíferos que habitavam essa região (como as antas e queixadas) já foram extintos devido a sobrecaça (Silva & Tabarelli 2000). É importante ressaltar que toda essa região passa por um ciclo anual do plantio e queima da cana-de-açúcar, que pode propiciar características ecológicas singulares e naturezas de estresses singulares, principalmente em relação às áreas mais próximas às bordas dos fragmentos que sofrem mais intensamente com as queimadas, realizadas após a colheita da cana. E podem intensificar os efeitos da fragmentação florestal e dos efeitos de borda por conseqûencia dessas queimas periódicas.

1.5 Biogeografia dos subtrópicos do leste da América do Sul

No sudoeste da América do Sul, dados palinológicos (Behling 1998, Behling et al. 2005) e fitogeográficos (Rambo 1961, Joly et al. 1991) sugerem que uma maciça recolonização por espécies arbóreas ocorreu apenas após a última glaciação na atual região subtropical. Esta recolonização iniciou ao redor de 5.000 – 10.000 atrás (Behling et al. 2005), sugerindo que condições mais frias impediam o desenvolvimento das comunidades arbóreas nos subtrópicos. As espécies arbóreas eram escassas durante os períodos paleoclimáticos mais frios (Behling et al. 2005), e no máximo da última era glacial os campos substituíram as florestas em direção ao norte até 20° S de latitude (Behling et al. 2005). Este processo é um indicativo de que as espécies arbóreas, apresentam em sua maioria nichos climáticos tropicais (Giehl & Jarenkow 2012). Poucas espécies e linhagens mudaram seus nichos em direção aos subtrópicos, e o *pool* de espécies e linhagens restritas ao sítios tropicais é bem maior que as presentes nos subtrópicos. Apenas uma pequena porcentagem de linhagens, famílias e espécies são exclusivas a sítios subtropicais (Giehl & Jarenkow 2012; Oliveira-Filho et al. 2014). Deste modo, muitas evidências apontam para a existência de uma clara associação de uma maior diversidade de espécies arbóreas com climas mais tropicais e quentes. Além disso, devemos considerar que a riqueza de espécies vegetais é limitada pela existência de filtros ambientais, sendo um dos mais significativos a restrição de disponibilidade hídrica, que normalmente é menos limitante nos trópicos, embora não seja necessariamente bem distribuída ao longo do ano (Kreft e Jetz 2007; Qian e Ricklefs 2008).

Rambo (1961) reconheceu duas correntes migratórias da flora tropical em direção ao sul: a do oeste, através das bacias dos rios Uruguai e Paraná, com um caráter mesófilo (sazonal),e a do leste, ao longo da costa Atlântica, com um caráter mais higrófilo. Ele argumenta que a primeira alcançou as regiões mais ao Sul bem antes das última, e esta está em complete concordância com o registro polínico que indica a presença de densas florestas nas planícies da Argentina ao redor de 8.000 anos antes do presente (iriondo e Garcia 1993), enquanto as florestas ombrófilas litorâneas não foram registradas para os subtrópicos antes de 7.000 anos antes do presente (Ledru et al. 2008). A subsequente expansão das florestas ombrófilas, e das suas espécies “quente-úmido”, ao longo da costa poderia ter empurrado as espécies do contingente “quente-sazonal” em direção ao interior do continente, e desde então, as florestas sazonais terem se concentrados nas áreas mais continentais, embora algumas espécies bem higrófilas penetraram bem adentro do continente (Behling et al. 2005; Behling and Negrelle 2001; Klein 1975; Lorscheitter 2003), como a ocorrência do palmito (*Euterpe edulis*) no Parque de Moconá na Argentina (Davi et al. 1999).

Giehl e Jarenkow (2012) postulam que a dispersão de espécies de regiões tropicais para subtropicais, na porção oriental da America do Sul, não é bem sucedida pela amplamente distribuída falta de capacidade de espécies e linhagens de tolerar os mínimos de temperatura que ocorrem no inverno. Estes autores encontraram a menor riqueza em sítios subtropicais que apresentaram as menores temperaturas médias além das maiores taxas de sazonalidade da temperatura, mas chuvas bem distribuídas ao longo do ano. Também encontraram que o turnover latitudinal de espécies e linhagens segue amplamente mudanças na sazonalidade de temperatura e precipitação, padrão altamente correlacionado com a diminuição na riqueza. Resultados similares, que corroboram estas hipóteses também foram encontrados por Higuchi et al. (2013), Gonçalves & Souza (2014) e Oliveira-Filho et al. (2014). A menor riqueza observada nos subtrópicos se daria devido às diferentes taxas de especiação e extinção entre as linhagens que habitam os trópicos em comparação às dos subtrópicos (Giehl & Jarenkow 2012), além do fato que os sítios subtropicais tiveram uma área e distribuição variável nos últimos 55 milhões de anos, o que pode ter interagido com o conservatismo filogenético de nichos tropicais para explicar as diferenças nos padrões de diversificação das linhagens tropicais e subtropicais (Fine et al. 2008).

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2 ESTRUTURA DA TESE

Esta tese está subdividida em dois capítulos principais. No primeiro capítulo, procuramos analisar se existem diferenças significativas nas respostas das florestas à fragmentação florestal através do seguinte delineamento: amostramos, em cada uma das três formações florestais (Floresta Ombrófila Densa, Floresta Mista Mista e Floresta Estacional Decidual), 10 fragmentos florestais, alocando uma parcela de 10x100 metros exatamente no centro geométrico de cada fragmento. Além destas, amostramos 10 parcelas de mesma extensão em áreas de referência de florestas maduras, que foram amostradas dentro das Unidades de Conservação. Para este fim, foram selecionadas as áreas que apresentassem os remanescentes de florestas maduras mais bem preservados, de cada formação florestal, nos estados do Rio Grande do Sul e Santa Catarina. Como principal vantagem desse delineamento tivemos a padronização do posicionamento das parcelas, que no caso das Unidades de Conservação sempre respeitaram uma distância mínima de 250 metros da borda florestal mais próxima, e no caso dos fragmentos, as parcelas foram posicionadas no centro geométrico dos mesmos. Tivamos a devida atenção para que as distâncias entre as parcelas de referência dentros das UCs, fossem em uma escala muito similar às distâncias entre os fragmentos florestais amostrados. Como principal limitação desse delineamento, tivemos a falta de repetição em nível de paisagens, pois foi amostrada apenas uma região para cada formação florestal. Esta limitação foi devida a falta de outras UCs, que apresentassem florestas maduras em ótimo estado de conservação (similares às amostradas) para serem usadas como referência. Por exemplo, nos estados do RS e SC, não temos outra UC de proteção integral que apresente significativas áreas de floresta maudura da Floresta Estacial

Decidual em excelente estado de preservação, além do Parque Estadual do Turvo, que foi amostrado.

No segundo capítulo, usamos a robusta base de dados do Inventário Florístico Florestal de Santa Catarina. Como grande vantagem tivemos um alto número de parcelas (389 parcelas de 0,4 ha cada) e fragmentos florestais amostrados, gerando repetições em nível de paisagem, e possibilitando conclusções mais robuustas em relação aos três tipos de floreta. A grande maioria das parcelas respeitou uma distância mínima de 10 km entre ela. Além de estarem distribuídos por praticamente toda a extensão do estado, que apresenta uma área de 95.346 km^2. Desse modo, também pudemos avaliar a variação dos atributos funcionais das espécies arbóreas também em relação a variáveis climáticas e da paisagem. Como uma limitação, se é que podemos considerar dessa maneira, poderíamos considerar a falta de padronização espacial em termos de posicionamento das parcelas dentro dos fragmentos, além de terem sido amostrados fragmentos florestais dos mais variados estádios de regeneração. Variáveis que foram controladas no primeiro capítulo, pois limitamos à amostragem apenas aos fragmentos florestais bem preservados das regiões analisadas. Desta maneira, perdemos alguns graus de liberdade nas análises para contemplar estas variáveis. Contudo claramente, esta robusta base de dados nos permitiu uma excelente oportunidade de avaliarmos os efeitos das variáveis climáticas e da paisagem em relação à: densidade de indivíduos; riqueza de espécies; proporção de indivíduos e espécies pioneiras, emergentes e zoocóricas; além do tamanho das sementes e da densidade da madeira das comunidades arbóreas - atributos funcionais que também foram considerados no primeiro capítulo.

Markedly divergent tree assemblage responses to forest fragmentation across a strong seasonality gradient

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Running title: Divergent tree responses to fragmentation

ABSTRACT

We examine the effects of forest fragmentation on the structure and composition of tree assemblages within three seasonal and aseasonal forest types of southern Brazil, including evergreen, Araucaria and deciduous forests. We sampled three southernmost Atlantic Forest landscapes, including the largest continuous protected forest areas within each forest type. Tree assemblages were sampled in each forest type within 10 plots of 0.1 ha in both continuous forests and 10 adjacent forest fragments. All trees within each plot were assigned to trait categories describing their regeneration strategy, vertical stratification, seed-dispersal mode, seed size, and wood density. We detected differences between both forest types and landscape contexts in terms of overall tree species richness, and the density and species richness of different functional groups of regeneration strategy, seed dispersal mode and woody density. Overall, evergreen forest fragments exhibited the largest deviations from continuous forest plots in assemblage structure. Evergreen, Araucaria and deciduous forests diverge in the functional composition of tree floras, particularly in relation to regeneration strategy and stress tolerance. By supporting a more diversified light-demanding and stress-tolerant flora with reduced richness/abundance of shade-tolerant, old-growth species, both deciduous forest and Araucaria tree assemblages are more intrinsically resilient to contemporary human-disturbances, including fragmentation-induced edge effects, in terms of species erosion and functional shifts. We suggest that these intrinsic differences in responses to changes in landscape structure between forest types should guide conservation strategies.

1. Introduction

The widespread conversion of old-growth tropical forests into small forest fragments [1], and mounting pressure to increase food production over the next decades is expected to further replace natural habitat with farmland in perhaps 1 billion ha [2]. In fact, current and past rates of forest conversion clearly indicate that most unprotected old-growth tropical forests will be eventually phased out, leaving a complex mosaic of agricultural areas and forest fragments under varying successional stages [3], [4], challenging applied ecologists to examine organismal responses to human disturbance and the role played by anthropogenic landscapes as biodiversity repositories [5].

Overall, habitat loss and fragmentation can dramatically alter the composition and structure of tree assemblages across forest edges and edge-dominated small forest fragments [6], [7]. Changes in tree assemblage structure can be largely explained by either positive or negative abundance responses of functional groups sharing divergent life histories and morpho-ecological traits, such as seed-size, dispersal mode and regeneration strategy [7]. Recent studies have shown that, compared to core mature forest areas, edge-dominated small fragments typically exhibit reduced abundances and species richness of emergent trees [8], [7], slow-growing, heavy-wooded trees [9], large-seeded vertebrate-dispersed plants [10], [11], shade-tolerant species sensitive to desiccation [12], and those exhibiting supra-annual flowering [13]. Conversely, fast-growing pioneer or successional species are predisposed in light gaps, often proliferate at multiple spatial scales, and have been described as ‘native winners’ [14]. Ecological filtering imposed by physical edge effects, and dispersal limitation at multiple spatial scales may explain most shifts experienced by tree assemblages in human-modified landscapes [15], but plant species erosion may be aggravated by fires, logging and climate change [13], [16].

Consequently, edge-dominated landscapes are likely to (1) retain only a small, non-random subset of the original flora [6], [17], (2) experience a proliferation of native pioneers and biotic homogenization [14], and (3) move further towards successional-systems [17], [18]. Despite these emergent patterns from studies in Amazonia and Atlantic Forest [6], [13], biological responses to habitat loss and fragmentation and the conservation value of human-modified landscapes remain obscure because tropical biotas differ in their physical environment, evolutionary history, and past and contemporary exposure to both natural and human-mediated disturbances [19], [20]. In other words, tropical floras differ in their natural abundance and diversity of disturbance-adapted or stress-tolerant species and, consequently, their inherent susceptibility to contemporary human disturbances. Yet fragmentation ecology research has been spatially concentrated in the Neotropical region [20], particularly in evergreen forests (e.g. PDBFF in Central Amazonia), and susceptibility to human disturbances have been traditionally addressed at species level (see syntheses in Bierregaard [21], [22]). Despite these potential limitations, comparisons across forest domains can elucidate functional responses to human disturbance as climate change proceeds apace, forest die-off follows the aftermath of severe droughts [16], and the land-use 'agricultural bomb' approaches.

The Atlantic Forest once covered ~150 million ha, straddling across both tropical and subtropical regions of South America with a long history of highly heterogeneous baseline environmental conditions. Briefly, this unique biogeographic region consists of both seasonally-dry deciduous forests, away from the coast, and relatively aseasonal evergreen tropical rain forests subjected to more constant orographic precipitation near the coast. This once vast biome has been reduced to less than 12% of its original forest cover [23], and is currently one of the world's most imperilled biodiversity hostpots [24]. The abundance of human-modified landscapes with a long history of human-disturbances associated with a relatively well-known regional biota in terms of both taxonomy and life-history attributes provide a key opportunity to address dynamic drivers of biodiversity persistence in modified landscapes for a myriad of taxa and ecological scenarios [13], [23], [25].

Here, we examine the effects of forest fragmentation on the structure and composition of tree assemblages across the three dominant forest types of the Atlantic Forest region of southern Brazil: evergreen, Araucaria and deciduous forest. Assemblage attributes, such as species richness, species composition and functional groupings – within classes of regeneration strategy, forest stratification, seed-dispersal mode and seed size – are compared between both habitat context (continuous forest vs. forest fragments) and forest types. We expected tangible differences between bioclimatic forest types in the abundance of functional groups affected by forest fragmentation, particularly due to baseline floristic differences in the abundance/diversity of stress-tolerant species as indicated in the description of these forest types [26]–[29]. Finally, we examine the theoretical and practical implications of our findings.

2. Methods

2.1. Study design

Our study encompassed three landscapes distributed across the three main southern Brazilian Atlantic Forest domains: evergreen, Araucaria and deciduous forests (Fig. 1). These forest types are referred to as Ombrophilous Dense Forest, Ombrophilous Mixed Forest, and Deciduous Forest, respectively, according to the Brazilian vegetation classification [30]. Deciduous trees account for fewer than 25% of all canopy species in evergreen forests but over half of the tree flora in deciduous forests [30]. In our study design, these three forest types span a wide seasonality gradient in terms of temperature and rainfall distribution, but mean total annual rainfall in all study areas is similar (1,500 – 2,000 mm yr^{-1}).

In each forest type we selected one landscape containing one large patch of strictly protected old-growth forest used as a 'control' in addition to 10 small forest patches (1.5 to 85 ha in size), which were located within 20 km from the perimeter of each control area. Landscape pre-selection was based on an extensive analysis of satellite imagery, field surveys and the information provided by a digital map of Brazilian vegetation types [31]. Our study landscapes, which ranged from 176 to 486 km^2 in size, spanned a geographic polygon of 82,800 km^2. We next describe each landscape briefly.

Evergreen forest: the Serra do Tabuleiro State Park (STSP: 87,405 ha) served as a control since it is the largest protected area in this region and consists primarily of old-growth forest patches. The regional climate is humid mesothermal, with a hot summer and well distributed rainfall throughout the year (Cfa in Köppen-Geiser's classification [32]. Elevations ranged from 220 to 490 m asl, mean rainfall was ~1500 mm/yr, and mean annual temperature is ~20ºC [33]. The non-forest matrix outside forest patches is dominated by pasture and cropland.

Araucaria forest: The Mata Preta Ecological Station (MPES: 6,563 ha) served as a control area as it is the last large remnant of Araucaria Forest in southern Brazil. Araucaria or candelabra tree are vernacular names of this iconic southern Brazilian conifer (*Araucaria angustifolia*, Araucariaceae), which forms the emergent stratum (up to 40 m) of this forest type, whereas canopy and understory plants typically consist of broadleaved Atlantic Forest species [34]. The regional climate is also moist subtropical with hot summers (Cfa in Köppen's classification [32], with a mean annual temperature of ~18.7ºC, a mean rainfall of ~2,002 mm/yr, and regular frosts between June and August [35]. Cattle pastures and cropland dominate the landscape matrix which was once a vast continuous area of Araucaria forest.

Deciduous forest: The Turvo State Park (TSP: 17,491 ha), located in the north-western state of Rio Grande do Sul, served as a control. All Atlantic Forest patches in this region are classified as deciduous forests [30]. TSP is the largest remaining contiguous old-growth tract of deciduous forest in southern Brazil [36]. The regional climate is subtropical sub-humid with relatively dry summers, with a mean rainfall of ~1,900 mm, and a marked hydrological deficit from late spring to early summer [37]. Frosts regularly occur between June and August and the mean annual temperature is 18-20°C [38]. Forest fragments sampled were embedded within the area surrounding the park, which had been largely converted into an intensively farmed landscape dominated by soybean and maize agriculture without any buffer zone protection.

Although these three landscapes have different histories of human disturbance, we only selected small forest fragments if they clearly lacked any evidence of human disturbance (e.g. wildfires, timber extraction, and cattle intrusion). Due to the landscape configuration available to us, our study design is limited to only a single forest landscape (i.e. no landscape replicates) per forest type. The Araucaria forest originally covered ~42.5% of the State of Santa Catarina, but this forest type has been reduced to only 1-4% of its original tracts since the expansion of modern agriculture [39]. The deciduous forest has experienced a similar land-use trajectory and the TSP is the only available regional-scale area of old-growth forest [36]. Despite these limitations, (1) the landscapes assessed here provide the last opportunity for a comparative analysis of the ecological biogeography of southern Brazilian forests, and (2) regional tree floras are well-documented taxonomically and ecologically (i.e. Flora Ilustrada Catarinense).

2.2. Tree assemblages

Tree assemblages were sampled across the three landscapes using 0.1 ha (10m x 100m) plots including 10 plots within each control area of core forest and one plot in each forest fragment, amounting to 60 plots (or 6 hectares) sampled. These relatively small plots have been widely adopted across the Atlantic Forest to detect fragmentation-related effects (Santos [7], [13]. Core forest plots were located at least 250 m from the nearest forest edge and with no detectable influence of forest borders as following: (1) the 10 plots sampled at STSP were randomly placed at least 250 m from the reserve boundaries; (2) the 10 plots sampled at MPES were sited perpendicularly to, and at least 250 m from an unpaved road within the park; and (3) the 10 plots sampled at TSP were sited perpendicularly to, and at least 250 m from the two unpaved roads linking the two park entrances with the Uruguay River. Our definition of core forest areas follows Laurance et al. [40] who showed that edge effects rarely penetrate 200 m from the nearest forest edge. One 0.1-ha plot was located at the geometric centre of each forest fragment as previously implemented elsewhere [7]. All plots were georeferenced using a handheld GPS. All trees ≥10 cm DBH were measured and identified in situ and voucher specimens of any ambiguous stems were collected, compared with vouchers deposited at the Federal University of Rio Grande do Sul (UFRGS) ICN Herbarium in Porto Alegre, and all vouchers without unambiguous identification were sent to family specialists. Four highly credible plant taxonomists - Marcos Sobral, Martin Grings, Márcio Verdi and Martin Molz - assisted in the species identification process.

2.3. Tree species attributes

All individuals were assigned to mutually exclusive categories of functional groups describing their seed size, vertical stratification, seed-dispersal mode, regeneration strategy, and wood density based on a comprehensive literature compilation, including books, papers, monographs of the regional flora and MSc and PhD dissertations [41], several volumes of the Flora Ilustrada Catarinense and Flora Fanerogâmica do Estado de São Paulo). These sources were supplemented by our own combined lifetime personal knowledge on the life-history traits of southern Brazilian tree species and online sources (e.g. Global Wood Density database [42]).

Functional groups of tree species were classified according to criteria adopted elsewhere in the Atlantic Forest [7], [43]–[45], as following: (a) Regeneration strategy – *Pioneer species* were defined as species requiring high light environments as viable regenerating sites such as forest edges and treefall gaps. This group included both large and long-lived pioneer species, in addition to short-lived pioneers (*sensu* Whitmore [46], and is equivalent to 'successional species' [6], [47]). *Shade-tolerant species* are those capable of regenerating in shaded environments, such as the shaded understory of old-growth forests . Juveniles of these species may survive in shade for several years ; (b) Forest stratification – *Understory species* comprised small trees flowering and fruiting in the lowest forest layer (<11 m); *Canopy species* occurred in the forest subcanopy and canopy; and *Emergent species* occurred in the highest forest layer [48]. Seed-dispersal mode – *Vertebrate-dispersed species* are those bearing diaspores attached to a fleshy pulp, aril, or other features typically associated with vertebrate seed dispersal vectors; and *Abiotically-dispersed species* are those producing winged seeds, plumes, other wind-dispersal devices that slow the rate of seed fall, those dispersed entirely by free fall, or seeds propelled explosively from the fruit [49]; *Seed size of vertebrate-dispersed species* – seeds were grouped according to a logarithmic scale of seed size, considering its longest dimension: < 1mm; 1-5mm; 5-10mm; 10-20mm; ≥ 20mm, scored from 1 to 5, respectively. *Wood specific gravity* (WSG) or wood density – recorded according to Chave [50] and by consulting the species-specific regional-scale literature (e.g. Lorenzi [51]).

Tree assemblages within each plot were thus characterized in terms of the following attributes: (1) stem density; (2) tree species richness; and the percentage of (3) pioneer species; (4) pioneer stems; (5) emergent species; (6) canopy species; (7) understorey species; (8) vertebrate-dispersed species; and (9) mean size of vertebrate-dispersed seeds.

2.4. Patch and landscape metrics

We used three spatial metrics as explanatory variables for changes in tree assemblage attributes: (i) forest patch area, the total forest area within each fragment or continuous forest; (ii) patch connectivity, expressed as the total amount of surrounding forest cover within a 1-km external matrix buffer from each patch; and (iii) distance to continuous forest, the straight-line distance from each fragment to the continuous forest within the large protected areas. These metrics were measured using ArcGis 9.2 and ERDAS Imagine 8, following a supervised classification of a set of Landsat 5TM (2002) satellites images, and a mosaic of 45 supplementary images dating from 2007 to 2013, available from Google Earth 7. Elevation for each plot was calculated based on high-resolution digital topographic maps and the digital elevation surface available from the Shuttle Radar Topography Mission (SRTM). Soil types for each site were obtained according to the Brazilian soil classification system [52].

2.5. Data analysis

Differences in tree assemblage attributes were examined within each habitat context (continuous forests vs. fragments) and across the three forest types as following: One-way ANOVAs followed by Tukey post-hoc comparisons for differences in stem density, species richness and functional species composition. Differences in stem density and species richness within seed size classes were examined using contingency tables (G-test). Generalized linear models (GLMs) were used to detect the effects of explanatory variables on tree assemblage attributes considering all 60 plots. The following explanatory variables were considered: forest patch size, patch connectivity, distance to the nearest continuous forest, elevation, habitat context, and soil type. We excluded from final models any explanatory variables exhibiting high collinearity ($r^2 \geq 0.7$) and/or variables that were not significant in explaining any of the functional abundance responses.

We performed non-metric multidimensional scaling (NMDS) ordinations of the 20 plots in each forest landscape using the Bray-Curtis (BC) dissimilarity matrix of taxonomic species abundance [53]. We allowed the ordination to be rotated and centered, using the function *metaMDS* of the *vegan* package in R v. 2.15 [54] to perform the NMDS. The percentage of pioneer stems within each plot was regressed against the first axis of the NMDS ordinations to detect the influence of pioneer species on multivariate patterns of species composition and abundance within each landscape (i.e. control and forest fragments). To test the hypothesis that plots placed within either control forests or forest fragments were taxonomically more similar to one another across the tree landscapes/forest types, we constructed a BC similarity matrix of species composition across all plots, and calculated the average (± SE) pairwise BC values for three groups of comparisons: (1) between plots in forest fragments within any given landscape ($N = 45$); (2) between plots within the continuous of each landscape ($N = 45$); and (3) between any continuous forest plots and any forest fragment plots ($N = 100$). We compared differences in BC dissimilarities between the groups using permutational multivariate analysis of variance (PERMANOVA), using PAST v. 2.11 [55], with 9,999 permutations and Bonferroni-corrected p-values. We performed an indicator species analyses (sensu Dufrêne and Legendre [56]) based on six sets of plots: control forest and fragment plots across the three landscapes. Finally, we ran Mantel tests, through randomization tests (using the *rtest* function of the *ade4* package in R) to address potential effects of plot spatial location on their taxonomic similarity.

3. Results

A total of 3,972 trees belonging to 270 species and 72 families were recorded across all 60 plots. Evergreen forest plots exhibited the highest species richness (165), followed by deciduous forest (105) and Araucaria forest (87). Overall, continuous control plots in evergreen forest supported the most species-rich tree assemblages, but contained lower proportions of pioneers, both in terms of species and individuals, compared to either Araucaria or deciduous forest plots (Table 1). There were also differences in the abundance and diversity of other functional groups between forest types (Table 1). In particular, tree assemblages exhibited different responses to forest fragmentation across the three forest types (Table 1). There were marked differences between small fragments and continuous forest plots in all forest types in terms of stem density, tree species richness, the prevalence of pioneer species and individuals, and stem wood density. However, these shifts in assemblage structure were more evident and almost entirely restricted to evergreen forests, in which mean species richness in fragments was one-third lower and pioneer stems were six-fold more abundant (from 5.5% to nearly 30% of all stems) compared to continuous forest plots at STSP. Other attributes, such as the abundance of vertebrate-dispersed, large-seeded, and emergent trees, exhibited no detectable differences between fragments and continuous forests regardless of vegetation type, although evergreen forest fragments contained a higher proportion of stems bearing seeds >10 mm in length (Fig. 6, $G = 59.55$, $df = 4$, $p > 0.001$). Finally, GLM models explained between 16% and 62% of the variation in tree assemblage attributes, which were affected by both forest type and forest patch area (Table 2). Again, stem density and species richness of taxa defined as pioneers exhibited marked responses to forest patch size, particularly in evergreen forest plots. Although overall tree species richness was higher in increasingly larger forest patches (Fig. 2a), pioneer species declined regardless of the vegetation type (Fig. 2b-c). Finally, the amount of forest cover in the surrounding matrix had a significantly negative effect on the stem density and diversity of pioneers.

In terms of floristic composition considering both continuous forests and fragments, the three forest types exhibited marked baseline differences as the Myrtaceae, Lauraceae and Rubiaceae were more prevalent in evergreen forest (36% of all species), whereas Fabaceae, Myrtaceae, Rutaceae and Euphorbiaceae dominated deciduous forests (40% of all species), and Myrtaceae, Fabaceae and Lauraceae dominated Araucaria forests (29% of all species) (see supplementary material, Table S1). Although the three forest types were only a few hundred kilometers apart (at most ~520 km), they shared only 4% of all species (12); evergreen and deciduous forests shared 24 species (10%), Araucaria and deciduous forests shared 45 species (31%), and Araucaria and evergreen forests shared 30 species (14%). Within-habitat species similarity was relatively low and never exceeded 40%. Furthermore, pairwise comparisons between continuous forest and fragment plots exhibited very low levels of species similarity, ranging from 3.57 to 9.26% across the three forest types (Fig. 3). All pairwise comparisons in species similary between core forest and fragments plots exhibited significant differences (PERMANOVA, $F = 8.918$, $p \leq 0.05$), with similarity scores between plots in continuous forest and fragments 30% lower than those within each habitat context. Mantel tests failed to uncover any large-scale spatial effect on the taxonomic similarity for 5 of the 6 groups of plots examined here. The proportion of species in each landscape that occurred in continuous forest plots but were missing in small fragments varied from 40% in evergreen forest to 18% in deciduous forest, which exhibited the highest levels of species similarity between plots in continuous forest and fragments ($F=20.33$, $p < 0.0001$).

Differences in floristic responses to forest fragmentation across the three forest domains were confirmed by the NMDS ordination of tree assemblages. In short, two clusters of forest plots emerged separating the large control areas and small forest fragments. However, the spatial segregation of these clusters was much less marked in deciduous forest than in less seasonal forest types (Fig. 4). These ordinations were supported by low stress levels ranging from 0.15 to 0.22. Linear regression models between the first NMDS axis describing community structure and the percentage of pioneer species occurring in each plot suggested that compositional changes across landscape contexts in evergreen and Araucaria forests are largely related to pioneer abundance ($R^2 = 0.63\text{-}0.7$; *p* values < 0.001; Fig. 5), but no such relationship was found in the seasonally-dry deciduous forest ($R^2 = 0.012$; $p = 0.650$). Indicator species analyses within forest types underscored the occurrence of 56 species, 24 of which in core evergreen forest. Small sets of indicator species emerged for evergreen forest fragments (8 species), Araucaria core forest (5) and forest fragments (9), and core deciduous forest (5) and fragments (5 species; Table S2), with a strong tendency for replacement of shade-tolerant species by pioneers from core forest areas to small forest fragments across all three forest types. Note that only one pioneer species (a long-lived emergent) was identified as an indicator species across continuous forest plots, whereas 15 were detected in fragments. Conversely, 33 shade-tolerant species could be defined as indicators of core continuous forest plots, whereas only 7 species emerged as indicators of forest fragments.

4. Discussion

In the context of tree assemblages in tropical forests, only the most aseasonal sites studied here (evergreen forests) clearly support the notion that forest fragmentation (1) reduces the species richness, (2) induces the proliferation of some pioneer or successional species, (3) changes the stem abundance and species richness of different functional groups, and (4) drastically alters the taxonomic composition of tree assemblages, resulting in the emergence of a new set of indicator species [9], [40], [57], [58]. These taxonomic and functional shifts are usually correlated with both patch and landscape metrics [59], suggesting that community-wide shifts result from fragmentation-related processes, particularly responses to edge effects, rather than baseline differences, such as soil types, between core and edge-affected forest habitats [7], [12], [60]. However, we documented marked differences between forest types in both the magnitude (number of attributes exhibiting shifts) and intensity (ecological deviation) of tree-assemblage responses to habitat fragmentation. As expected, these responses were consistent with a climatic gradient from relatively aseasonal to a markedly seasonal climate, and far more evident in evergreen forest than in either deciduous or Araucaria forest. A much larger proportion of species were shared between fragments and continuous forest in seasonal deciduous forest (Fig. 3 and 4) compared to the two relatively aseasonal forest types. We particularly note the three-fold increase in the relative species richness of pioneers in evergreen forest fragments. Unfortunately, we were unable to replicate our sampling program across landscapes within each forest type due to the very low availability of remaining continuous forest patches in southern Brazil that could serve as control forests. Abundance and compositional shifts in small forest remnants could therefore be potentially attributed to baseline differences associated, for instance, with soil type, landscape structure and historical land use [59]. However, these forest types are likely to be inherently different in their respective degrees of sensitivity to habitat fragmentation due to ecological and biogeographic differences in their baseline flora. As such while other neotropical studies have shown that tree assemblages in small evergreen forest fragments gradually lose old-growth tree species, become dominated by a small set of pioneer species, and are poorly represented in terms of tree functional groups typical of large tracts of primary forest, [6], [7], [40], [43], this is the first study using a standardized sampling design to provide evidence that seasonal and aseasonal forests have divergent responses to landscape change in terms of the functional and taxonomic shifts in the tree flora.

Tree species in southern Brazilian Araucaria and deciduous forests exhibit a higher proportion of light-demanding species as recorded in our study landscapes (51% and 49% of all species, respectively) compared to only 21% in evergreen forest. We differentiate two light-demanding regeneration guilds. The first typically consists of fast-growing, short- and long-lived pioneer species (sensu Whitmore [46]) or successional species with natural dynamics associated with treefall gaps in old-growth forest, but that can recruit in edge habitats [6]. Species within this group allocate higher investments to reproduction and population growth by inhabiting resource-unlimited habitats, compared to long-lived but shade-tolerant species that recruit in the forest understory. Such light-demanding forest species (including the genera *Albizia, Alchornea, Ceiba, and Cedrela*) take advantage of well illuminated understory underneath a more deciduous canopy in addition to the naturally discontinuous forest canopy in deciduous forest [61], and may benefit from elevated light and drier conditions in edge-affected habitats in forest fragments [58].

The second light-demanding tree strategy in Aracauria and deciduous forests includes species that can invade open-habitats such as southern grasslands (i.e. *campos sulinos*) and maintain viable populations in small forest patches and gallery forests, such as the natural "forest islands" of many semi-natural forest-grassland mosaics of southern Brazil [62], [63]. In these natural mosaics and ecotones, tree species are exposed to intense light exposure, extreme temperatures (including frosts), and water stress associated with droughts and shallow soils [27]. This light-demanding but stress-tolerant nucleating generalist flora exhibits high colonization ability [27], [64]. This guild is mainly represented by *Araucaria angustifolia* and its affiliated species, some of which have biogeographic analogues in Austral-Antarctic and Andean floras [34], [65], and are related to other species shared with deciduous/semi-deciduous patches of Atlantic forest [63]. These are represented by several species of *Sebastiana,* (Euphorbiaceae), *Solanum* (Solanaceae), *Parapiptadenia* (Leguminosae), and *Zanthoxylum* (Rutaceae), (see Table S1 in supplementary material; [64]).

Placing these life-history strategies into a conservation context, these light-demanding species operate as key drivers of forest expansion in southern Brazil [64]. These species may be defined as disturbance-adapted, by either lacking significant demographic responses or responding positively to habitat fragmentation as they have long been exposed to a wide amplitude in abiotic conditions that are comparable to those induced by edge creation in human-modified landscapes. Accordingly, the Araucaria and deciduous forest did not exhibit any increment in pioneer species richness or abundance in forest fragments despite modest shifts in taxonomic composition. In fact, it has long been proposed that light-demanding plant strategies (1) are more tolerant to stress caused by light exposure, water shortage and climatic extremes [66], [67], and (2) are expected to be poorly diversified and less abundant in evergreen forests, where shade-tolerance prevails due to predominantly humid and shaded conditions in old-growth forest [68]. Moreover, plant species in seasonally-dry forests should be inherently more tolerant to desiccation than those in evergreen forests [69], [70].

In synthesis, the evergreen, Araucaria and deciduous forests of the southern Atlantic Forest biome diverge in the ecological profile of their tree floras, particularly in terms of regeneration strategy and tolerance to microclimatic stress. By supporting a naturally more diversified light-demanding and stress-tolerant flora with reduced richness and abundance of shade-tolerant, old-growth species, both deciduous and Araucaria forests are expected to be more resilient to contemporary human disturbances, in terms of species erosion and functional shifts. In other words, these forest types are intrinsically predisposed to the emergence of human-modified landscapes due to an elevated number of disturbance-adapted species at multiple spatial scales, leading to some theoretical implications. Differences in sensitivity to habitat loss and fragmentation partly result from differences in the relative contribution of disturbance-adapted species to the baseline flora. In the case of tropical tree species, sensitivity to habitat fragmentation and associated disturbances involves life-history traits related to adult stature [40], sexual system and reproductive phenology, pollination and seed dispersal strategies [13], [47]. Additional life-history strategies may include physiological performance during environmental stress due to either resource limitation or climatic extremes. From an ecological perspective, seasonally-dry and transitional forests are expected to support a higher proportion of stress-tolerant species — that therefore confers them more resilience to forest fragmentation — than core old-growth evergreen forests and their extraordinary diversity of shade-tolerant species.

If corroborated by future studies elsewhere, our results have direct implications to the best conservation strategies whereby efforts employed in each forest domain should be guided by the evolutionary history of the tree flora. In relatively aseasonal forests, the preservation of large tracts of forest is crucial to retain most of the species diversity. This is consistent with several studies showing that small, edge-dominated forest patches are at best ill-suited to retain the bulk of the species diversity associated with moist, shaded environments of core, closed-canopy forests [15], [40], [43]. Conversely, setting-aside a large number of forest fragments (in addition to the large reserves), of varying sizes can be considered a valid conservation strategy in seasonal forests [71], [72]. Large continuous seasonal forest stands (>3,000 ha) are no longer available outside protected areas of southern Brazil, where >95% of the forest cover has been converted to agriculture and what remains is heavily degraded [73]. This is consistent with all seasonal tropical forests which currently retain only 2% of their original extent, are heavily fragmented [74], and are the most threatened forest type anywhere [75], because of their high agricultural value due to high soil fertility and gentle slopes [76], [77]. Given this sorry state of affairs, we therefore end on a high note in extolling the conservation value of even small seasonally-dry forest fragments in retaining the biodiversity of the southern Atlantic forest biome.

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TABLES AND FIGURES

Table 1 – Tree assemblages attributes (mean ± SD) in 0.1-ha plots located in forest fragments and core old-growth forest in southern Brazil.

Assemblage attributes	FOD continuous (n = 10)	FOD fragments (n = 10)	FOM continuos (n = 10)	FOM fragments (n = 10)	FED continuous (n = 10)	FED fragments (n = 10)
Stem density (per 0.1 ha)	93.3 ± 13.9 ^{a}	74.5 ± 13.0 ^{b}	65.8 ± 25.5 ^{b,c}	65.0 ± 9.6 ^{b,c}	46.3 ± 7.6 ^{d}	52.3 ± 9.3 ^{c,d}
Total species richness	39.8 ± 5.2 ^{a}	27.4 ± 3.7 ^{b}	18.5 ± 5.1 ^{c}	21.3 ± 3.0 ^{c,d}	24.5 ± 3.7 ^{b,d}	24.8 ± 4.3 ^{b,d}
Pioneer species (%)	9.1 ± 5.2 ^{a}	25.9 ± 12.2 ^{b}	41.2 ± 12.3 ^{c}	57.0 ± 8.4 ^{d}	32.2 ± 12.0 ^{b,c}	35.0 ± 6.6 ^{b,c}
Pioneer stems (%)	5.5 ± 5.1 ^{a}	29.4 ± 20.7 ^{b}	29.3 ± 16.2 ^{b}	60.0 ± 13.3 ^{c}	25. 9 ± 12.4 ^{b}	35.5 ± 11.3 ^{b}
Emergent species (%)	5.5 ± 1.4 ^{a}	7.2 ± 3.7 ^{a,b}	8.4 ± 4.2 ^{a,b}	8.7 ± 3.0 ^{a,b}	9.0 ± 4.8 ^{a,b}	12.0 ± 6.6 ^{b}
Canopy species (%)	62.8 ± 8.0	64.7 ± 8.1	61.8 ± 7.1	61.4 ± 10.7	62.9 ± 3.7	62.1 ± 10.3
Understorey species (%)	31.8 ± 7.3	28.1 ± 8.6	29.8 ± 7.4	29.9 ± 11.3	28.1 ± 4.4	25.8 ± 11.0
Vertebrate-dispersed species (%)	83.4 ± 4.5 ^{a}	84.2 ± 3.3 ^{a}	75.0 ± 6.8 ^{a,b}	71.0 ± 9.0 ^{b,c}	61.9 ± 9.5 ^{c}	63.3 ± 13.3 ^{c}
Vertebrate-dispersed seed size	3.34 ± 0.21 ^{a,b}	2.95 ± 0.25 ^{a}	3.17 ± 0.28 ^{a,b}	3.29 ± 0.36 ^{a,b}	3.47 ± 0.38 ^{b}	3.38 ± 0.35 ^{b}
Mean wood density (g/cm³)	0.70 ± 0.026 ^{a}	0.63 ± 0.030 ^{b}	0.62 ± 0.021 ^{b}	0.67 ± 0.054 ^{a,b}	0.67 ± 0.049 ^{a,b}	0.66 ± 0.066 ^{a,b}

Significant differences in post hoc comparisons (Tukey tests) between habitat types are indicated by different letters in a same row. Values in bold denote sig

Table 2 – Generalized linear model results explaining seven assemblage-wide tree species attributes across 60 plots sampled within three forest types of southern Brazil. E = Evergreen; A = Araucaria; S = Seasonal.

Assemblage attributes	Explanatory variables	Estimate (± SE)	z value	p-Value	R^2 whole model
Stem density (per 0.1 ha)	Vegetation type (E - A)	-0.310 (± 0.048)	-6.387	**< 0.0001**	0.529
	Vegetation type (E - S)	-0.600 (± 0.050)	-11.946	**< 0.0001**	
	Fragment area (log$_{10}$ ha)	0.010 (± 0.010)	1.009	0.313	
	Surrounding forest cover	-0.348 (± 0.126)	-2.765	**0.006**	
Species richness	Vegetation type (E - A)	-0.594 (± 0.079)	-7.474	**< 0.0001**	0.609
	Vegetation type (E - S)	-0.370 (± 0.075)	-4.955	**< 0.0001**	
	Fragment area (log$_{10}$ ha)	0.020 (± 0.016)	1.262	0.207	
	Surrounding forest cover	-0.464 (± 0.195)	-2.372	**0.017**	
Pioneer stems (%)	Vegetation type (E - A)	1.247 (± 0.102)	12.171	**< 0.0001**	0.620
	Vegetation type (E - S)	0.951 (± 0.114)	8.368	**< 0.0001**	
	Fragment area (log$_{10}$ ha)	-0.156 (± 0.021)	-7.405	**< 0.0001**	
	Surrounding forest cover	1.397 (± 0.243)	5.755	**< 0.0001**	
Vertebrate-dispersed species (%)	Vegetation type (E - A)	-0.158 (± 0.093)	-1.694	0.090	0.555
	Vegetation type (E - S)	-0.339 (± 0.090)	-3.784	**0.0001**	
	Fragment area (log$_{10}$ ha)	0.001 (± 0.189)	0.04	0.968	
	Surrounding forest cover	-0.146 (± 0.231)	-0.631	0.528	
Emergent stems (%)	Vegetation type (E - A)	0.468 (± 0.180)	2.603	**0.009**	0.178
	Vegetation type (E - S)	0.482 (± 0.187)	2.573	**0.010**	
	Fragment area (log$_{10}$ ha)	-0.057 (± 0.036)	-1.58	0.114	
	Surrounding forest cover	-0.505 (± 0.454)	-1.114	0.265	
Vertebrate-dispersed seed size	Vegetation type (E - A)	0.132 (± 0.130)	1.015	0.314	0.167
	Vegetation type (E - S)	0.302 (± 0.128)	2.357	**0.022**	
	Fragment area (log$_{10}$ ha)	0.045 (± 0.026)	1.727	0.090	
	Surrounding forest cover	-0.002 (± 0.325)	-0.006	0.995	
Mean wood density (g/cm^2)	Vegetation type (E - A)	-0.009 (± 0.042)	-0.437	0.664	0.068
	Vegetation type (E - S)	0.008 (± 0.020)	0.393	0.696	
	Fragment area (log$_{10}$ ha)	0.006 (± 0.004)	1.472	0.147	
	Surrounding forest cover	0.0165 (± 0.050)	0.328	0.744	

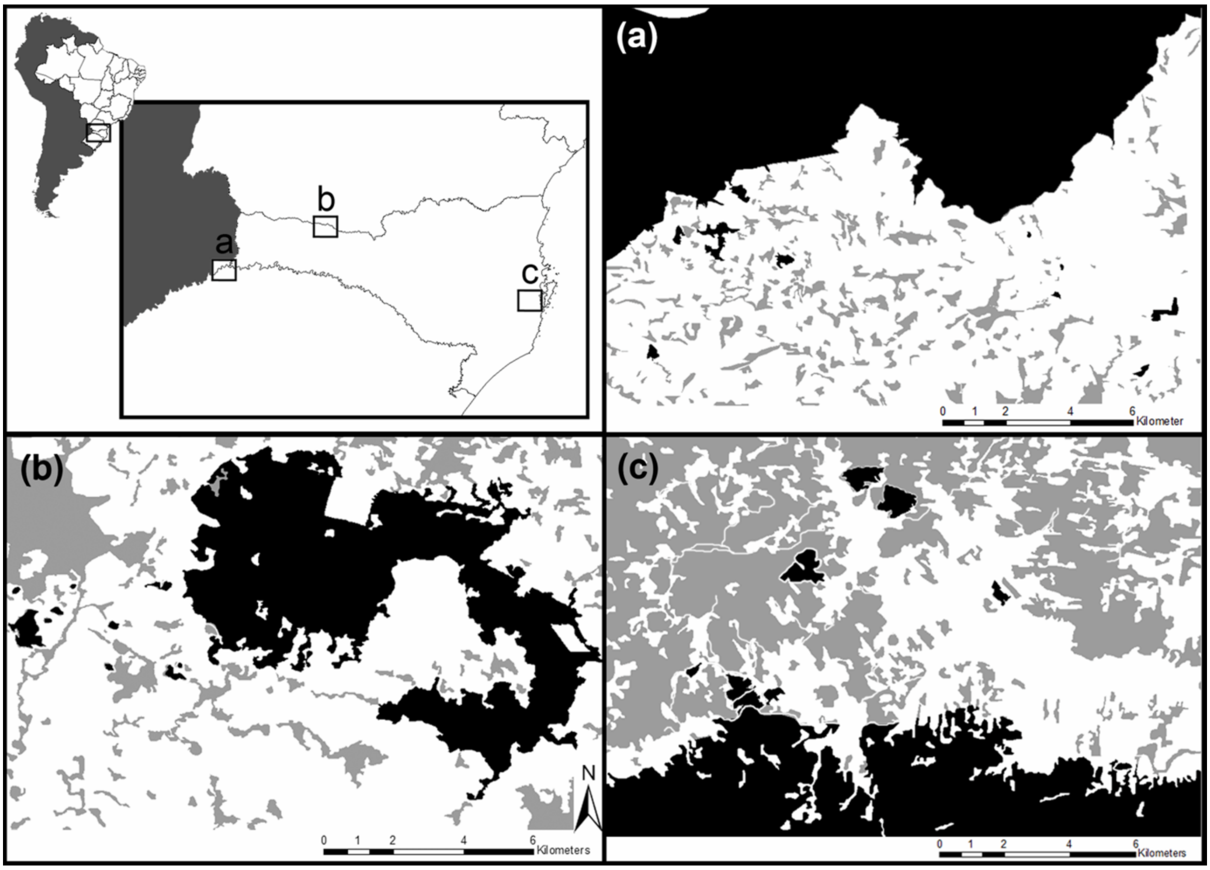
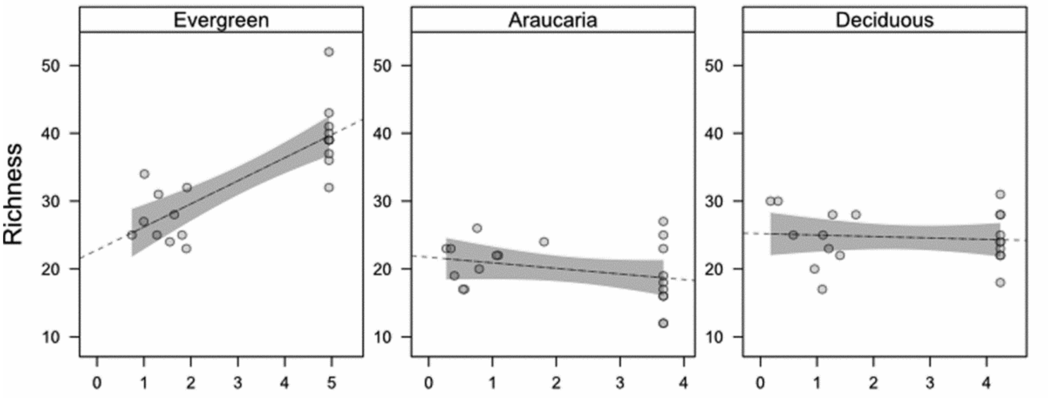
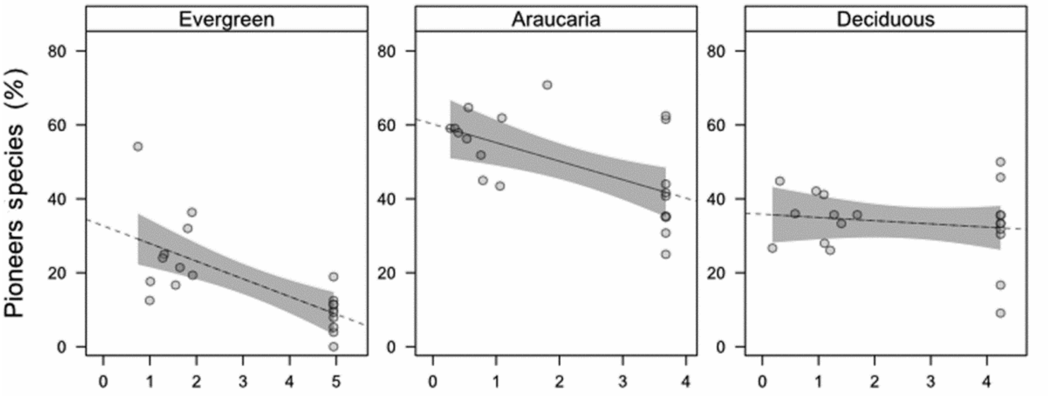


Figure 1. **Landscapes observed in three different forest types in the Atlantic Forest domain of southern Brazil.** Location of the three landscapes examined across three different forest types in the Atlantic Forest domain of southern Brazil. Large black polygons represent the three protected areas used as control forests; small black polygons indicate the 10 forest fragments sampled in each landscape. Grey areas refer to other forest fragments in the region. (a) Seasonal Deciduous Forest, including the Turvo State Park; (b) Araucaria Mixed Forests, including the Mata Preta Ecological Station; and (c) Moist/Ombrophilous Dense Forest, including the Serra do Tabuleiro State Park.

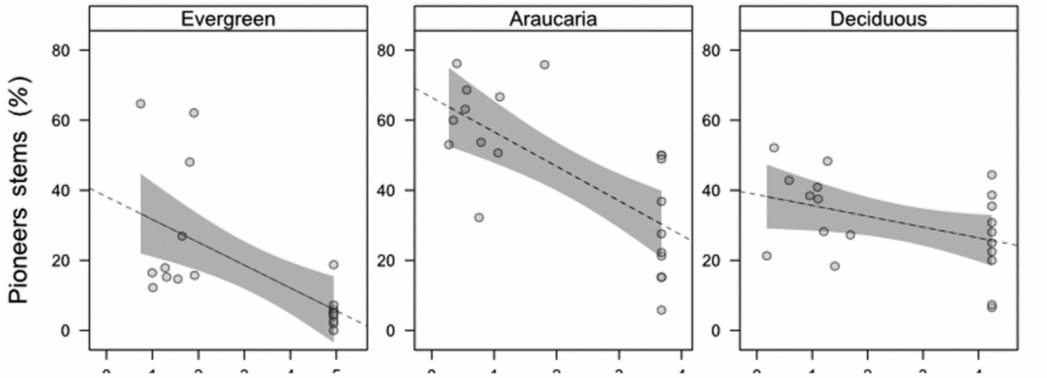
(a) Species richness



(b) Percentage of pioneers species (%)



(c) Percentage of pioneers stems



(d) Mean wood density (g/cm²)

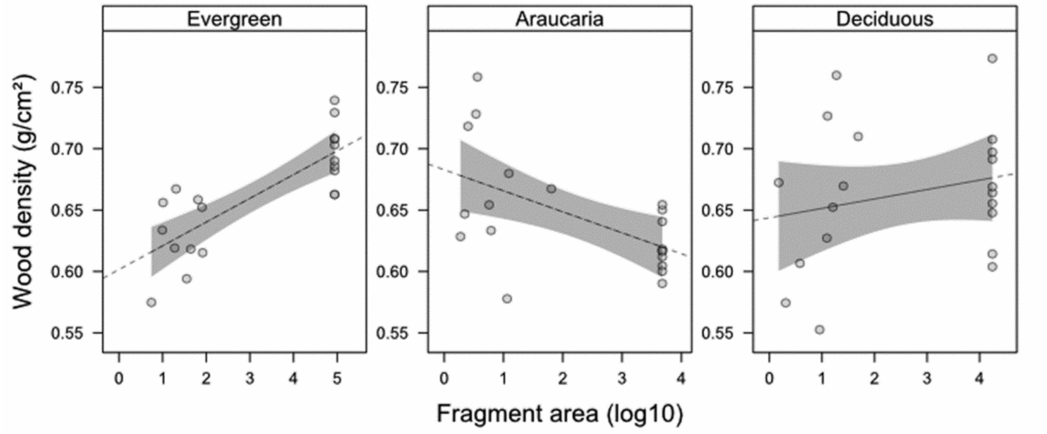


Figure 2. **Relationships between patch area and tree species attributes.** Relationships between $\log_{10}$ patch area (m^2) and (a) tree species richness, (b) percentage of pioneer tree species, (c) percentage of pioneer stems, and (d) mean wood density (g/cm^2) across three forest types of southern Brazil. Data points represent the 0.1-ha plots sampled in small forest fragments and core areas of continuous old-growth forest.

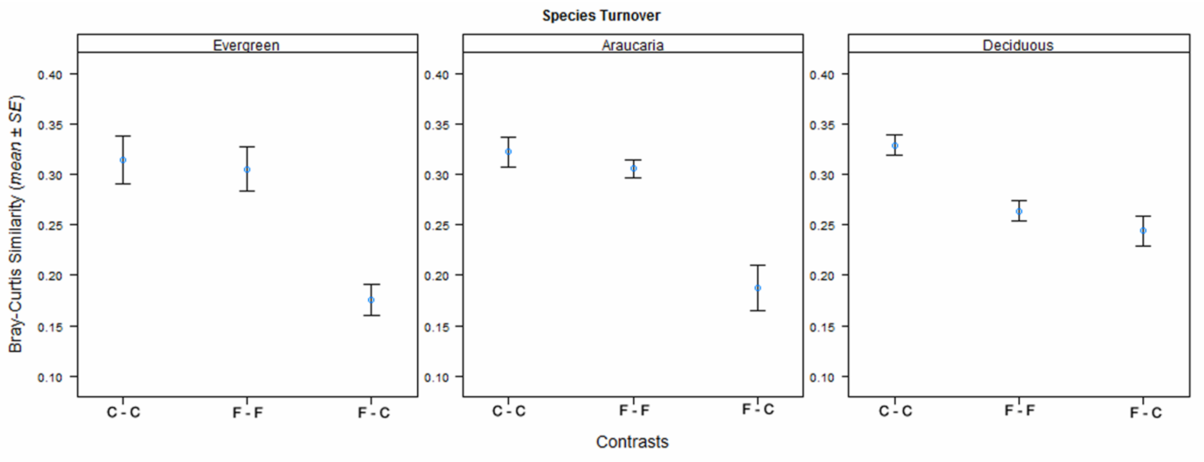


Figure 3. **Bray-Curtis similarity values between landscape contexts across three forest types.** Bray-Curtis similarity values (mean ± SE) in species composition using abundance data both within and between landscape contexts across three forest types of southern Brazil: between core forest plots (C-C); between forest fragment plots (F-F); and between forest fragment and core forest plots (F-C).

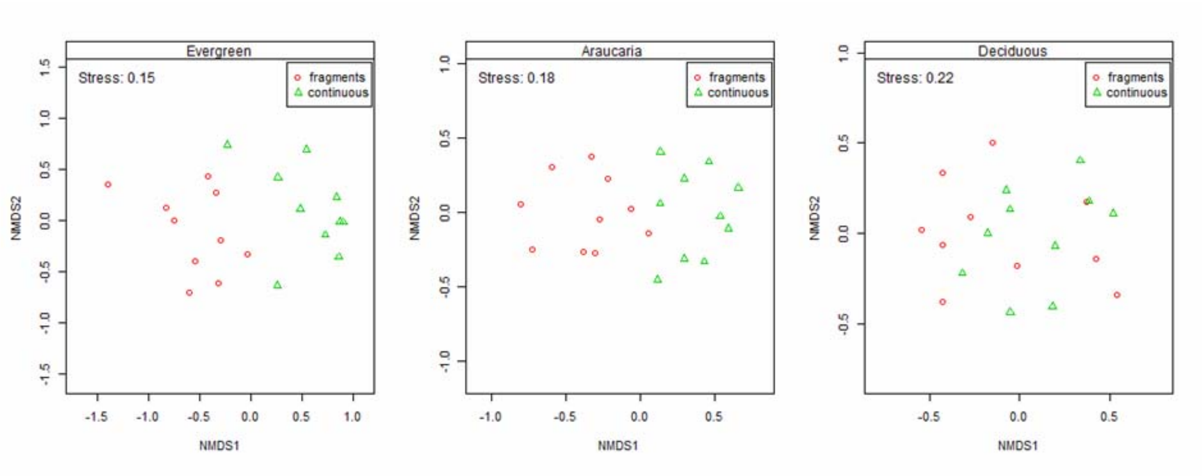


Figure 4. **NMDS ordination of forest fragments and continuous old-growth core plots.** Non-metric multidimensional scaling (NMDS) ordination of sixty 0.1-ha plots located within forest fragments and core areas of continuous old-growth forest in three forest types in southern Brazil.

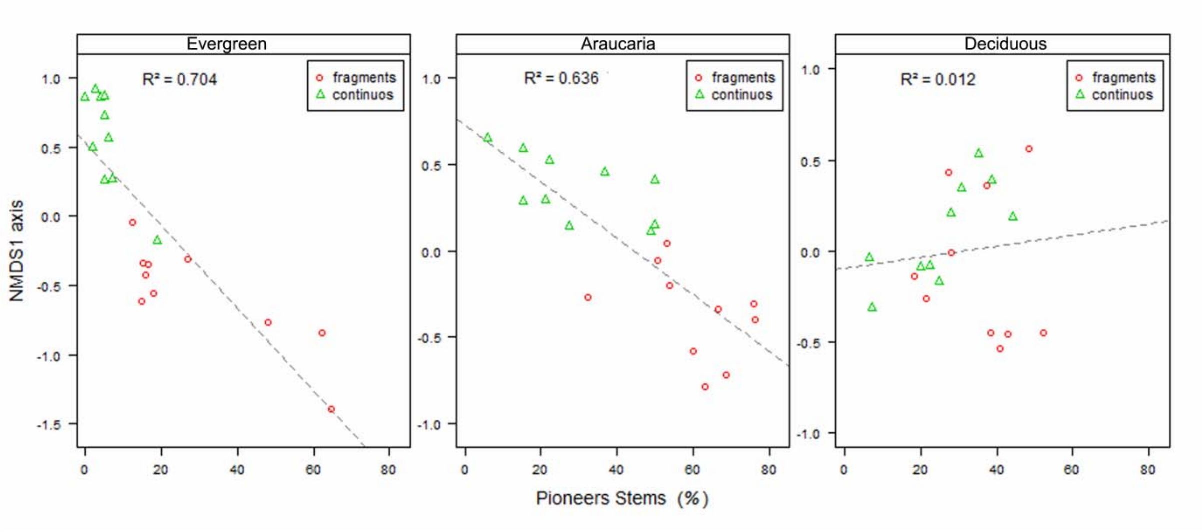


Figure 5. **Relationship between the first axis of the NMDS and the percentage of pioneer stems.** Relationship between the first NMDS ordination axis (see Fig. 4) and the percentage of pioneer stems in 0.1-ha plots within forest fragments (red circles) and continuous forests (green triangles) in each of the three forest types. R^2 values refer to linear regression models.

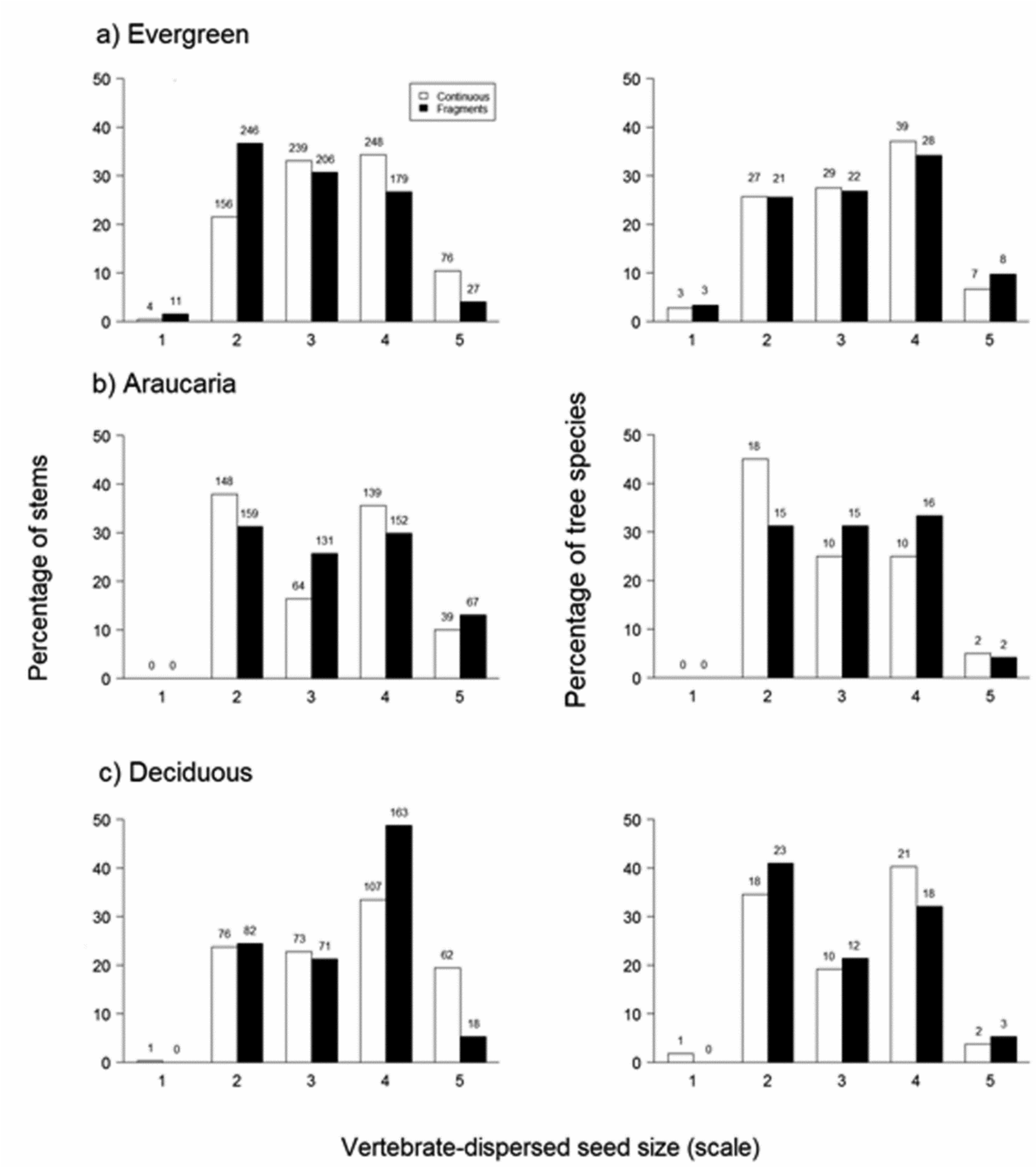


Figure 6. **Percentage of stems and species concerning seed size classes in the three forest types**. Average percentage of stems and species in each category of vertebrate-dispersed seeds of different size classes in forest fragments (solid bars) and core areas of continuous old-growth forest (open bars) in three forest types of southern Brazil. Numbers above each bar refer to the number of stems (left bars) and species (right bars).

SUPPLEMENTARY MATERIAL

Table S1. Abundance of all sampled tree species occurring in forest fragments and core old-growth continuous forest at three forest types in southern Brazil. A total of 10 forest plots of 0.1 ha each were sampled for each landscape context in each forest type. F = fragments; C = continuous forest plots.

	Evergreen		Araucaria		Deciduous	
Species	F	C	F	C	F	C
Achatocarpus praecox Griseb.	0	0	0	0	6	0
Actinostemon concolor (Spreng.) Müll.Arg.	0	3	0	0	0	10
Aegiphila brachiata Vell.	0	0	0	0	3	0
Agonandra excelsa Griseb.	0	0	0	0	1	0
Aiouea saligna Meisn.	3	2	0	0	0	0
Albizia edwallii (Hoehne) Barneby & J.W. Grimes	1	1	0	0	2	2
Albizia niopoides (Spruce ex Benth.) Burkart	0	0	0	0	0	1
Alchornea glandulosa Poepp.	9	0	0	0	0	0
Alchornea triplinervia (Spreng.) Müll. Arg.	8	5	2	0	0	2
Allophylus edulis (A.St.-Hil., Cambess. & A. Juss.) Radlk.	0	0	4	2	6	9
Allophylus puberulus (Cambess.) Radlk.	0	0	1	0	0	0
Aloysia virgata (Ruiz & Pav.) Juss.	0	0	0	0	11	2
Alsophila setosa Kaulf.	3	38	0	24	8	0
Amaioua intermedia Mart.	11	8	0	0	0	0
Andira fraxinifolia Benth.	4	1	0	0	0	0
Aniba firmula (Nees & C. Mart.) Mez	0	5	0	0	0	0
Annona cacans Warm.	1	0	0	0	0	0
Annona neosalicifolia H. Rainer	0	0	10	0	9	6
Annona neosericea H. Rainer	13	11	0	0	0	0
Annona rugulosa (Schltdl.) H. Rainer	2	0	3	3	2	0
Aparisthmium cordatum (A. Juss.) Baill.	0	3	0	0	0	0
Apuleia leiocarpa (Vogel) J.F. Macbr.	0	0	0	0	8	7
Aralia warmingiana (Marchal) J. Wen	0	0	0	0	1	4
Araucaria angustifolia (Bertol.) Kuntze	0	0	62	37	0	0
Aspidosperma australe Müll. Arg.	1	53	0	1	4	0
Attalea dubia (Mart.) Burret	2	0	0	0	0	0
Balfourodendron riedelianum (Engl.) Engl.	0	0	0	0	9	11
Banara tomentosa Clos	0	0	2	9	2	2
Bathysa australis (A. St.-Hil.) Hook. f. ex K. Schum.	14	14	0	0	0	0
Bauhinia forficata Link	0	0	0	0	4	0
Brosimum lactescens (S. Moore) C.C.Berg	2	1	0	0	0	0
Butia eriospatha (Mart. ex Drude) Becc.	0	0	1	0	0	0

Byrsonima ligustrifolia A. Juss.	1	19	0	0	0	0
Cabralea canjerana (Vell.) Mart.	12	8	0	0	26	9
Calliandra foliolosa Benth.	0	0	0	0	3	2
Callisthene kuhlmannii H.F. Martins	0	1	0	0	0	0
Calyptranthes concinna DC.	0	0	19	0	0	0
Calyptranthes grandifolia O. Berg	0	17	0	0	0	0
Calyptranthes lucida Mart. ex DC.	1	16	0	0	0	0
Calyptranthes strigipes O. Berg	1	12	0	0	0	0
Calyptranthes tricona D. Legrand	0	0	0	0	0	26
Campomanesia guazumifolia (Cambess.) O.Berg	0	0	5	0	0	3
Campomanesia xanthocarpa O. Berg	0	0	55	3	8	3
Campomanesia guaviroba (DC.) Kiaersk.	1	0	0	0	0	0
Cinnamodendron dinisii Schwanke	0	0	3	6	0	0
Casearia decandra Jacq.	0	0	22	15	5	1
Casearia obliqua Spreng.	1	5	33	20	0	0
Casearia sylvestris Sw.	15	2	3	1	8	5
Cecropia glaziovii Snethl.	5	1	0	0	0	0
Cedrela fissilis Vell.	6	6	8	1	21	8
Ceiba speciosa (A. St.-Hil.) Ravenna	0	0	0	0	0	4
Chionanthus filiformis (Vell.) P.S. Green	0	3	0	0	0	0
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	0	0	0	0	15	23
Chrysophyllum inornatum Mart.	0	3	0	0	0	0
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	0	0	0	0	5	24
Chrysophyllum viride Mart. & Eichler	0	2	0	0	0	0
Cinnamomum amoenum (Nees & Mart.) Kosterm.	0	0	4	0	0	0
Cinnamomum glaziovii (Mez) Kosterm.	2	1	0	0	0	0
Citharexylum myrianthum Cham.	1	0	0	0	0	0
Citronella paniculata (Mart.) R.A. Howard	0	0	0	0	0	2
Clethra scabra Pers.	5	1	11	1	0	0
Clusia criuva Cambess.	13	9	0	0	0	0
Coccoloba warmingii Meisn.	0	2	0	0	0	0
Colubrina glandulosa Perkins	1	1	0	0	0	0
Copaifera trapezifolia Hayne	0	2	0	0	0	0
Cordia americana (L.) Gottschling & J.S.Mill.	0	0	2	0	1	0
Cordia ecalyculata Vell.	0	0	0	0	7	2
Cordia trichotoma (Vell.) Arráb. ex Steud.	0	0	0	1	12	3
Cordiera concolor (Cham.) Kuntze	0	5	0	3	0	0
Coussapoa microcarpa (Schott) Rizzini	1	0	0	0	0	0
Coussarea contracta (Walp.) Müll.Arg.	1	4	11	47	0	0
Coutarea hexandra (Jacq.) K. Schum.	0	0	0	2	0	0
Cryptocarya aschersoniana Mez	10	8	0	0	0	0
Cupania vernalis Cambess.	8	1	40	64	27	0
Cyathea corcovadensis (Raddi) Domin	2	8	0	0	0	0
Cyathea delgadii Sternb.	0	10	0	0	0	0
Cyathea phalerata Mart.	0	5	0	0	0	0

Cybistax antisyphilitica (Mart.) Mart.	1	1	0	0	0	0
Dalbergia frutescens (Vell.) Britton	2	0	2	0	8	7
Dasyphyllum spinescens (Less.) Cabrera	0	0	2	0	0	0
Diatenopteryx sorbifolia Radlk.	0	0	2	4	4	8
Dicksonia sellowiana Hook.	0	0	2	172	0	0
Diospyros inconstans Jacq.	0	0	0	0	0	2
Drimys brasiliensis Miers	0	0	0	2	0	0
Duguetia lanceolata A. St.-Hil.	0	12	0	0	0	0
Enterolobium contortisiliquum (Vell.) Morong	0	0	0	0	1	0
Erythrina falcata Benth.	0	0	0	0	1	1
Erythroxylum deciduum A.St.-Hil.	0	0	1	0	1	0
Esenbeckia grandiflora Mart.	0	1	0	0	0	0
Eugenia beaurepairiana (Kiaersk.) D. Legrand	0	5	0	0	0	0
Eugenia burkartiana (D. Legrand) D. Legrand	1	0	0	0	0	0
Eugenia cereja D. Legrand	1	0	0	0	0	0
Eugenia excelsa O. Berg	0	1	0	0	0	0
Eugenia handroana D. Legrand	0	1	0	0	0	0
Eugenia hiemalis Cambess.	0	0	0	0	0	1
Eugenia involucrata DC.	0	0	6	0	0	1
Eugenia multicostata D. Legrand	0	1	0	0	0	0
Eugenia nutans O. Berg	0	1	0	0	0	0
Eugenia pyriformis Cambess.	0	0	12	0	1	1
Eugenia ramboi D.Legrand	0	0	0	2	1	0
Eugenia subterminalis DC.	0	0	0	0	1	0
Eugenia uniflora L.	0	0	24	0	5	1
Euterpe edulis Mart.	66	18	0	0	0	0
Faramea montevidensis (Cham. & Schltdl.) DC.	3	3	0	0	0	0
Ficus adhatodifolia Schott ex Spreng.	5	1	0	0	0	0
Ficus arpazusa Casar.	1	0	0	0	0	0
Ficus citrifolia Mill.	0	0	0	0	0	1
Ficus luschnathiana (Miq.) Miq.	2	0	0	0	3	1
Ficus organensis Miq.	0	2	0	0	0	0
Garcinia gardneriana (Planch. & Triana) Zappi	1	7	0	0	0	0
Gleditsia amorphoides (Griseb.) Taub.	0	0	0	0	1	0
Guapira opposita (Vell.) Reitz	11	40	0	0	0	0
Guarea macrophylla Vahl	5	0	0	0	0	1
Guatteria australis A. St.-Hil.	6	8	0	0	0	0
Hedyosmum brasiliense Miq.	0	2	0	0	0	0
Heisteria silvianii Schwacke	2	7	0	0	0	0
Helietta apiculata Benth.	0	0	0	0	12	6
Heliocarpus popayanensis Kunth	0	0	0	0	0	1
Hennecartia omphalandra J.Poiss.	0	0	0	0	1	0
Hirtella hebeclada Moric. ex DC.	3	51	0	0	0	0
Holocalyx balansae Micheli	0	0	0	0	11	15
Hovenia dulcis Thunb.	0	0	0	1	0	0

Hyeronima alchorneoides Allemão	74	13	0	0	0	0
Ilex brevicuspis Reissek	3	0	2	1	0	0
Ilex dumosa Reissek	0	1	0	0	0	0
Ilex microdonta Reissek	0	0	2	4	0	0
Ilex paraguariensis A. St.-Hil.	0	5	4	23	0	0
Ilex taubertiana Loes.	0	1	0	0	0	0
Ilex theezans Mart. ex Reissek	11	3	3	1	0	0
Inga marginata Willd.	2	1	0	0	2	4
Inga vera Willd.	0	0	0	2	0	2
Inga virescens Benth.	0	0	1	0	0	0
Jacaranda micrantha Cham.	2	0	0	1	0	0
Jacaranda puberula Cham.	6	1	6	2	0	0
Jacaratia spinosa (Aubl.) A.DC.	0	0	0	0	1	4
Lamanonia ternata Vell.	0	3	27	12	0	0
Laplacea fruticosa (Schrad.) Kobuski	1	0	0	0	0	0
Lithraea brasiliensis Marchand	0	0	21	1	0	0
Lonchocarpus campestris Mart. ex Benth.	0	0	0	0	4	7
Luehea divaricata Mart. & Zucc.	0	0	3	1	12	16
Machaerium hirtum (Vell.) Stellfeld	0	0	0	0	0	1
Machaerium nyctitans (Vell.) Benth.	0	1	0	0	0	0
Machaerium paraguariense Hassl.	0	0	1	1	2	3
Machaerium stipitatum (DC.) Vogel	0	0	1	2	15	11
Maclura tinctoria (L.) D.Don ex Steud.	4	0	0	0	1	5
Magnolia ovata (A. St.-Hil.) Spreng.	2	6	0	0	0	0
Manihot grahamii Hook.	0	0	0	0	2	0
Marlierea excoriata Mart.	2	2	0	0	0	0
Marlierea sylvatica (Gardner) Kiaersk.	2	4	0	0	0	0
Matayba elaeagnoides Radlk.	0	0	14	19	3	0
Matayba intermedia Radlk.	29	16	0	0	0	0
Maytenus muelleri Schwacke	0	0	0	1	0	0
Maytenus robusta Reissek	1	9	0	0	0	0
Meliosma sellowii Urb.	0	7	0	0	0	0
Miconia cabussu Hoehne	44	12	0	0	0	0
Miconia cinnamomifolia (DC.) Naudin	41	4	0	0	0	0
Miconia cubatanensis Hoehne	0	1	0	0	0	0
Miconia pusilliflora (DC.) Naudin	0	0	0	0	1	0
Mimosa scabrella Benth.	0	0	3	0	0	0
Mollinedia triflora (Spreng.) Tul.	1	1	0	0	0	0
Myrcia brasiliensis Kiaersk.	7	4	0	0	0	0
Myrcia dichrophylla D. Legrand	0	10	0	0	0	0
Myrcia glabra (O.Berg) D. Legrand	2	0	0	0	0	0
Myrcia guianensis (Aubl.) DC.	0	3	2	0	0	0
Myrcia oblongata DC.	0	0	51	0	0	0
Myrcia pubipetala Miq.	12	15	0	0	0	0
Myrcia pulchra (O. Berg) Kiaersk.	0	1	3	0	0	0

Myrcia racemosa (O. Berg) Kiaersk.	0	2	0	0	0	0
Myrcia richardiana (O. Berg) Kiaersk.	0	3	0	0	0	0
Myrcia selloi (Spreng.) N. Silveira	0	0	1	0	0	0
Myrcia spectabilis DC.	0	2	0	0	0	0
Myrcia splendens (Sw.) DC.	5	0	0	0	0	0
Myrcia tijucensis Kiaersk.	1	8	0	0	0	0
Myrciaria floribunda (West ex Willd.) O. Berg	3	0	3	0	0	0
Myrocarpus frondosus Allemão	0	0	0	0	3	2
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult	3	0	1	9	0	0
Myrsine guianensis (Aubl.) Kuntze	0	0	0	2	1	2
Myrsine umbellata Mart.	0	2	0	0	0	0
Nectandra oppositifolia Nees & Mart.	0	0	4	1	19	0
Nectandra megapotamica (Spreng.) Mez	0	0	4	26	20	4
Nectandra oppositifolia Nees & Mart.	22	10	0	0	0	0
Neomitranthes glomerata (D. Legrand) D. Legrand	0	1	0	0	0	0
Ocotea aciphylla (Nees) Mez	1	13	0	0	0	0
Ocotea catharinensis Mez	0	7	0	0	0	0
Ocotea corymbosa (Meisn.) Mez	0	2	0	0	0	0
Ocotea diospyrifolia (Meisn.) Mez	0	0	6	45	5	5
Ocotea elegans Mez	0	2	0	0	0	0
Ocotea indecora (Schott) Mez	0	4	0	0	0	0
Ocotea lancifolia (Schott) Mez	0	6	0	0	0	0
Ocotea mandioccana A. Quinet	1	2	0	0	0	0
Ocotea nectandrifolia Mez	0	7	0	0	0	0
Ocotea odorifera Rohwer	0	3	0	0	0	0
Ocotea porosa (Nees & Mart.) Barroso	0	1	0	0	0	0
Ocotea puberula (Rich.) Nees	8	0	5	3	8	0
Ocotea pulchella Mart.	0	1	14	0	0	0
Ocotea pulchra Vattimo-Gil	0	2	0	0	0	0
Ocotea silvestris Vattimo	0	5	0	0	0	0
Ormosia arborea (Vell.) Harms	2	3	0	0	0	0
Ouratea sellowii Engl.	0	2	0	0	0	0
Parapiptadenia rigida (Benth.) Brenan	0	0	3	1	5	4
Pausandra morisiana (Casar.) Radlk.	0	2	0	0	0	0
Peltophorum dubium (Spreng.) Taub.	0	0	0	0	1	0
Pera glabrata (Schott) Poepp. ex Baill.	60	37	0	0	0	0
Phytolacca dioica L.	0	0	0	0	3	0
Picramnia parvifolia Engl.	0	0	0	0	0	1
Picrasma crenata (Vell.) Engl.	0	0	0	1	2	4
Pilocarpus pennatifolius Lem.	0	0	0	0	6	4
Pimenta pseudocaryophyllus (Gomes) Landrum	0	2	0	0	0	0
Piptadenia gonoacantha (Mart.) J.F.Macbr.	1	0	0	0	0	0
Piptocarpha angustifolia Dusén ex Malme	0	2	2	14	0	0
Piptocarpha sellowii (Sch. Bip.) Baker	4	0	9	5	2	0
Pisonia zapallo Griseb.	1	4	0	0	3	5

Plinia cordifolia (D. Legrand) Sobral	0	2	0	0	0	0
Plinia edulis (Vell.) Sobral	2	0	0	0	0	0
Plinia rivularis (Cambess.) Rotman	0	0	0	0	2	2
Podocarpus sellowii Klotzsch ex Endl.	0	1	0	0	0	0
Posoqueria latifolia (Rudge) Roem. & Schult.	5	13	0	0	0	0
Pouteria venosa (Mart.) Baehni	1	0	0	0	0	0
Protium kleinii Cuatrec.	0	28	0	0	0	0
Prunus myrtifolia (L.) Urb.	0	0	18	10	18	2
Psychotria carthagenensis Jacq.	0	15	0	0	0	0
Psychotria suterella Müll. Arg.	0	1	0	0	0	0
Psychotria vellosiana Benth.	25	8	0	0	0	0
Qualea cryptantha (Spreng.) Warm.	0	1	0	0	0	0
Qualea minor (Mart.) Spreng.	0	1	0	0	0	0
Quiina glazovii Engl.	1	1	0	0	0	0
Randia ferox (Cham. & Schltdl.) DC.	0	0	0	0	1	1
Roupala montana Aubl.	1	7	2	0	0	0
Rudgea jasminoides (Cham.) Müll. Arg.	0	3	0	0	0	0
Rudgea recurva Müll. Arg	0	4	0	0	0	0
Ruprechtia laxiflora Meisn.	0	0	1	1	2	2
Sapium glandulosum (L.) Morong	0	0	14	0	0	0
Schefflera angustissima (Marchal) Frodin	0	8	0	0	0	0
Schefflera calva (Cham.) Frodin & Fiaschi	1	0	0	0	4	2
Schinus terebinthifolius Raddi	0	0	1	0	0	0
Sebastiania brasiliensis Spreng.	0	0	0	0	14	17
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	0	0	9	0	5	6
Seguieria aculeata Jacq.	0	0	0	1	0	0
Seguieria langsdorffii Moq.	1	0	0	0	0	0
Sloanea guianensis (Aubl.) Benth.	32	34	0	0	0	0
Sloanea monosperma Vell.	0	1	0	4	0	0
Solanum pseudoquina A.St.-Hil.	0	0	0	0	2	0
Solanum sanctae-catharinae Dunal	0	0	1	1	1	0
Sorocea bonplandii (Baill.) W.C. Burger, Lanjouw & Boer	0	6	0	0	8	15
Strychnos brasiliensis (Spreng.) Mart.	0	0	2	1	0	0
Styrax acuminatus Pohl	1	0	0	0	0	0
Styrax leprosus Hook. & Arn.	0	0	15	7	3	5
Syagrus romanzoffiana (Cham.) Glassman	2	0	3	2	15	60
*Symplocos tenuifolia*Brand	0	0	0	7	0	0
Symplocos tetrandra Mart.	0	0	0	1	2	0
Symplocos trachycarpa Brand	2	0	0	0	0	0
Syzygium jambos (L.) Alston	1	0	0	0	0	0
Tabernaemontana catharinensis A.DC.	3	0	0	0	0	3
Tapirira guianensis Aubl.	4	0	0	0	0	0
Tetrorchidium rubrivenium Poepp.	4	0	0	0	3	3
Trema micrantha (L.) Blume	0	0	0	1	2	2
Trichilia catigua A.Juss.	0	0	0	0	3	7

Trichilia claussenii C.DC.	0	0	0	0	17	20
Trichilia lepidota Mart.	3	2	0	0	0	0
Urera baccifera (L.) Gaudich. ex Wedd.	0	0	0	0	23	4
Vantanea compacta (Schnizl.) Cuatrec.	0	29	0	0	0	0
Vasconcellea quercifolia A.St.-Hil.	0	0	0	0	2	0
Vernonanthura discolor (Spreng.) H.Rob.	0	0	26	8	0	0
Virola bicuhyba (Schott ex Spreng.) Warb.	6	8	0	0	0	0
Vitex megapotamica (Spreng.) Moldenke	0	0	2	4	1	1
Xylopia brasiliensis Spreng.	8	19	0	0	0	0
Xylosma pseudosalzmannii Sleumer	0	0	0	0	2	2
Zanthoxylum fagara (L.) Sarg.	0	0	0	0	1	1
Zanthoxylum petiolare A.St.-Hil. & Tul.	0	0	0	0	0	1
Zanthoxylum rhoifolium Lam.	1	0	1	0	0	1

Table S2. Indicator species analysis of tree assemblages recorded in old-growth continuous forest and fragment plots in three forest types (n=60 plots) in southern Brazil.

Indicator species	Family	Regeneration strategy	Indicator value (IV)	*p*
Evergreen - continuous				
Hirtella hebeclada	Chrysobalanaceae	s-Tolerant	0.972	0.001
Aspidosperma australe	Apocynaceae	s-Tolerant	0.899	0.001
Protium kleinii	Burseraceae	s-Tolerant	0.894	0.001
Calyptranthes lucida	Myrtaceae	s-Tolerant	0.868	0.001
Schefflera angustissima	Araliaceae	s-Tolerant	0.837	0.001
Vantanea compacta	Humiriaceae	s-Tolerant	0.837	0.001
Byrsonima ligustrifolia	Malpighiaceae	s-Tolerant	0.815	0.001
Calyptranthes grandifolia	Myrtaceae	s-Tolerant	0.775	0.001
Duguetia lanceolata	Annonaceae	s-Tolerant	0.775	0.001
Calyptranthes strigipes	Myrtaceae	s-Tolerant	0.744	0.001
Maytenus robusta	Celastraceae	s-Tolerant	0.735	0.001
Myrcia tijucensis	Myrtaceae	s-Tolerant	0.73	0.002
Eugenia beaurepairiana	Myrtaceae	s-Tolerant	0.707	0.001
Meliosma sellowii	Sabiaceae	s-Tolerant	0.707	0.002
Myrcia dichrophylla	Myrtaceae	s-Tolerant	0.707	0.001
Heisteria silvianii	Olacaceae	s-Tolerant	0.683	0.001
Ocotea aciphylla	Lauraceae	s-Tolerant	0.681	0.003
Garcinia gardneriana	Clusiaceae	s-Tolerant	0.661	0.002
Aniba firmula	Lauraceae	s-Tolerant	0.632	0.003
Ocotea catharinensis	Lauraceae	s-Tolerant	0.632	0.004
Ocotea indecora	Lauraceae	s-Tolerant	0.632	0.004
Ocotea nectandrifolia	Lauraceae	s-Tolerant	0.632	0.006
Ocotea silvestris	Lauraceae	s-Tolerant	0.548	0.024
Rudgea recurva	Rubiaceae	s-Tolerant	0.548	0.028
Evergreen - fragments				
Miconia cinnamomifolia	Melastomataceae	Pioneer	0.799	0.001
Miconia cabussu	Melastomataceae	s-Tolerant	0.793	0.001
Psychotria vellosiana	Rubiaceae	s-Tolerant	0.778	0.001
Ilex theezans	Aquifoliaceae	Pioneer	0.654	0.001
Alchornea glandulosa	Euphorbiaceae	Pioneer	0.632	0.002
Myrcia splendens	Myrtaceae	Pioneer	0.548	0.017
Cecropia glaziovii	Urticaceae	Pioneer	0.500	0.049
Guarea macrophylla	Meliaceae	s-Tolerant	0.500	0.048
Araucaria - continuous				
Dicksonia sellowiana	Dicksoniaceae	s-Tolerant	0.832	0.001
Ocotea diospyrifolia	Lauraceae	s-Tolerant	0.815	0.001

Coussarea contracta	Rubiaceae	s-Tolerant	0.773	0.002
Ilex paraguariensis	Aquifoliaceae	s-Tolerant	0.758	0.001
Symplocos tenuifolia	Symplocaceae	s-Tolerant	0.548	0.026
Araucaria - fragments				
Myrcia oblongata	Myrtaceae	Pioneer	0.894	0.001
Campomanesia xanthocarpa	Myrtaceae	s-Tolerant	0.847	0.001
Sapium glandulosum	Euphorbiaceae	Pioneer	0.837	0.001
Eugenia pyriformis	Myrtaceae	s-Tolerant	0.717	0.001
Lithraea brasiliensis	Anacardiaceae	Pioneer	0.691	0.001
Calyptranthes concinna	Myrtaceae	Pioneer	0.632	0.003
Ocotea pulchella	Lauraceae	Pioneer	0.611	0.006
Eugenia uniflora	Myrtaceae	Pioneer	0.566	0.017
Albizia niopoides	Fabaceae	Pioneer	0.548	0.016
Seasonal - continuous				
Chrysophyllum marginatum	Sapotaceae	s-Tolerant	0.863	0.001
Gymnanthes concolor	Euphorbiaceae	s-Tolerant	0.62	0.003
Trichilia catigua	Meliaceae	s-Tolerant	0.592	0.003
Calyptranthes tricona	Myrtaceae	s-Tolerant	0.548	0.024
Ceiba speciosa	Malvaceae	Pioneer	0.548	0.019
Seasonal - fragments				
Cordia trichotoma	Boraginaceae	s-Tolerant	0.671	0.001
Urera baccifera	Urticaceae	Pioneer	0.653	0.002
Bauhinia forficata	Fabaceae	Pioneer	0.632	0.001
Cordia ecalyculata	Boraginaceae	s-Tolerant	0.624	0.007
Achatocarpus praecox	Achatocarpaceae	Pioneer	0.548	0.022

CAPÍTULO 2

Forest fragmentation and divergent tree assemblages responses to landscape variables in southern Brazil

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Running title: Forest fragmentation and divergent tree assemblages responses

ABSTRACT

We examine the influences of landscape metrics (forest area, shape and isolation) and climatic variables (precipitation, temperature and seasonality) on the structure and composition of tree assemblages within three seasonal and aseasonal forest types of southern Brazil, including evergreen, Araucaria and deciduous forests. Trees assemblages were sampled in 389 plots of 0.4 ha forest fragments off all sizes, in the southernmost Atlantic Forest region, southern Brazil (between 26° and 29° S and 48° and 53° W). The sampled plots included protected and private properties. All trees ≥ 10 cm DBH within each plot were measured, identified to species level, and assigned to trait categories describing their regeneration strategy, vertical stratification, seed-dispersal mode, seed size and wood density. Spatial landscape metrics and climatic variables were used as explanatory variables to examine the variation in functional attributes and composition of tree assemblages. A total of 97,512 trees (97.13% identified to species level) belonging to 658 species and 86 families were recorded across the 389 plots. Evergreen forest plots exhibited the highest species richness, followed by Araucaria and deciduous forest. Most tree assemblages attributes showed significant differences among forest types, the major differences comprised: species richness, stem density, the proportion of pioneer species and stems, and the proportion of understorey and vertebrate-dispersed species. The forest types demonstred markedly divergent responses to patch and landscape variables. The evergreen, Araucaria and deciduous forests diverge in the ecological/biogeographic composition of tree floras, particularly in the relative species contribution of functional groups in relation to regeneration strategy and stress tolerance. Our data strongly suggests that this confers to these forest floras markedly different levels of resilience and tolerance to contemporary human-disturbances.

Key-words: Araucaria; Atlantic Forest; edge effects; patch; habitat loss; seasonal forest.

1. Introduction

The understanding of succession under different forest types and dimensions of human impacts is one of the key challenges for the promotion and development of effective programs for biodiversity conservation in the future (Gardner et al., 2009; Quesada et al., 2009). Interpreting biodiversity research findings is frequently made harder by constrained study designs, low congruence in species responses to disturbance, difficulty of selecting and collecting reliable information from a highly diverse biota, besides shifting baselines and an overdependence on comparatives inferences from a small number of well studied localities (Gardner et al. 2009; Metzger 2009). Financial and logistical constraints severely limit the quality and amount of information we are able to gather about the natural world (Gardner et al. 2009). Marked ecological differences between forest types could have deep implications for the best conservations efforts and strategies that should be adopted.

A landscape perspective is essential for understanding modified forest ecosystems because most species, at some point in their life cycle, experience their surroundings at spatial scales beyond the plot level, and biological fluxes (e.g. dispersal and pollination) within and between areas of forest and the managed matrix are common (Kupfer et al. 2006; Laurance 2008; Perfecto & Vandenmeer 2008; Tscharntke et al. 2008). Although much of landscape ecology has been conducted at the patch scale, differences in landscape mosaic properties, such as the amount and spatial configuration of native forest cover, are vital in understanding the value of modified forest landscapes for biodiversity conservation (Tscharntke et al. 2005; Bennett et al. 2006). Even when different landscapes are defined by similar environmental characteristics, small initial differences in disturbance regimes and human impacts can precipitate marked and cumulative divergences in species composition and ecosystem functioning through time (Laurance et al. 2007). In the search for expediency there is a real danger that just some context-specific ecological narratives can be propagated from a small limited set of studies and localities, leading to inappropriate knowledge transfers and misleading paradigms (Laurance et al. 2007; Gardner et al. 2009). In this study we present the ecological analyses of a robust and comprehensive database gathered along understudied localities – the subtropics of the South America, in the southern distribution of the Brazilian Atlantic Forest.

Recent biogeographical analyses have shown that the flora from the subtropical region in the South of Brazil have different biogeographical origins (Waechter 2002; Giehl & Jarenkow 2012; Gonçalves & Silva 2014; Oliveira-Filho et al. 2014). These areas of origin have different climatic conditions that conferred to these floras, through evolutionary time, particular physiologies and tolerances to, sometimes, challenging climatic conditions (Engelbrecht 2007; Oliveira-Filho et al. 2014). We expect that the different composition blends of tree species, with their different origins and climatic affinities, in each of the three forest types that characterize this region (Oliveira-Filho et al. 2014), will have different levels of tolerances concerning both adverse natural climatic conditions such as frosts, periods of droughts and different soil conditions, and therefore also to the human induced alterations of landscapes and patch configurations (imposed primarily by land conversion and forest fragmentation). We could expect that these environment tolerances are more pronounced in pioneers species, because they normally have to deal with greater daily and year-round microclimatic fluctuations (Bazzaz 2000; Laurance et al. 2002). We expect that these physiological adaptations (especially drought and frost tolerances) confers to these groups of species higher tolerances to the edge-effects, ubiquitous in human-modified landscapes. More specifically we could expect a higher proportion of: 1) frost and drought-tolerant species associated with Seasonal Decidual Forests; 2) frost tolerant species associated with Araucaria Forests; and 3) a richer, shade tolerant, wet affiliated, and frost and drought intolerants species associated with the evergreen (Ombrophilous Dense Forest). Therefore we could expect a gradient os assemblages sensitivities to forest fragmentation, being the evergreen the more sensitive and deciduous forests the least sensitive. It is important to highlight that we expect that all three forest types presents, some degree, deleterious responses to forest fragmentation (in the form of decreased diversity and an increased proportion of pioneer species), but we also expect different intensities of the responses in each forest type considering their different presumed tolerances to altered microclimatic conditions (especially prevalent in small forest fragments).

2. Methods

2.1. Study design

This is one of the most comprehensive quantitative forest fragmentation studies ever conducted in South America, where we analysed quantitative data from 389 plots in forest fragments scattered throughout 95,346 km^2, totalizing more than 155 ha of sampled area and 97.000 adult trees. Our study encompassed the landscapes distributed across the three main Atlantic Forest domains of southern Brazil, these forest types are referred to as Ombrophilous Dense Forest, Ombrophilous Mixed Forest, and Deciduous Forest according to the Brazilian vegetation classification (Veloso et al., 1991), hereafter refered as evergreen, Araucaria and deciduous forests, respectively. The study area was defined as the southern Brazilian state of Santa Catarina, located between latitudes 26º and 29º S and between longitudes 48º and 53º W, comprising an area of 95,346 km^2 (Fig. 1). 389 0.4 - ha plots were selected from the Santa Catarina Forest and Floristic Inventory (IFFSC) database (Vibrans et al. 2010). Each sampling plot consisted of a cluster of four crosswise 1000-m^2 subplots (20-m x 50-m), each at 30 meters distance from one centre point, to collect field data of forest composition and structure. In each plot all trees ≥10 cm DBH were measured and identified.

The Atlantic Forest original distribution covered around 150 million ha, and extends across both tropical and subtropical regions of South America. Briefly, this region consists of both seasonally-dry deciduous forests, away from the coast, and relatively aseasonal evergreen tropical rain forests subjected to more constant orographic precipitation near the coast. This biome has been reduced to less than 12% of its original forest cover (Ribeiro et al., 2009). Vibrans et al. (2013) estimated the remaining forest cover of the forests types in the state of Santa Catarina (in relation to each original distribution): of 22.0 % for Araucaria, 40.4 % for evergreen and 16.3% for Deciduous forests, and overall 27.7 % of remaining forest cover for the whole state. The abundance of human-modified landscapes with a long history of human-disturbances associated with a relatively well known biota in terms of both taxonomy and life-history attributes in the regions analized provide a key opportunity to address dynamic drivers of biodiversity persistence in modified landscapes for a myriad of taxa and ecological scenarios (see Faria et al. 2007; Ribeiro et al. 2009; Tabarelli et al. 2010). The Araucaria forests once covered large extents of the inner highlands of the three southern Brazilian states, and also the Missiones province in Argentina (Oliveira-Filho et al. 2014). At higher altitudes and near shallower soils, the easily recognized Araucaria forests (through the emergent chandelier-like crowns of the gymnosperm *Araucaria angustifolia* (Bertol.) Kuntze) form vegetation mosaics with highland grasslands and meet Atlantic cloud forests along the crests of the coastal hill ranges (Klein 1990; Jarenkow & Budke 2009; Oliveira-Filho et al. 2014). Seasonal deciduous forests cover the largest area and make up most of the extensions of both tropical and subtropical Atlantic forests that meet the neighbouring Biogeographic Domains dominated by open and seasonally dry vegetation types (Oliveira-Filho et al. 2014). These hinterland expanses of deciduous forests become increasingly larger towards the south where they go as far as eastern Paraguay and north-eastern Argentina and border the vegetation of the Chaco and Espinal Domains to the west and the hyper-seasonal prairies of the Pampa Domain to the south (Oliveira-Filho et al. 2014).

2.2. Tree species attributes

All individuals trees were assigned to mutually exclusive categories of functional groups describing their seed size, vertical stratification, seed-dispersal mode, regeneration strategy, and wood density based on a comprehensive literature review, including books, papers, monographs of the regional flora and MSc and PhD dissertations (e.g. Sobral et al., 2006, several volumes of the Flora Ilustrada Catarinense and Flora Fanerogâmica do Estado de São Paulo). These sources were supplemented by our own lifetime personal knowledge on the life-history traits of tree species of southern Brazilian forests (e.g. Jarenkow & Baptista, 1987; Jarenkow & Waechter, 2001), and online sources (e.g. Global Wood Density database: Chave et al., 2009).

Functional groups of tree species were defined according to categories and criteria adopted elsewhere in the Atlantic Forest (Silva & Tabarelli, 2000; Tabarelli & Peres, 2002; Santos et al., 2008; Santo-Silva et al., 2013), as following: (a) Regeneration strategy – *Pioneer species* were defined as species requiring high light environments as viable regenerating sites such as forest edges and treefall gaps. This group included both large and long-lived pioneer species in addition to short-lived pioneers (*sensu* Whitmore, 1989) and is equivalent to 'successional species' as referred to in the literature (Laurance et al., 2006a, 2006b). *Shade-tolerant species* are those capable of regenerating in shaded environments, such as the shaded understorey of old-growth forests (Hartshorn, 1978). Juveniles of these species may survive in shade for several years (Whitmore, 1989); (b) Forest stratification – *Understorey species* comprised small trees flowering and fruiting in the lowest forest layer (<11 m); *Canopy species* occurred in the forest subcanopy and canopy; and *Emergent species* occurred in the highest forest layer (Wilson, 1989). Seed-dispersal mode - *Vertebrate-dispersed species* are those bearing diaspores attached to a fleshy pulp, aril, or other features typically associated with vertebrate seed dispersal vectors; and *Abiotically-dispersed species* are those producing winged seeds, plumes, other wind-dispersal devices that slow the rate of seed fall, those dispersed entirely by free fall, or those propelled explosively by a fruit that opens suddenly, often triggered by a trip-lever (van der Pijl, 1982); *Seed size of vertebrate-dispersed species* – seeds were grouped according to a logarithmic scale of seed size, considering its longest dimension: < 1mm; 1-5mm; 5-10mm; 10-20mm; ≥ 20mm, scored from 1 to 5, respectively. *Wood specific gravity* (WSG) or wood density – recorded according to Chave et al., (2006) and by consulting specific regional-scale literature (e.g. Lorenzi, 1992), when data from the species was not available, we used the average of the genus, if that was also not available (in only a few cases), we used the average of the family (considering the genus data).

Tree assemblages within each plot were thus characterized in terms of the following attributes: (1) stem density; (2) species richness; and the percentage of (3) pioneer species; (4) pioneer stems; (5) understorey species; (6) canopy species; (7) emergent species; (8) vertebrate-dispersed species; and (9) size of vertebrate-dispersed seeds, and (10) wood density.

2.3. Patch and landscape metrics

We used three spatial metrics as explanatory variables for tree assemblage attributes: (i) forest patch area, the continuous forested area within a 2.8 km buffer zone from the center of each sampling plot; (ii) index of shape of the fragment (iii), and the distance to nearest neighbour, the straight-line distance from the forest fragment to the closest neighbor fragment. More information concerning the methodological details of the landscape metrics can be obtained in Schaadt (2012). Soil types for each site were obtained according to the Brazilian soil classification system (EMBRAPA, 2011). Climatic variables were obtained from the WorldClim database (Hijmans et al. 2005). We also used the actual evapotranspiration (mm) derived from WorldClim layers by Zomer et al. (2006).

2.4. Data analysis

Differences in climatic variables, landscape metrics and tree assemblage attributes among the three forest types were compared using one-way ANOVA followed by Tukey post hoc comparisons (Table 1). Generalized linear models (GLMs) were adopted to detect the effects of explanatory variables on tree assemblage attributes considering all 389 (0.4 ha) plots (Table 2). We excluded from final models any explanatory variables exhibiting high collinearity ($r^2 \geq 0.7$) and/or variables that were not significant in explaining any of the functional abundance responses. The following explanatory variables were considered: annual precipitation, precipitation seasonality, temperature seasonality, the mean temperature of the coldest month (MTCM), evapotranspiration, forest patch size, shape index of the fragment, distance to the nearest forest fragment neighbour, distance to the nearest forest border, forest type and soil type. The variables mean annual temperature and altitude were excluded from the analyses because they presented high collinearity with MTCM. Spatial autocorrelation of GLM residuals was examined by Moran's I in the ape package (Paradis et al., 2004) in R. In all instances, Moran's I was not significant ($P > 0.05$). In order to analyse whether the forest type responds differently to the explanatory variables, we performed generalized linear models averaging, using the MuMln package (Bartón 2013), to detect which variables was significantly correlated with the variation in the functional attributes of the tree assemblages (Table 3).

We plotted the cumulative number of species against the number of patches added, we sorted the patches from smallest to largest, and largest to smallest. We performed an indicator species analyses (sensu Dufrêne and Legendre, 1997) based on all the plots of the three forests. The *fidelity* (table S.1) refers to the probability of finding the species in sites belonging to the forest type, and *specificity* is the probability that the surveyed site belongs to the forest type group given the fact that the species has been found. We performed two non-metric multidimensional scaling (NMDS) ordinations of the 389 plots using the Bray-Curtis (BC), the first we used the dissimilarity index matrix of taxonomic species abundance (Krebs, 1989), and the second with the climatic variables described in Table 1. Environmental factors were fitted to the second ordination (Figure 3 - b)) using the *envfit* function of the vegan package in R v. 2.15 (R Core Development Team, 2012). We allowed the ordination to be rotated and centered, and used the function *metaMDS* of the *vegan* package in R (R Development Core Team, 2012). Finally, the percentage of pioneer stems in each plot was regressed against the first axis of the first NMDS ordination to detect the influence of pioneer species on multivariate patterns of species composition and abundance within each forest type (Figure 6).

3. Results

A total of 97,512 trees (97.1% identified to species level) belonging to 648 species and 86 families were recorded across all 389 plots. Evergreen forest plots exhibited the highest species richness (574), followed by Araucaria (336) and deciduous forest (195). This order of species richness was supported by the rarefaction analyses (Fig. 2). 129 species occurred in all three forest types, evergreen forest had the greatest number of exclusive species (271), followed by Araucaria (38), and deciduous forest with only 12 exclusive species. Evergreen and Araucaria forests shared 144 species, evergreen and deciduous shared

30 species, and Araucaria and deciduous forests shared 24 species. Besides the low number of exclusive species for Araucaria and deciduous forests, the indicator species analyses indicated 58 species for Araucaria and 70 species for deciduous forests and 161 species for evergreen forests (Table S.1).

The NMDS ordination of all plots, considering the species composition (Figure 3a), has also shown a clear separation of the three forest types, with just a small level of overlap between them. The NMDS ordination, using the climatic (plus altitude) variables, have shown a higher overlap, especially between the Araucaria and evergreen forest plots. The DCA have shown that separation between these forests are related to the temperature variables (e.g. annual mean temperature (AMT), mean temperature of the coldest month (MTCM) and altitude, Figure 3b). On the other hand, the precipitation related variables (e.g. precipitation seasonality, evapotranspiration, precipitation of the driest month and annual precipitation) are the main drivers separating these two and the deciduous forests plots. It is worth stressing here that rainfall seasonality, in the whole regions, is more related to a significant increased precipitation volume in the summer compared with that of the winter. In other words, a higher seasonality is more related to a period of excessive rain in summer instead of a significant rainless period. Table 1 shown that there is marked differences, considering climatic variables among forest types. The regression between the scores of the first axis of the NMDS ordination and percentage of pioneers stems in each plot had a significant relationship in all forest types (Figure 6).

Major differences in assemblages attributes among forest types comprised: stem density, tree species richness, the proportion of pioneer species and pioneer individuals, and the proportion of understorey and vertebrate-dispersed species. Most tree assemblages attributes showed significant differences among forest types (Table 1, Figure 4). GLM models based on these explanatory variables explained between 58.22% and 18.74% of the variation in tree assemblage attributes (Table 2). The variable forest type was a significant variable in 6 of the 8 tree assemblage attributes models (Table 2). Patch and landscape metrics had, at least one significant variable in the models, for only three of the nine tree assemblages attributes analysed in deciduous forests (Table 3), while for evergreen and deciduous they were for seven and six, respectively. Concerning species richness, patch and landscape metrics were important only for Araucaria and evergreen forests (Table 3).

The graphic of the cumulative species number in relation to the number of patches added (ordered from small to large, and large to small in fragment area) showed a distinc pattern in the deciduous forests compared to the Araucaria and evergreen, while for evergreen and Araucaria the small to large accumulation species curves were always under the large to small curves, in the deciduous forest this clear distinction didn't exist (Figure 4). Reinforcing that deciduous forests shows different responses to patch metrics when compared to Araucaria and evergreen forests.

Discussion

This study is one of the first quantification of tree assemblages functional groups and its relationships with environmental and landscapes factors in South American subtropical Atlantic Forests. The data supported our hypotheses of a gradient of forests sensitivities to habitat loss and forest fragmentation. We documented differences between forest types on the magnitude (number of attributes exhibiting shifts) and intensity (ecological deviation) of tree-assemblage responses to habitat fragmentation. As expected, tree assemblage responses correlated with the climatic gradient from relatively aseasonal to a marked seasonal climate, and were more evident in evergreen forest than in either deciduous or Araucaria forest. The separation between the Araucaria and evergreen forests were correlated mainly to the temperature related variables and altitude as expected, as well as the seasonality and precipitation variance being closely related to the separation between the deciduous and evergreen plots (Figure 2b). These climatic variables were also strongly related to variations in species richness between plots (Table 2), similar results were also found by other studies with different datasets (Higuchi et al. 2013; Oliveira-Filho et al. 2014; Gonçalves & Souza 2014). However, none of these mentioned studies have incorporated landscape and patch variables in their analyses. As we expected, all forest types floras showed some degree of response to the landscapes metrics concerning forest fragmentation. But they differed, quite markedly, on the magnitude and intensity of tree-assemblage responses to habitat fragmentation (Table 2).

We can relate these differential responses to the different biogeographical origins of the species blends that form each forest type (Fiaschi & Pirani 2009; Oliveira-Filho et al 2014), and their different tolerances to microclimatic conditions. The Deciduous forest is composed (not taking into account the shared flora) mainly of species with “warm-seasonal” and “cool-seasonal” affinities (Waechter 2002; Oliveira-Filho et al. 2013). These species had to evolve physiological adaptations to cope with drought periods in their former distribution, with a markedly seasonal climate and a rainless period. The fact that several species of the Deciduous forests shed their leaves during the cold season, even where there isn’t a significant water deficit, could be no more than a preserved ecological trait (Leite and Klein 1990; Marchioretto et al 2007; Martins 2009). The leaf deciduousness of the group with the “warm-seasonal” affinity is probably related to its ability to handle both low temperatures extremes in the subtropics and periods of drought in the tropics (Oliveira-Filho 2014). This way, we could relate the observed responses, like the less evident drop in species richness in relation to fragment area (figure 5) and the observed similar trend of cumulative species number independently of patch size for Deciduous forest plots (Fig. 4), with the more widespread drought tolerance between the Deciduous forests species, and with their higher proportion of pioneer species concerning the whole pool of species.

In human-altered environments forest species have to deal with altered microclimatic conditions (Laurance et al. 2002; Pinto et al. 2010; Ewers & Banks-Leite 2013). In what was once large continuous old-growth forest tracts are now a myriad of (mainly small) forest fragments scattered in the landscapes, with all kinds of shapes and sizes, along the whole original distribution of Atlantic Forest (Ribeiro et al. 2009). The remaining forest species that still inhabit these altered landscapes have to deal with very different microclimatic conditions compared with their original ones (Laurance et al. 2002; Ewers & Banks-Leite 2013). In this sense, pioneer species (species that can establish and grow in full sunlight) have better odds to remain in these altered environments (because they normally have a greater physiological plasticity and tolerance to drier and hotter conditions (Engelbrecht 2007)). In this study, evergreen forests have the smallest percentage of pioneers species concerning the pool of species of each forest type (only 29.84% of all tree species, compared with 40.51% for Deciduous and 36.28% for Araucaria forests). Araucaria and Deciduous forests species have to obligatorily deal with some climatic filters of species diversity, mainly frost tolerance, but also drought tolerance in places where particular determined soil conditions promotes considerable water deficits. The evergreen forests have the greatest number of species, what could be expected since the species that inhabit these regions are not limited by these climatics filters (frosts and droughts), they can afford to don’t have the physiological adaptations to tolerate these conditions (which could probably be related also to a competition disadvantage in favourable environments, promoting slower rates of growth or metabolic trade-offs). In this sense, evergreen forests are expected to have the greater parcel of susceptible species to edge-effects and forest fragmentation.

Implications for conservation

The different responses to forest loss and fragmentation, found in this study, suggests that different strategies, concerning nature conservation purposes, could be adopted in each forest type (at least when it comes to trees). The preservation of large core old-growth forest patches seems crucial to the preservation of the majority of the high species diversity of non-seasonal forests. Besides our results for the evergreen forest, several papers have already showed that small forest patches, mainly dominated by forest edges effects, are unsuitable to preserve the larger number of species adapted to the moist and shaded environment of the interior of these dense closed canopy forests (Laurence et al. 2002; Girão et al. 2007; Tabarelli et al. 2012; Santo-Silva et al. 2013). While for Seasonal forests the preservation of a large number of forest fragments (in addition to the large reserves), of varying sizes, can also be considered a plausible option (Halffter, 2005; Castillo-Campos et al. 2008, Arroyo-Rodriguez et al. 2009). What is positive on one hand, if we consider that seasonal forests are the most endangered forest type in the world (Jansen 1988), where currently only 2% of the original cover remains, and it is completely fragmented (Werneck & Colli, 2006), due to the high fertility of the soils and the gentle slope, which are very useful to agriculture and cattle ranching (Murphy and Lugo 1986; Prado & Gibbs 1993). There are no more large continuous forest stands (over 3,000 ha) outside of protected areas in South Brazil nowadays. In all the region, over 95% of the original forest has been destroyed and what remains is heavily degraded (Fontana et al., 2003; Vibrans et al. 2013), so it is not bad news for this forest type that forest fragments can also help to maintain the persistence of species in these highly deforested and fragmented landscapes. But is important to highlight that there must be, at least, a minimal gene flow between the forest remnants at the landscape scale (Leibold, 2004), to avoid the deleterious processes in the long run, as genetic drift and stochastic population fluctuations that can lead to extinctions.

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TABLES AND FIGURES

Table 1. Abiotic and biotic variables registered in each sample plot in the three forest types. Significant differences in post hoc comparisons (Tukey tests) of variables are indicated by different letters in the same row, where differences were significant within analysis of variance ($p > 0.05$).

	Evergreen (n = 200)		Araucaria (n = 127)		Deciduous (n = 62)	
Variables	Mean (± SD)	Range	Mean (± SD)	Range	Mean (± SD)	Range
Abiotic variables						
Annual mean temperature (ºC)	18.43 (± 1.37) a	14.97-21.16	15.78 (± 1.08) b	12.60 - 18.30	18.77 (± 0.86) a	16.72 - 20.15
Annual precipitation (mm)	1577.6 (± 96.4) a	1325.1 -1875.4	1642.6 (± 162.7) b	1317.9 - 2168.5	1906.8 (± 109.9) c	1709.0 - 2206.3
Precipitation seasonality	25.24 (± 5.61) a	9.95-39.79	15.80 (± 3.79) b	10.37 - 25.61	12.16 (± 3.31) c	8.18 - 20.02
Precipitation Driest month (mm)	86.0 (± 6.0) a	74.2 - 116.7	103.3 (± 15.4) b	72.6 - 147.0	130.1 (± 10.7) c	108.5 - 156.8
Evapotranspiration (mm)	1251.7 (± 76.2) a	1066.0 - 1388.0	1280.9 (± 93.9) b	1057.0 - 1476.0	1449.1 (± 60.6) c	1350 - 1553.0
Mean temperature coldest month (ºC)	9.40 (± 1.72) a	4.74 - 13.39	5.68 (± 0.98) b	3.87 - 8.81	8.39 (± 1.01) c	6.01 - 10.11
Temperature seasonality	2945.3 (± 94.1) a	2684 - 3195	3012.2 (± 200.8) b	2499 - 3366	3132.3 (± 133.5) c	2897 - 3371
Fragment area (ha)	1455.58 (± 702.68) a	11.10 - 2461.76	939.73 (± 687.60) b	2.60 - 2316.47	296.57 (± 280.50) c	7.38 - 1083.54
Fragment core area (ha)	1042.67 (± 730.99) a	0.23- 2374	603.84 (± 603.36) b	0.14 - 2146.05	50.68 (± 55.16) c	0.15 - 207.54
Distance from the closest border	49.90 (± 42.68)	5.00 - 262.88	60.41 (± 69.23)	5.00 - 499.81	55.96 (± 37.97)	5.0 - 227.48
Distance nearest neighbour	335.87 (± 429.32) a	2.96-2738.32	193.08 (± 198.18) b	9.95 - 919.89	75.63 (± 44.97) c	2.54 - 183.59
Total core area (ha)	1259.13 (± 588.47) a	50.85 - 2374.42	848.20 (± 512.99) b	50.39 - 2146.05	351.43 (± 118.70) c	155.51 - 682.05
Biotic variables						
Stems density (per 0.4 ha)	270.4 (± 77.90) a	108 - 609	254.76 (± 116.77) a	35 - 589	178.87 (± 63.28) b	46 - 316
Richness	55.79 (± 14.20) a	23 -90	32.17 (± 10.72) b	7 - 52	36.90 (± 8.79) c	12 - 59
Pioneers species (%)	32.16 (± 10.24) a	13.51 - 60.00	45.53 (± 12.43) b	13.33 - 87.50	41.14 (± 8.46) b	23.53 - 63.16
Pioneers stems (%)	33.35 (± 14.70) a	6.93 - 75.28	44.04 (± 21.53) b	4.76 - 97.62	44.61 (± 15.12) c	16.90 - 80.00
Shade-tolerants species (%)	67.84 (± 10.24) a	40.00 - 86.49	54.47 (± 12.43) b	12.50 - 86.67	58.86 (± 8.46) c	36.84 - 76.47
Understorey species (%)	32.39 (± 6.25) a	0 - 46.94	35.15 (± 10.08) b	9.52 - 62.86	26.85 (± 6.97) c	10.53 - 42.11
Canopy species (%)	64.61 (± 5.69) a	48.98 - 87.50	61.07 (± 10.89) b	25.00 - 85.71	68.16 (± 6.92) c	51.52 - 89.47
Emergents spp (%)	2.97 (± 2.13) a	0 - 11.54	3.79 (± 2.61) b	0 - 14.29	4.99 (± 2.85) c	0 - 13.79
Vertebrate-dispersed species (%)	77.71 (± 7.30) a	56.10 - 95.45	75.01 (± 8.08) b	59.09 - 96.15	65.47 (± 7.82) c	41.67 - 81.25
Mean wood density (g/cm^3)	0.63 (± 0.038) a	0.49 - 0.78	0.63 (± 0.062) a	0.48 - 0.84	0.65 ± (0.056) b	0.53 - 0.81

Table 2 – Results from generalized linear models applied to tree assemblages attributes in all three forest types (n=389 plots) in southern Brazil. E = evergreen; A = Araucaria; D = deciduous.

Assemblage attributes	Explanatory variables	Estimate	Std. Error	z value	p-value		R^2 (%) whole model
Species richness	Annual Precipitation	3.891	1.409	2.761	0.006	**	58.22
	Precipitation Seasonality	7.54E-04	1.06E-04	7.103	1.22E-12	***	
	Temperature Seasonality	-3.52E-03	3.32E-03	-1.06	0.289		
	MTCM	6.11E-04	1.06E-04	5.771	7.87E-09	***	
	Evapotranspiration	0.033	7.85E-03	4.168	3.08E-05	***	
	Longitude	7.72E-04	2.02E-04	3.826	0.0001	***	
	Latitude	0.134	0.032	4.196	2.72E-05	***	
	Forest.types (E-A)	-0.063	0.018	-3.57	0.0004	***	
	Forest.types (E-D)	-0.516	0.036	-14.233	< 2e-16	***	
	Soil types	-0.498	0.066	-7.514	5.75E-14	***	
	Successional stage	0.100	0.014	7.127	1.03E-12	***	
	Fragment area	4.69E-05	1.68E-05	2.786	0.005	**	
	Shape index	1.42E-04	4.39E-03	0.032	0.974		
	Distance nearest border	9.37E-05	2.60E-05	3.604	0.0003	***	
	Nearest neighbour	1.86E-04	1.65E-04	1.128	0.259		
Stem density (per 0.4 ha)	Annual Precipitation	5.02E-04	4.55E-05	11.024	< 2e-16	***	34.92
	Precipitation Seasonality	8.18E-05	1.45E-03	0.057	0.955		
	Temperature Seasonality	-3.31E-06	4.22E-05	-0.078	0.938		
	MTCM	-0.045	3.39E-03	-13.356	< 2e-16	***	
	Evapotranspiration	-3.18E-04	8.75E-05	-3.635	2.78E-04	***	
	Longitude	0.087	0.014	6.239	4.40E-10	***	
	Latitude	-0.153	7.70E-03	-19.919	< 2e-16	***	
	Forest.types (E-A)	-0.225	0.015	-15.223	< 2e-16	***	
	Forest.types (E-D)	-0.205	0.027	-7.607	2.81E-14	***	
	Soil types	0.286	0.082	4.361	4.08E-08	***	
	Successional stage	0.110	5.98E-03	18.458	< 2e-16	***	
	Fragment area	6.04E-05	7.05E-06	8.576	< 2e-16	***	
	Shape index	-9.93E-03	1.86E-03	-5.345	9.06E-08	***	
	Distance nearest border	-6.14E-05	1.18E-05	-5.204	1.95E-07	***	
	Nearest neighbour	-1.84E-04	6.77E-05	-2.719	0.007	**	
Pioneer stems (%)	Annual Precipitation	-3.27E-04	7.63E-05	-4.289	1.79E-05	***	30.58
	Precipitation Seasonality	-0.002	2.32E-03	-0.996	0.319		
	Temperature Seasonality	6.28E-04	6.97E-05	9.005	< 2e-16	***	
	MTCM	0.078	5.54E-03	14.132	< 2e-16	***	
	Evapotranspiration	-7.30E-04	1.42E-04	-5.128	2.93E-07	***	
	Longitude	-0.004	0.023	-0.163	0.871		
	Latitude	-0.103	0.013	-7.853	4.06E-15	***	
	Forest.types (E-A)	0.574	0.026	22.445	< 2e-16	***	
	Forest.types (E-D)	0.467	0.043	10.925	< 2e-16	***	
	Soil types	0.286	0.082	4.3612	4.08E-08	***	
	Successional stage	-0.103	0.010	-10.326	< 2e-16	***	
	Fragment area	-6.49E-05	1.20E-05	-5.434	5.50E-08	***	
	Shape index	-7.62E-03	3.08E-03	-2.472	0.013	*	
	Distance nearest border	-1.89E-04	2.50E-05	-7.55	4.36E-14	***	
	Nearest neighbour	6.27E-04	1.09E-04	5.765	8.18E-09	***	
Pioneer species (%)	Annual Precipitation	-1.53E-04	1.77E-04	-0.865	0.387		44.06
	Precipitation Seasonality	1.28E-03	5.51E-03	0.232	0.816		
	Temperature Seasonality	1.65E-04	1.78E-04	0.924	0.356		
	MTCM	0.014	0.013	1.086	0.278		
	Evapotranspiration	-2.58E-04	3.38E-04	-0.762	0.446		
	Longitude	-0.036	0.053	-0.689	0.491		
	Latitude	-0.066	0.030	-2.173	0.030	*	
	Forest.types (E-A)	0.468	0.059	7.989	1.36E-15	***	
	Forest.types (E-D)	0.265	0.102	2.602	0.009	**	
	Soil types	0.131	0.194	0.818	0.326		
	Successional stage	-0.089	0.024	-3.756	0.0002	***	
	Fragment area	-2.68E-05	2.90E-05	-0.926	0.354		
	Shape index	-0.006	7.32E-03	-0.821	0.412		
	Distance nearest border	-1.56E-04	5.24E-05	-2.979	0.003	**	
	Nearest neighbour	-9.02E-05	2.80E-04	-0.322	0.747		

cont. Table 2.

Emergent species (%)	Annual Precipitation	-8.00E-04	5.73E-04	-1.397	0.163	18.45
	Precipitation Seasonality	0.028	0.018	1.594	0.111	
	Temperature Seasonality	-6.95E-04	6.02E-04	-1.153	0.249	
	MTCM	0.126	0.043	2.898	0.004 **	
	Evapotranspiration	3.98E-04	1.12E-03	0.355	0.723	
	Longitude	-0.286	0.167	-1.712	0.087 .	
	Latitude	-0.016	0.102	-0.154	0.878	
	Forest types (E-A)	0.584	0.201	2.904	0.004 **	
	Forest types (E-D)	0.398	0.341	1.165	0.244	
	Soil types	0.131	0.194	0.818	0.326	
	Successional stage	0.043	0.080	0.535	0.592	
	Fragment area	1.05E-04	9.89E-05	1.062	0.288	
	Shape index	0.032	0.023	1.385	0.166	
	Distance nearest border	-1.14E-04	1.73E-04	-0.659	0.510	
	Nearest neighbour	9.65E-04	9.03E-04	1.068	0.285	
Vertebrate-dispersed stems (%)	Annual Precipitation	1.02E-04	5.63E-05	1.808	0.071 .	27.23
	Precipitation Seasonality	-3.32E-03	1.73E-03	-1.92	0.055 .	
	Temperature Seasonality	3.02E-04	5.24E-05	5.758	8.49E-09 ***	
	MTCM	0.060	4.05E-03	14.729	< 2e-16 ***	
	Evapotranspiration	2.41E-05	1.05E-04	0.23	0.818	
	Longitude	0.073	0.017	4.274	1.92E-05 ***	
	Latitude	2.39E-03	9.38E-03	0.255	0.799	
	Forest.types (E-A)	-0.019	0.019	-1.014	0.310	
	Forest.types (E-D)	-0.099	0.034	-2.89	0.004 **	
	Soil types	-0.025	0.047	-0.657	0.232	
	Successional stage	0.023	7.29E-03	3.149	0.002 **	
	Fragment area	0.000	8.54E-06	-17.647	< 2e-16 ***	
	Shape index	-2.72E-03	2.29E-03	-1.187	0.235	
	Distance nearest border	1.14E-04	1.46E-05	7.799	6.23E-15 ***	
	Nearest neighbour	-1.43E-05	8.42E-05	-0.169	0.866	
Vertebrate-dispersed species (%)	Annual Precipitation	5.71E-05	1.25E-04	0.458	0.647	40.60
	Precipitation Seasonality	-0.005	3.87E-03	-1.413	0.158	
	Temperature Seasonality	1.36E-06	1.25E-04	0.011	0.991	
	MTCM	0.015	9.16E-03	1.63	0.103	
	Evapotranspiration	-1.09E-04	2.33E-04	-0.467	0.641	
	Longitude	0.042	0.038	1.127	0.260	
	Latitude	0.008	0.020	0.382	0.703	
	Forest.types (E-A)	-0.016	0.040	-0.386	0.699	
	Forest.types (E-D)	-0.094	0.077	-1.216	0.224	
	Soil types	-0.095	0.116	-0.855	0.381	
	Successional stage	0.028	0.016	1.775	0.076	
	Fragment area	-1.13E-05	1.94E-05	-0.582	0.560	
	Shape index	-6.11E-03	5.11E-03	-1.195	0.232	
	Distance nearest border	2.06E-05	2.98E-05	0.691	0.490	
	Nearest neighbour	4.60E-05	1.93E-04	0.239	0.811	
Mean wood density (g/cm³)	Annual Precipitation	8.15E-05	3.27E-05	2.49	0.013 *	19.48
	Precipitation Seasonality	-3.92E-04	1.06E-03	-0.372	0.710	
	Temperature Seasonality	6.87E-05	3.22E-05	2.132	0.034 *	
	MTCM	0.012	2.52E-03	4.659	4.48E-06 ***	
	Evapotranspiration	-2.05E-05	6.72E-05	-0.305	0.761	
	Longitude	-1.68E-03	9.89E-03	-0.170	0.865	
	Latitude	-1.84E-03	5.87E-03	-0.313	0.755	
	Forest.types (E-A)	0.010	0.011	0.904	0.367	
	Forest.types (E-D)	-0.034	0.019	-1.766	0.078 .	
	Soil types	0.035	0.030	1.2755	0.209	
	Successional stage	0.014	4.46E-03	3.212	0.001 **	
	Fragment area	-1.32E-05	5.38E-06	-2.457	0.014 *	
	Shape index	-4.42E-04	1.37E-03	-0.323	0.747	
	Distance nearest border	1.85E-05	9.43E-06	1.957	0.051 .	
	Nearest neighbour	-7.55E-05	5.03E-05	-1.500	0.134	

Assemblage attributes	Explanatory variables	Estimate	Std. Error	z value	p-value		R² (%) whole model
Stem density (per 0.4 ha)	Annual Precipitation	5.02E-04	4.55E-05	11.024	< 2e-16	***	34.54
	Precipitation Seasonality	8.18E-05	1.45E-03	0.057	0.954849		
	Temperature Seasonality	-3.31E-06	4.22E-05	-0.078	0.937534		
	MTCM	-4.52E-02	3.39E-03	-13.356	< 2e-16	***	
	Evapotranspiration	-3.18E-04	8.75E-05	-3.635	0.000278	***	
	Longitude	8.75E-02	1.40E-02	6.239	4.40E-10	***	
	Latitude	-1.53E-01	7.70E-03	-19.919	< 2e-16	***	
	Forest.types (E-A)	-2.25E-01	1.48E-02	-15.223	< 2e-16	***	
	Forest.types (E-D)	-2.05E-01	2.69E-02	-7.607	2.81E-14	***	
	Soil types	0.286	0.082	4.361	4.075E-08	***	
	Successional stage	1.10E-01	5.98E-03	18.458	< 2e-16	***	
	Fragment area	6.04E-05	7.05E-06	8.576	< 2e-16	***	
	Shape index	-9.93E-03	1.86E-03	-5.345	9.06E-08	***	
	Distance nearest border	-6.14E-05	1.18E-05	-5.204	1.95E-07	***	
	Nearest neighbour	-1.84E-04	6.77E-05	-2.719	0.006547	**	
Species richness	Annual Precipitation	3.89E+00	1.41E+00	2.761	0.005764	**	58.22
	Precipitation Seasonality	7.54E-04	1.06E-04	7.103	1.22E-12	***	
	Temperature Seasonality	-3.52E-03	3.32E-03	-1.06	0.289188		
	MTCM	6.11E-04	1.06E-04	5.771	7.87E-09	***	
	Evapotranspiration	3.27E-02	7.85E-03	4.168	3.08E-05	***	
	Longitude	7.72E-04	2.02E-04	3.826	0.00013	***	
	Latitude	1.34E-01	3.19E-02	4.196	2.72E-05	***	
	Forest.types (E-A)	-6.32E-02	1.77E-02	-3.57	0.000356	***	
	Forest.types (E-D)	-5.16E-01	3.62E-02	-14.233	< 2e-16	***	
	Soil types	-4.98E-01	6.63E-02	-7.514	5.75E-14	***	
	Successional stage	1.00E-01	1.41E-02	7.127	1.03E-12	***	
	Fragment area	4.69E-05	1.68E-05	2.786	0.00534	**	
	Shape index	1.42E-04	4.39E-03	0.032	0.974187		
	Distance nearest border	9.37E-05	2.60E-05	3.604	0.000314	***	
	Nearest neighbour	1.86E-04	1.65E-04	1.128	0.259444		
Pioneer stems (%)	Annual Precipitation	-3.27E-04	7.63E-05	-4.289	1.79E-05	***	30.76
	Precipitation Seasonality	-2.31E-03	2.32E-03	-0.996	0.319329		
	Temperature Seasonality	6.28E-04	6.97E-05	9.005	< 2e-16	***	
	MTCM	7.82E-02	5.54E-03	14.132	< 2e-16	***	
	Evapotranspiration	-7.30E-04	1.42E-04	-5.128	2.93E-07	***	
	Longitude	-3.71E-03	2.28E-02	-0.163	0.870701		
	Latitude	-1.03E-01	1.31E-02	-7.853	4.06E-15	***	
	Forest.types (E-A)	5.74E-01	2.56E-02	22.445	< 2e-16	***	
	Forest.types (E-D)	4.67E-01	4.28E-02	10.925	< 2e-16	***	
	Soil types	2.86E-01	8.17E-02	4.36117	4.08E-08	***	
	Successional stage	-1.03E-01	1.00E-02	-10.326	< 2e-16	***	
	Fragment area	-6.49E-05	1.20E-05	-5.434	5.50E-08	***	
	Shape index	-7.62E-03	3.08E-03	-2.472	0.013431	*	
	Distance nearest border	-1.89E-04	2.50E-05	-7.55	4.36E-14	***	
	Nearest neighbour	6.27E-04	1.09E-04	5.765	8.18E-09	***	
Pioneer species (%)	Annual Precipitation	-1.53E-04	1.77E-04	-0.865	0.386786		44.76
	Precipitation Seasonality	1.28E-03	5.51E-03	0.232	0.81615		
	Temperature Seasonality	1.65E-04	1.78E-04	0.924	0.355599		
	MTCM	1.44E-02	1.33E-02	1.086	0.277606		
	Evapotranspiration	-2.58E-04	3.38E-04	-0.762	0.446236		
	Longitude	-3.65E-02	5.29E-02	-0.689	0.49112		
	Latitude	-6.55E-02	3.02E-02	-2.173	0.029795	*	
	Forest.types (E-A)	4.68E-01	5.86E-02	7.989	1.36E-15	***	
	Forest.types (E-D)	2.65E-01	1.02E-01	2.602	0.009255	**	
	Soil types						
	Successional stage	-8.87E-02	2.36E-02	-3.756	0.000173	***	
	Fragment area	-2.68E-05	2.90E-05	-0.926	0.354264		
	Shape index	-6.01E-03	7.32E-03	-0.821	0.411618		
	Distance nearest border	-1.56E-04	5.24E-05	-2.979	0.002892	**	
	Nearest neighbour	-9.02E-05	2.80E-04	-0.322	0.747233		

Table 3 – Results from generalized linear models averaged (P values) applied to tree assemblages attributes in the three forest types in southern Brazil. E = evergreen; A = Araucaria; D = deciduous.

	Stem density (per 0.1 ha)			Species richness			Pioneer stems (%)			Pioneer species (%)		
Variables	E	A	D	E	A	D	E	A	D	E	A	D
Annual Precipitation	**< 0.001**	**< 0.001**	**0.018**	**0.019**	**< 0.001**	**0.009**	**< 0.001**	**< 0.001**	**< 0.001**	**0.003**	0.133	**0.047**
Precipitation Seasonality	0.130	**< 0.001**	**< 0.001**	0.888	**0.002**	0.081	0.090	0.993	**< 0.001**	0.384	0.960	0.713
MTCM	**< 0.001**	0.458	**< 0.001**	0.676	**0.045**	0.071	**< 0.001**	**< 0.001**	0.081	0.928	0.731	0.811
Evapotranspiration	**0.000**	**0.005**	**0.001**	**0.024**	**< 0.001**	0.543	0.080	0.217	**0.002**	0.467	0.134	0.971
Longitude	0.388	**< 0.001**	**< 0.001**	0.675	0.951	0.328	0.343	**< 0.001**	0.144	**0.025**	0.272	0.809
Latitude	**< 0.001**	**0.003**	0.285	**0.008**	0.795	0.106	**< 0.001**	**< 0.001**	0.170	0.283	**0.009**	0.886
Successional stage	**< 0.001**	**< 0.001**	**0.001**	**< 0.001**	**0.004**	**0.025**	**< 0.001**	**< 0.001**	**0.037**	**< 0.001**	0.335	0.780
Fragment area	0.357	**< 0.001**	0.881	**0.000**	**< 0.001**	0.286	**< 0.001**	**< 0.001**	0.214	0.951	**0.022**	0.958
Shape index	**< 0.001**	**< 0.001**	**0.048**	0.188	0.613	0.242	0.851	**< 0.001**	**< 0.001**	0.711	0.991	0.818
Distance nearest border	**0.011**	**< 0.001**	**< 0.001**	**0.043**	**0.027**	0.337	**< 0.001**	**0.002**	0.427	**< 0.001**	0.373	0.240
Nearest neighbour	0.568	**< 0.001**	**< 0.001**	**0.042**	**< 0.001**	0.991	**< 0.001**	**< 0.001**	**< 0.001**	**0.008**	0.119	0.577

	Emergent species (%)			Vertebrate-dispersed stems (%)			Vertebrate-dispersed seed size			Mean wood density (g/cm²)		
	E	A	D	E	A	D	E	A	D	E	A	D
Annual Precipitation	**0.017**	0.916	0.374	0.143	**0.001**	0.251	**0.009**	0.098	**0.008**	0.393	0.250	0.794
Precipitation Seasonality	0.928	0.424	0.942	**< 0.001**	**0.005**	0.719	0.625	**0.007**	**0.048**	**0.014**	**0.003**	0.425
MTCM	**< 0.001**	0.465	0.512	**< 0.001**	0.411	**0.051**	0.130	**0.041**	**0.034**	0.352	**< 0.001**	0.069
Evapotranspiration	0.305	0.430	0.286	**0.026**	0.485	**0.029**	0.969	0.183	0.291	0.701	0.486	0.308
Longitude	0.407	0.725	0.486	**< 0.001**	**0.049**	**0.034**	0.267	0.093	0.669	0.625	0.307	0.422
Latitude	0.677	0.665	0.189	0.158	**0.013**	0.131	**0.001**	0.082	0.209	0.826	0.489	**0.050**
Successional stage	0.580	0.495	0.633	**< 0.001**	**< 0.001**	0.265	**0.002**	0.412	**0.035**	**0.025**	0.449	**0.051**
Fragment area	**0.019**	0.371	0.287	**0.007**	**< 0.001**	0.128	0.110	0.335	0.762	0.592	0.106	**0.008**
Shape index	0.096	0.868	0.256	**< 0.001**	**< 0.001**	0.649	0.144	**0.038**	0.356	0.100	0.062	0.201
Distance nearest border	0.210	0.803	0.402	**0.001**	**< 0.001**	**0.055**	0.071	0.336	0.130	**0.056**	0.554	0.659
Nearest neighbour	0.415	0.471	0.821	**< 0.001**	**0.002**	0.847	0.362	0.831	0.700	0.722	0.167	0.835

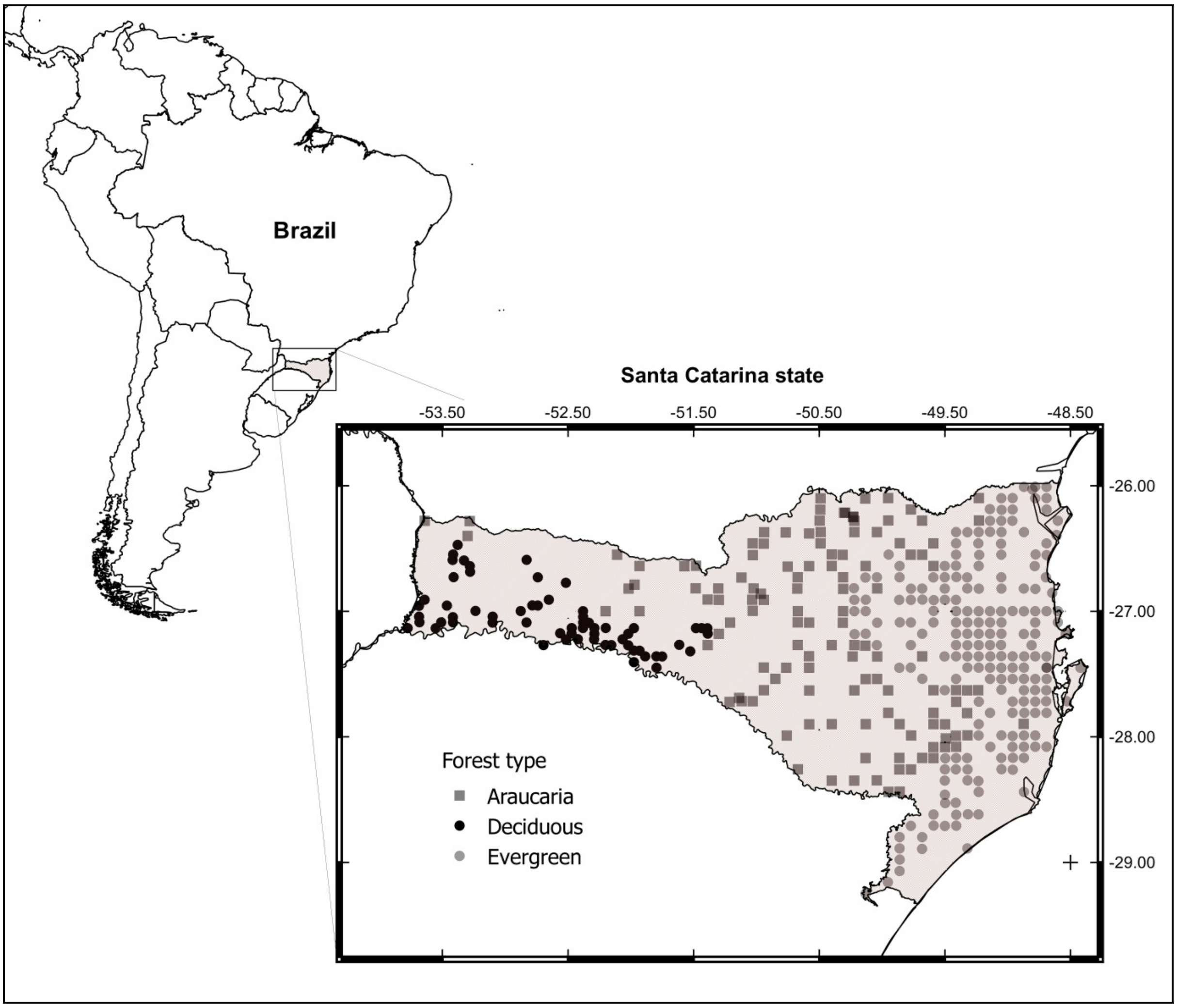


Figure 1. Map showing the location of the 389 0.4-ha plots located within forest fragments in three forest types in southern Brazil.

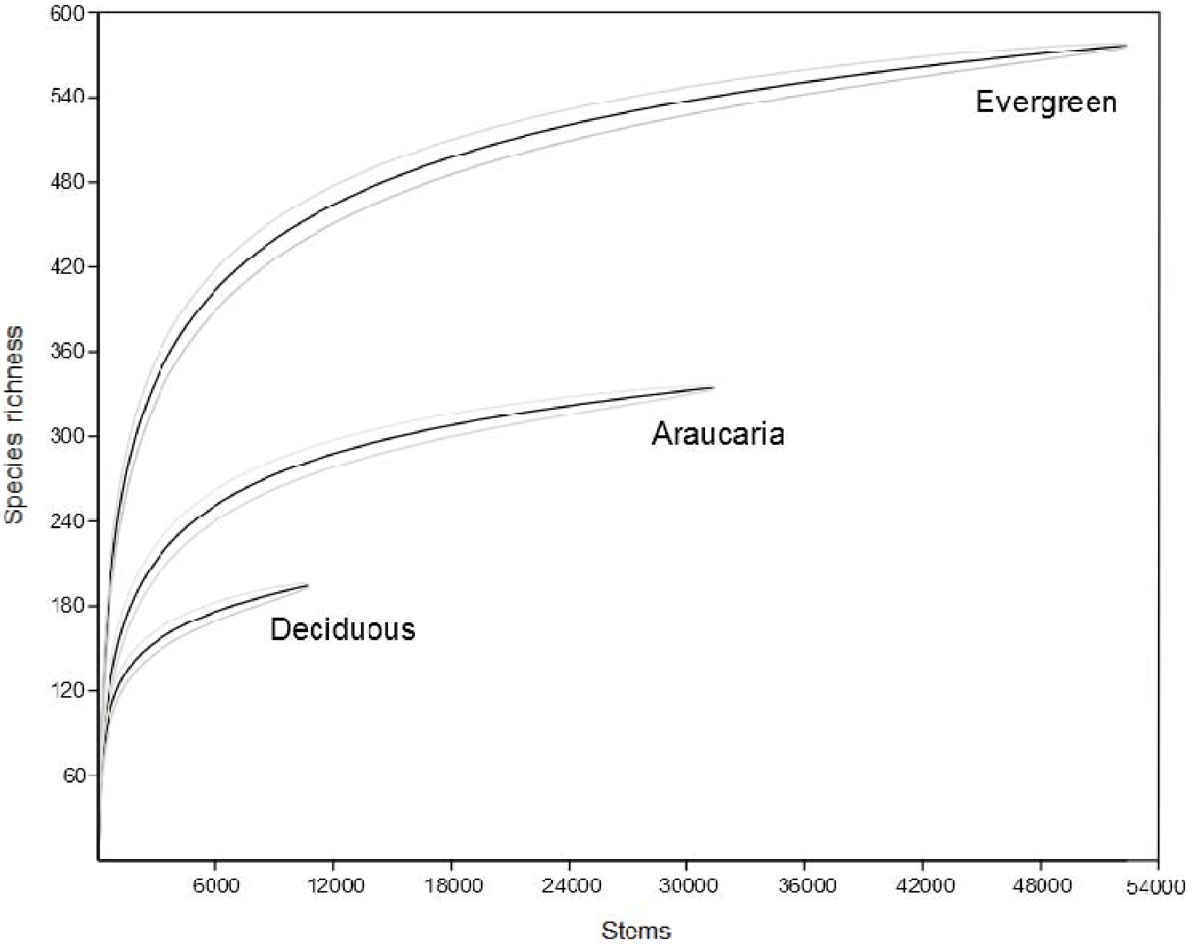


Figure 2. Density and species richness of adult trees, and the respective confidence intervals (95%) obtained by rarefaction, for the three forest types in southern Brazil.

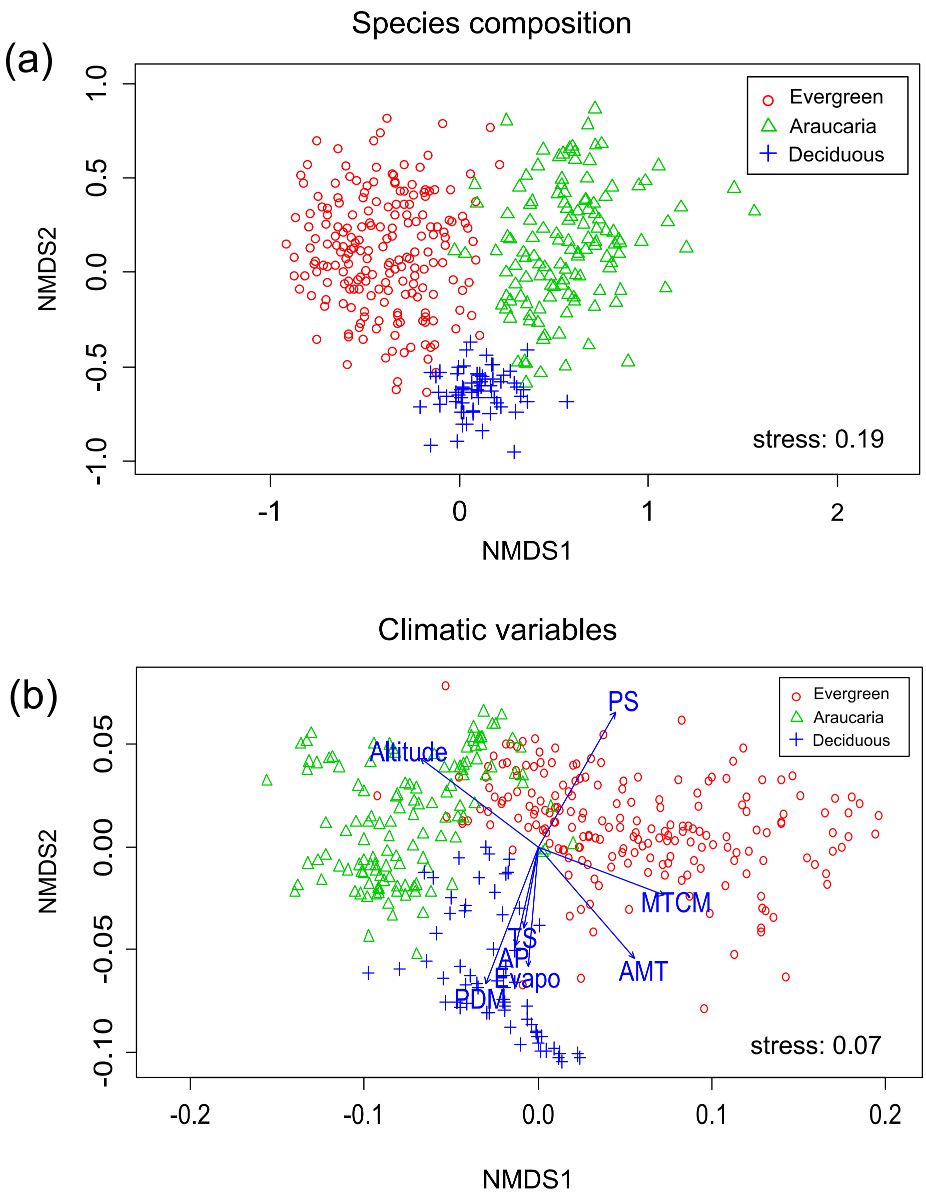


Figure 3. Non-metric multidimensional scaling ordination of the 389 0.4-ha plots located within forest fragments in three forest types in southern Brazil. Defined by their (a) species composition (using abundance data and Bray-Curtis dissimilarity), and (b) climatic variables (the seven climatic variables summarized in Table 1, plus altitude). The environmental predictors are shown as arrows pointing at the prevailing direction of increasing values and lengths proportional to their correlations with ordination scores. PS = precipitation seasonality; MTCM = mean temperature coldest month; AMT = annual mean temperature; AP = annual precipitation; evapo = evapotranspiration; PDM = precipitation driest month; TS = temperature seasonality.

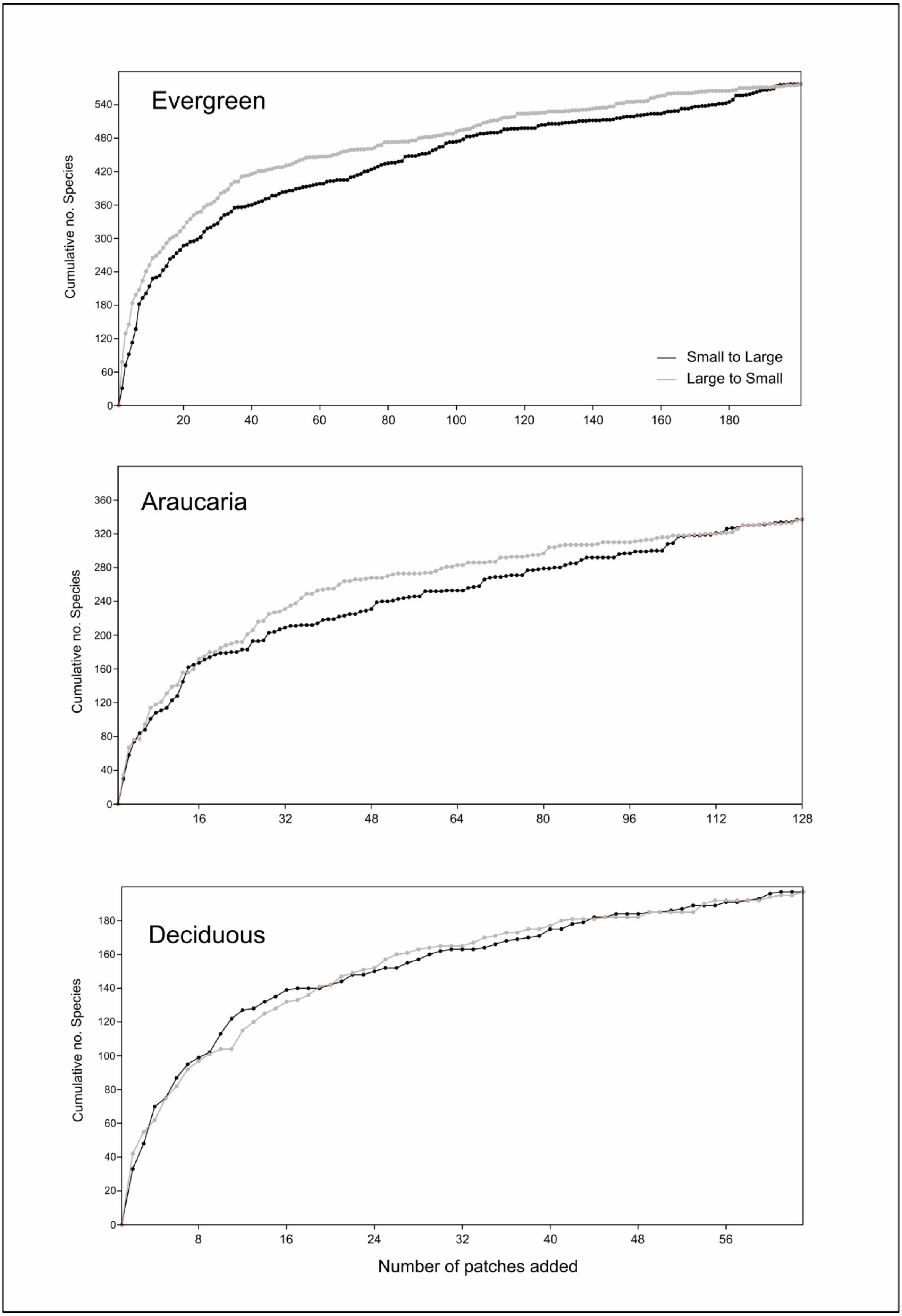
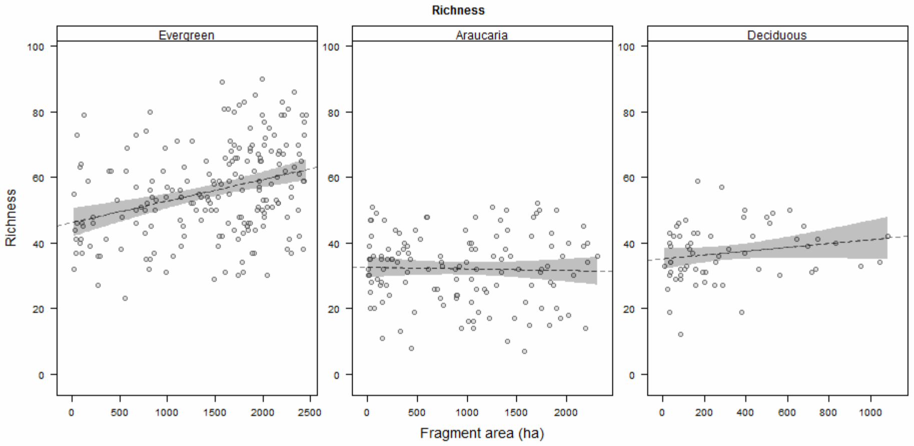
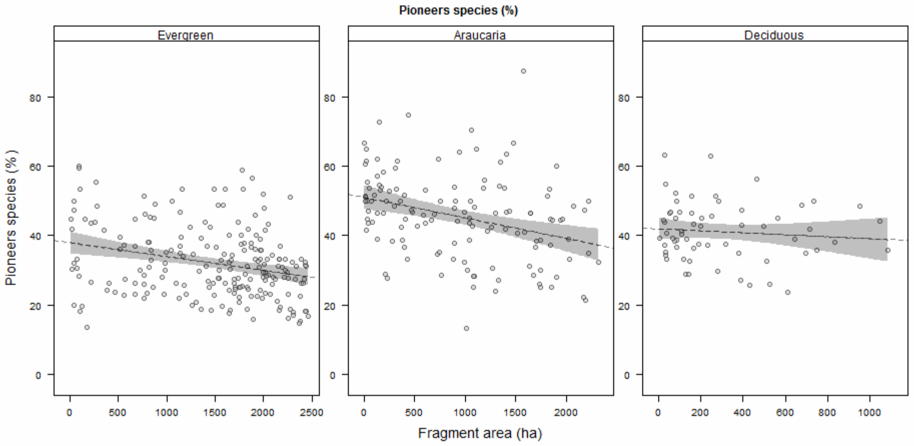
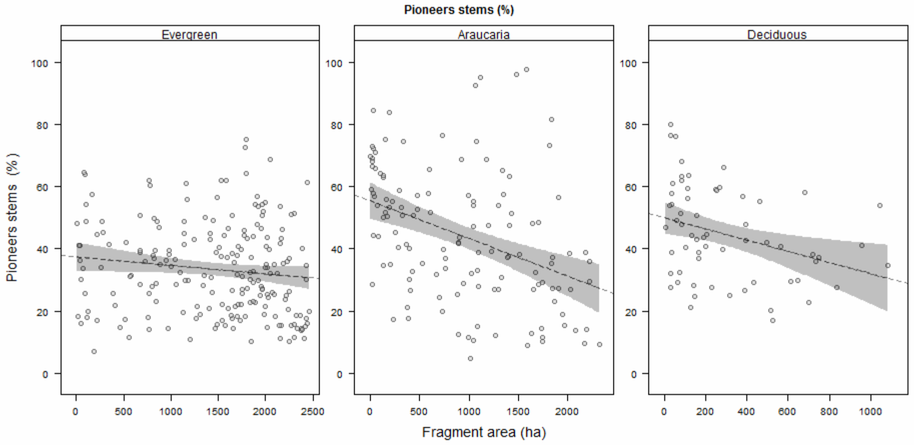

Evergreen
Cumulative no. Species
0
60
120
180
240
300
360
420
480
540
20
40
60
80
100
120
140
160
180
Small to Large
Large to Small
Araucaria
Cumulative no. Species
0
40
80
120
160
200
240
280
320
360
16
32
48
64
80
96
112
128
Deciduous
Cumulative no. Species
0
20
40
60
80
100
120
140
160
180
8
16
24
32
40
48
56
Number of patches added

Figure 4. Cumulative number of plant species sampled in 0.4 ha per patch versus cumulative number of patches added in the three forest types. Patches were added from small to large or large to small, respectively, and then corresponding cumulative species counts were obtained.


Richness


Pioneers species (%)


Pioneers stems (%)

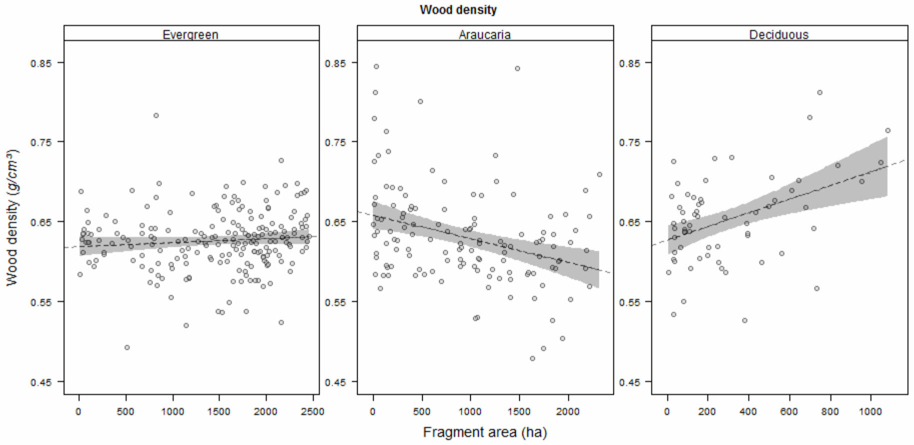

Wood density

Figure 5. Relationships between fragment area and (a) tree species richness, (b) percentage of pioneer tree species, (c) percentage of pioneer stems, and (d) mean wood density (g/cm²). Data points represent the 0.4-ha plots sampled forest fragments across three forest types of southern Brazil.

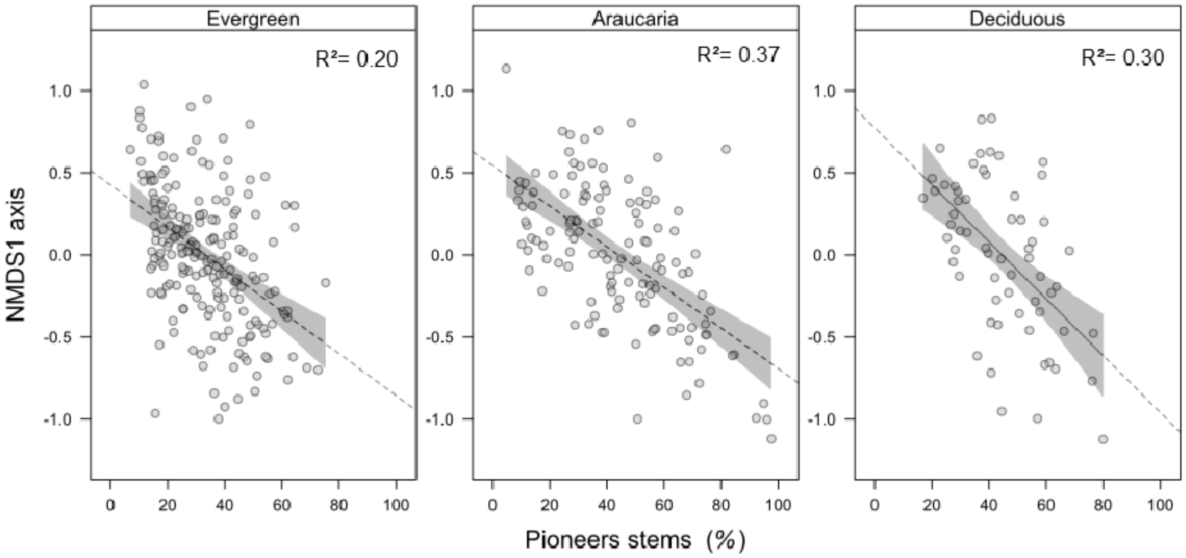


Figure 6. Relationship between the NMDS ordinations axis and the percentage of pioneer stems in 0.4-ha plots in forest fragments in each of three forest types. R² values refer to linear regression models.

Suplementary material

Table S.1 – Indicator species analysis of tree assemblages recorded in 389 forest fragment plots in three forest types in southern Brazil.

Indicator species	*specificity*	*fidelity*	Indicator value	*p*
Evergreen - 161 species				
Alchornea triplinervia (Spreng.) Müll.Arg.	0.95	0.76	0.85	0.001
Psychotria vellosiana Benth.	0.93	0.62	0.76	0.001
Nectandra oppositifolia Nees	0.97	0.60	0.76	0.001
Euterpe edulis Mart.	1.00	0.55	0.74	0.001
Matayba intermedia Radlk.	0.83	0.64	0.73	0.001
Guapira opposita (Vell.) Reitz	1.00	0.53	0.73	0.001
Guatteria australis A. St.-Hil.	0.97	0.54	0.72	0.001
Cecropia glaziovi Snethl.	1.00	0.51	0.71	0.001
Hieronyma alchorneoides Allemão	1.00	0.51	0.71	0.001
Alsophila setosa Kaulf.	0.94	0.53	0.70	0.001
Myrcia pubipetala Miq.	1.00	0.49	0.70	0.001
Cyathea phalerata Mart.	0.98	0.48	0.68	0.001
Ocotea elegans Mez	0.91	0.51	0.68	0.001
Annona neosericea H.Rainer	1.00	0.43	0.65	0.001
Pera glabrata (Schott) Poepp. ex Baill.	1.00	0.42	0.65	0.001
Bathysa australis (A.St.-Hil.) K.Schum.	1.00	0.42	0.64	0.001
Byrsonima ligustrifolia A.Juss.	1.00	0.42	0.64	0.001
Posoqueria latifolia (Rudge) Schult.	1.00	0.41	0.64	0.001
Aniba firmula (Nees & Mart.) Mez	1.00	0.39	0.62	0.001
Miconia cabussu Hoehne	1.00	0.39	0.62	0.001
Cryptocarya mandioccana Meisn.	0.92	0.42	0.62	0.001
Piptocarpha axillaris (Less.) Baker	0.79	0.48	0.61	0.001
Heisteria silvianii Schwacke	1.00	0.37	0.60	0.001
Ocotea catharinensis Mez	1.00	0.37	0.60	0.001
Sloanea guianensis (Aubl.) Benth.	0.97	0.38	0.60	0.001
Hirtella hebeclada Moric. ex DC.	1.00	0.36	0.60	0.001
Inga sessilis (Vell.) Mart.	1.00	0.36	0.60	0.001
Virola bicuhyba (Schott ex Spreng.) Warb.	1.00	0.36	0.60	0.001
Miconia cinnamomifolia (DC.) Naudin	1.00	0.35	0.59	0.001
Maytenus robusta Reissek	1.00	0.34	0.58	0.001
Protium kleinii Cuatrec.	1.00	0.34	0.58	0.001
Ocotea nectandrifolia Mez	0.96	0.31	0.55	0.001
Cyathea delgadii Sternb.	0.98	0.30	0.54	0.001
Myrcia brasiliensis Kiaersk.	0.92	0.29	0.52	0.001
Xylopia brasiliensis Spreng.	1.00	0.27	0.52	0.001
Ocotea silvestris Vattimo-Gil	0.98	0.27	0.51	0.001
Garcinia gardneriana (Planch. & Triana) Zappi	1.00	0.26	0.51	0.001

Magnolia ovata (A.St.-Hil.) Spreng.	1.00	0.26	0.51	0.001
Copaifera trapezifolia Hayne	1.00	0.25	0.50	0.001
Duguetia lanceolata A.St.-Hil.	1.00	0.25	0.50	0.001
Schefflera angustissima (Marchal) Frodin	0.98	0.25	0.50	0.001
Tapirira guianensis Aubl.	1.00	0.24	0.49	0.001
Ocotea odorifera (Vell.) Rohwer	0.69	0.35	0.49	0.003
Annona cacans Warm.	1.00	0.24	0.49	0.001
Myrcia tijucensis Kiaersk.	1.00	0.24	0.49	0.001
Ormosia arborea (Vell.) Harms	0.99	0.24	0.48	0.001
Tetrorchidium rubrivenium Poepp.	0.96	0.24	0.48	0.001
Aiouea saligna Meisn.	1.00	0.22	0.47	0.001
Pseudobombax grandiflorum (Cav.) A.Robyns	1.00	0.22	0.46	0.001
Calyptranthes grandifolia O. Berg	0.83	0.26	0.46	0.001
Meliosma sellowii Urb.	0.80	0.27	0.46	0.001
Coussapoa microcarpa (Schott) Rizzini	0.92	0.23	0.46	0.001
Ficus adhatodifolia Schott ex Spreng.	0.92	0.23	0.46	0.001
Calyptranthes lucida Mart. ex DC.	1.00	0.21	0.46	0.001
Clusia criuva Cambess.	1.00	0.21	0.46	0.001
Amaioua guianensis Aubl.	0.95	0.22	0.46	0.001
Brosimum lactescens (S.Moore) C.C.Berg	1.00	0.21	0.45	0.001
Ocotea aciphylla (Nees & Mart.) Mez	1.00	0.21	0.45	0.001
Coccoloba warmingii Meisn.	0.97	0.21	0.45	0.001
Nectandra membranacea (Sw.) Griseb.	0.90	0.21	0.43	0.002
Ocotea glaziovii Mez	0.97	0.19	0.43	0.001
Abarema langsdorffii (Benth.) Barneby & J.W. Grimes	1.00	0.18	0.42	0.001
Zollernia ilicifolia (Brongn.) Vogel	1.00	0.18	0.42	0.001
Alchornea glandulosa Poepp. & Endl.	0.99	0.18	0.42	0.001
Trichilia lepidota Mart.	1.00	0.17	0.41	0.001
Alchornea sidifolia Müll.Arg.	0.86	0.19	0.40	0.002
Chrysophyllum viride Mart. & Eichler	0.98	0.17	0.40	0.002
Eugenia ternatifolia Cambess.	1.00	0.16	0.40	0.001
Ocotea corymbosa (Meisn.) Mez	0.81	0.20	0.40	0.003
Ocotea pulchra Vattimo-Gil	1.00	0.16	0.39	0.001
Platymiscium floribundum Vogel	1.00	0.15	0.39	0.001
Laplacea fruticosa (Schrad.) Kobuski	0.85	0.18	0.39	0.004
Andira fraxinifolia Benth.	0.99	0.15	0.39	0.001
Aspidosperma tomentosum Mart.	0.95	0.16	0.39	0.002
Buchenavia kleinii Exell	1.00	0.15	0.38	0.001
Miconia budlejoides Triana	1.00	0.15	0.38	0.001
Seguieria langsdorffi Moq.	0.91	0.16	0.38	0.001
Vantanea compacta (Schnizl.) Cuatrec.	1.00	0.14	0.37	0.001
Aparisthmium cordatum (A.Juss.) Baill.	1.00	0.14	0.37	0.002
Calyptranthes strigipes O.Berg	1.00	0.14	0.37	0.001
Alseis floribunda Schott	0.84	0.16	0.36	0.001
Piptadenia gonoacantha (Mart.) J.F.Macbr.	0.99	0.13	0.36	0.002

Campomanesia guaviroba (DC.) Kiaersk.	0.95	0.13	0.35	0.001
Aegiphila integrifolia (Jacq.) Moldenke	0.90	0.14	0.35	0.003
Eugenia involucrata DC.	0.73	0.17	0.35	0.023
Brosimum glaziovii Taub.	1.00	0.12	0.35	0.001
Marlierea silvatica (O.Berg) Kiaersk.	1.00	0.12	0.35	0.001
Ocotea mandioccana A.Quinet	1.00	0.12	0.35	0.001
Pterocarpus rohrii Vahl	1.00	0.12	0.35	0.002
Citharexylum myrianthum Cham.	0.98	0.12	0.34	0.001
Psidium cattleianum Sabine	0.93	0.13	0.34	0.007
Myrcia aethusa (O.Berg) N.Silveira	0.97	0.12	0.34	0.001
Esenbeckia grandiflora Mart.	0.89	0.13	0.34	0.003
Schizolobium parahyba (Vell.) Blake	1.00	0.12	0.34	0.001
Eugenia cereja D.Legrand	1.00	0.11	0.33	0.001
Ficus cestrifolia Schott ex Spreng.	1.00	0.11	0.33	0.003
Myrcia glabra (O.Berg) D.Legrand	1.00	0.11	0.33	0.001
Podocarpus sellowii Klotzsch ex Endl.	0.89	0.12	0.33	0.001
Cordia silvestris Fresen.	1.00	0.11	0.32	0.003
Pouteria venosa (Mart.) Baehni	1.00	0.11	0.32	0.001
Chrysophyllum inornatum Mart.	0.96	0.11	0.32	0.005
Nectandra leucantha Nees	1.00	0.10	0.32	0.002
Pimenta pseudocaryophyllus (Gomes) Landrum	0.79	0.13	0.31	0.013
Eugenia brevistyla D.Legrand	1.00	0.10	0.31	0.003
Ocotea vaccinioides (Meisn.) Mez	0.98	0.10	0.30	0.002
Nectandra puberula (Schott) Nees	0.88	0.11	0.30	0.003
Myrcia pulchra (O. Berg) Kiaersk.	0.73	0.13	0.30	0.026
Myrsine parvula (Mez) Otegui	0.86	0.11	0.30	0.005
Psychotria carthagenensis Jacq.	0.95	0.10	0.30	0.005
Eugenia multicostata D.Legrand	1.00	0.09	0.30	0.003
Faramea montevidensis (Cham. & Schltdl.) DC.	1.00	0.09	0.30	0.003
Ocotea dispersa (Nees & Mart.) Mez	1.00	0.09	0.30	0.002
Marlierea excoriata Mart.	0.90	0.10	0.30	0.006
Marlierea obscura O.Berg	1.00	0.09	0.29	0.002
Miconia cubatanensis Hoehne	1.00	0.08	0.28	0.005
Piptadenia paniculata Benth.	1.00	0.08	0.28	0.011
Machaerium hirtum (Vell.) Stellfeld	0.91	0.09	0.28	0.007
Cariniana estrellensis (Raddi) Kuntze	1.00	0.08	0.27	0.004
Chionanthus trichotomus (Vell.) P.S.Green	1.00	0.08	0.27	0.007
Mollinedia schottiana (Spreng.) Perkins	1.00	0.08	0.27	0.004
*Myrcia dichrophyll*a D.Legrand	1.00	0.08	0.27	0.003
Myrcia spectabilis DC.	1.00	0.08	0.27	0.008
Quiina glazovii Engl.	1.00	0.08	0.27	0.004
Tibouchina pulchra Cogn.	0.93	0.08	0.27	0.024
Cedrela fissilis Vell.	0.92	0.08	0.27	0.011
Myrsine lancifolia Mart.	0.97	0.08	0.27	0.01
Inga sellowiana Benth.	0.94	0.08	0.27	0.006

Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.	1.00	0.07	0.27	0.005
Eugenia cerasiflora Miq.	1.00	0.07	0.27	0.005
Miconia valtheri Naudin	1.00	0.07	0.27	0.01
Mollinedia triflora (Spreng.) Tul.	1.00	0.07	0.27	0.005
Neomitranthes glomerata (D.Legrand) D.Legrand	1.00	0.07	0.27	0.007
Pourouma guianensis Aubl.	1.00	0.07	0.27	0.007
Eugenia handroana D.Legrand	0.73	0.10	0.26	0.028
Marlierea tomentosa Cambess.	1.00	0.07	0.26	0.007
Myrsine hermogenesii (Jung-Mend. & Bernacci) M.F.Freitas & Kin.-Gouv.	1.00	0.07	0.26	0.008
Ouratea vaccinioides (A.St.-Hil. & Tul.) Engl.	1.00	0.07	0.26	0.009
Psychotria suterella Müll.Arg.	0.92	0.07	0.25	0.009
Rudgea jasminoides (Cham.) Müll.Arg.	0.79	0.08	0.25	0.029
Cinnamomum pseudoglaziovii Lorea-Hern.	1.00	0.06	0.25	0.015
*Miconia pusilliflora (*DC.) Naudin	1.00	0.06	0.25	0.006
Cupania oblongifolia Mart.	1.00	0.06	0.24	0.023
Handroanthus umbellatus (Sond.) Mattos	1.00	0.06	0.24	0.015
Pausandra morisiana (Casar.) Radlk.	1.00	0.06	0.24	0.018
Banara parviflora (A. Gray) Benth.	0.89	0.06	0.23	0.045
Persea alba Nees & Mart.	0.88	0.06	0.23	0.039
Aspidosperma ramiflorum Müll. Arg.	1.00	0.05	0.22	0.021
Calophyllum brasiliense Cambess.	1.00	0.05	0.22	0.039
Cyathea atrovirens (Langsd. & Fisch.) Domin	1.00	0.05	0.22	0.012
Hedyosmum brasiliense Miq.	1.00	0.05	0.22	0.03
Mollinedia clavigera Tul.	0.94	0.05	0.22	0.038
Chionanthus micranthus (Mart.) Lozano & Fuertes	1.00	0.05	0.21	0.029
Cinnamomum hatschbachii Vattimo-Gil	1.00	0.05	0.21	0.035
Diospyros inconstans Jacq.	1.00	0.05	0.21	0.019
Inga striata Benth.	1.00	0.05	0.21	0.022
Marlierea reitzii D. Legrand	1.00	0.05	0.21	0.028
Ouratea parviflora (A.DC.) Baill.	1.00	0.05	0.21	0.029
Pachystroma longifolium (Nees) I.M.Johnst.	1.00	0.05	0.21	0.022
Aspidosperma parvifolium A.DC.	1.00	0.04	0.20	0.024
Boehmeria caudata Sw.	1.00	0.04	0.20	0.036
Myrcia anacardiifolia Gardner	1.00	0.04	0.20	0.029
Araucaria – 58 species				
Araucaria angustifolia (Bertol.) Kuntze	1.00	0.70	0.84	0.001
Dicksonia sellowiana Hook.	0.98	0.65	0.80	0.001
Ilex paraguariensis A.St.-Hil.	0.82	0.62	0.71	0.001
Ocotea pulchella (Nees & Mart.) Mez	0.86	0.55	0.69	0.001
Cinnamomum amoenum (Nees & Mart.) Kosterm.	0.98	0.48	0.69	0.001
Vernonanthura discolor (Spreng.) H.Rob.	0.68	0.69	0.68	0.001
Styrax leprosus Hook. & Arn.	0.88	0.46	0.64	0.001
Casearia decandra Jacq.	0.75	0.52	0.63	0.001
Lithraea brasiliensis Marchand	0.99	0.38	0.61	0.001
Cinnamodendron dinisii Schwacke	0.98	0.38	0.61	0.001

Mimosa scabrella Benth.	0.95	0.39	0.61	0.001
Drimys brasiliensis Miers	0.90	0.39	0.59	0.001
Ocotea porosa (Nees & Mart.) Barroso	0.95	0.37	0.59	0.001
Myrcia guianensis (Aubl.) DC.	0.93	0.28	0.51	0.001
Blepharocalyx salicifolius (Kunth) O.Berg	0.92	0.26	0.49	0.001
Ilex brevicuspis Reissek	0.64	0.33	0.46	0.003
Calyptranthes concinna DC.	0.99	0.19	0.43	0.001
Symplocos uniflora (Pohl) Benth.	0.92	0.20	0.43	0.001
Podocarpus lambertii Klotzsch ex Endl.	0.97	0.17	0.41	0.001
Scutia buxifolia Reissek	1.00	0.17	0.41	0.001
Allophylus guaraniticus (A. St.-Hil.) Radlk.	0.97	0.17	0.40	0.001
Myrcianthes gigantea (D.Legrand) D.Legrand	1.00	0.16	0.40	0.001
Myrcia palustris DC.	0.95	0.17	0.40	0.001
Myrceugenia miersiana (Gardner) D.Legrand & Kausel	0.83	0.17	0.38	0.001
Citronella gongonha (Mart.) R. A. Howard	1.00	0.14	0.38	0.001
Myrceugenia glaucescens (Cambess.) D.Legrand & Kausel	1.00	0.14	0.38	0.001
Myrsine gardneriana A.DC.	0.84	0.17	0.37	0.004
Inga lentiscifolia Benth.	0.97	0.14	0.37	0.001
Acca sellowiana (O. Berg) Burret	0.95	0.14	0.37	0.001
Myrcia oblongata DC.	1.00	0.13	0.36	0.001
Zanthoxylum kleinii (R.S.Cowan) P.G.Waterman	0.99	0.12	0.34	0.001
Weinmannia humilis Engl.	0.98	0.12	0.34	0.001
Symplocos tetrandra Mart.	0.79	0.14	0.33	0.003
Dasyphyllum spinescens (Less.) Cabrera	0.91	0.11	0.32	0.001
Eugenia handroi (Mattos) Mattos	0.89	0.11	0.31	0.003
Eugenia pluriflora DC.	0.98	0.09	0.30	0.002
Myrcia hatschbachii D.Legrand	0.92	0.09	0.30	0.003
Drimys angustifolia Miers	1.00	0.09	0.29	0.002
Myrceugenia euosma (O.Berg) D.Legrand	1.00	0.09	0.29	0.002
Dasyphyllum tomentosum (Spreng.) Cabrera	0.89	0.09	0.29	0.002
Solanum pabstii L.B.Sm. & Downs	0.95	0.09	0.29	0.001
Quillaja brasiliensis (A.St.-Hil. & Tul.) Mart.	1.00	0.08	0.28	0.002
Nectandra grandiflora Nees	0.82	0.09	0.28	0.023
Annona neosalicifolia H. Rainer	0.81	0.09	0.28	0.006
Myrceugenia alpigena (DC.) Landrum	0.97	0.08	0.28	0.004
Myrrhinium atropurpureum Schott	1.00	0.06	0.25	0.002
Schinus lentiscifolius Marchand	1.00	0.06	0.25	0.004
Machaerium vestitum Vogel	0.76	0.08	0.24	0.026
Escallonia bifida Link & Otto	0.83	0.07	0.24	0.006
Baccharis oreophila Malme	0.89	0.06	0.24	0.014
Maytenus boaria Molina	1.00	0.06	0.24	0.007
Schinus polygamus (Cav.) Cabrera	1.00	0.06	0.24	0.004
Siphoneugena reitzii D.Legrand	0.87	0.06	0.22	0.038
Oreopanax fulvus Marchal	0.90	0.05	0.21	0.025
Eugenia uruguayensis Cambess.	0.89	0.05	0.21	0.025

Aureliana fasciculata (Vell.) Sendtn.	0.93	0.04	0.19	0.031
Machaerium scleroxylon Tul.	1.00	0.03	0.18	0.033
Persea major (Meisn.) L.E.Kopp	1.00	0.03	0.18	0.032
Deciduous – 70 species				
Nectandra megapotamica (Spreng.) Mez	0.73	0.94	0.83	0.001
Luehea divaricata Mart. & Zucc.	0.82	0.84	0.83	0.001
Balfourodendron riedelianum (Engl.) Engl.	0.98	0.68	0.81	0.001
Machaerium stipitatum (DC.) Vogel	0.82	0.74	0.78	0.001
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	0.91	0.66	0.78	0.001
Myrocarpus frondosus Allemão	0.87	0.68	0.77	0.001
Trichilia claussenii C.DC.	0.93	0.63	0.77	0.001
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	0.95	0.60	0.75	0.001
Nectandra lanceolata Nees	0.79	0.69	0.74	0.001
Cordia americana (L.) Gottschling & J.S.Mill.	0.99	0.48	0.69	0.001
Apuleia leiocarpa (Vogel) J.F. Macbr.	0.99	0.47	0.68	0.001
Cordia trichotoma (Vell.) Arráb. ex Steud.	0.85	0.55	0.68	0.001
Diatenopteryx sorbifolia Radlk.	0.98	0.47	0.68	0.001
Machaerium paraguariense Hassl.	0.82	0.53	0.66	0.001
Pilocarpus pennatifolius Lem.	0.97	0.44	0.65	0.001
Urera baccifera (L.) Gaudich. ex Wedd.	0.99	0.42	0.64	0.001
Annona sylvatica A.St.-Hil.	0.83	0.50	0.64	0.001
Parapiptadenia rigida (Benth.) Brenan	0.91	0.45	0.64	0.001
Hovenia dulcis Thunb.	0.89	0.44	0.62	0.001
Phytolacca dioica L.	0.72	0.53	0.62	0.001
Lonchocarpus campestris Mart. ex Benth.	0.59	0.65	0.62	0.001
Sebastiania brasiliensis Spreng.	0.83	0.37	0.56	0.001
Picrasma crenata (Vell.) Engl.	0.76	0.39	0.54	0.001
Albizia edwallii (Hoehne) Barneby & J.W. Grimes	0.73	0.39	0.53	0.001
Strychnos brasiliensis Mart.	0.89	0.31	0.52	0.001
Solanum mauritianum Scop.	0.72	0.37	0.52	0.001
Aloysia virgata (Ruiz & Pav.) Juss.	1.00	0.26	0.51	0.001
Holocalyx balansae Micheli	0.98	0.26	0.50	0.001
Ocotea diospyrifolia (Meisn.) Mez	0.66	0.37	0.49	0.001
Actinostemon concolor (Spreng.) Müll.Arg.	0.77	0.31	0.49	0.001
Celtis iguanaea (Jacq.) Sarg.	0.91	0.26	0.48	0.001
Cordia ecalyculata Vell.	0.86	0.24	0.46	0.001
Banara tomentosa Clos	0.64	0.32	0.46	0.001
Rauvolfia sellowii Müll.Arg.	1.00	0.19	0.44	0.001
Trichilia catigua A.Juss.	1.00	0.19	0.44	0.001
Vasconcellea quercifolia A.St.-Hil.	0.99	0.19	0.44	0.001
Pisonia ambigua Heimerl	0.56	0.34	0.44	0.001
Ruprechtia laxiflora Meisn.	0.72	0.24	0.42	0.001
Campomanesia guazumifolia (Cambess.) O.Berg	0.72	0.24	0.42	0.001
Erythrina falcata Benth.	0.73	0.23	0.41	0.001
Peltophorum dubium (Spreng.) Taub.	1.00	0.16	0.40	0.001

Randia ferox (Cham. & Schltdl.) DC.	0.89	0.18	0.40	0.001
Eugenia uniflora L.	0.69	0.23	0.40	0.001
Helietta apiculata Benth.	0.74	0.21	0.39	0.001
Allophylus puberulus (Cambess.) Radlk.	0.95	0.16	0.39	0.001
Bauhinia forficata Link	0.50	0.31	0.39	0.001
Calliandra foliolosa Benth.	0.98	0.15	0.38	0.001
Myrcianthes pungens (O.Berg) D.Legrand	0.62	0.21	0.36	0.001
Eugenia rostrifolia D.Legrand	0.89	0.13	0.34	0.001
Ceiba speciosa (A. St.-Hil.) Ravenna	1.00	0.11	0.34	0.001
Zanthoxylum fagara (L.) Sarg.	0.61	0.18	0.33	0.001
Zanthoxylum petiolare A.St.-Hil. & Tul.	0.71	0.15	0.32	0.001
Enterolobium contortisiliquum (Vell.) Morong	0.81	0.11	0.30	0.001
Calyptranthes tricona D. Legrand	0.73	0.11	0.29	0.002
Sambucus australis Cham. & Schltdl.	0.72	0.11	0.29	0.001
Achatocarpus praecox Griseb.	1.00	0.08	0.28	0.001
Seguieria aculeata Jacq.	0.83	0.08	0.26	0.017
Picramnia parvifolia Engl.	1.00	0.06	0.25	0.003
Albizia niopoides (Spruce ex Benth.) Burkart	0.93	0.06	0.24	0.003
Ateleia glazioviana Baill.	0.90	0.06	0.24	0.005
Eugenia gracillima Kiaersk.	1.00	0.05	0.22	0.005
Bastardiopsis densiflora (Hook. & Arn.) Hassl.	0.99	0.05	0.22	0.009
Trichilia elegans A.Juss.	0.85	0.05	0.20	0.013
Jacaratia spinosa (Aubl.) A.DC.	0.76	0.05	0.19	0.021
Gleditsia amorphoides (Griseb.) Taub.	0.73	0.05	0.19	0.038
Aralia warmingiana (Marchal) J. Wen	1.00	0.03	0.18	0.024
Persea americana Mill.	0.99	0.03	0.18	0.016
Lonchocarpus nitidus (Vogel) Benth.	0.94	0.03	0.17	0.042
Coccoloba argentinensis Speg.	0.91	0.03	0.17	0.034
Erythrina crista-galli L.	0.91	0.03	0.17	0.033

5 DISCUSSÃO GERAL

A Mata Atlântica sul-brasileira apresenta uma elevada heterogeneidade espacial, tanto em termos de ambientes quanto de vegetação, que é, certamente, decorrente da sua complexa geomorfologia. No centro da região Sul do Brasil, temos o planalto sul-brasileiro com altitudes que decrescem suavemente a oeste, e com abruptas encostas no litoral, que se elevam do nível no mar até altitudes que chegam a 2800 m acima do nível do mar (Bigarella 1991; Ribeiro et al. 2009).

A abrupta e íngreme elevação das encostas ao longo da costa está diretamente relacionada a diferenciação entre a Floresta Ombrófila Densa e a Floresta Ombrófila Mista. Chuvas orográficas nas encostas formadas pela ascenção do ar úmido e quente provindo do oceano em direção ao continente, promovem chuvas abundantes ao longo de todo o ano e um superávit hídrico nas encostas, contudo existe um pico de precipitação durante o verão (Higuchi et al. 2013; Oliveira-Filho et al. 2014, Capítulo 2). Uma parcela menor das frentes oceânicas chega às regiões mais interioranas da região sul, particularmente no verão. Contudo ambas as regiões recebem precipitações adicionais das frentes provindas da Antártida, particularmente no inverno (Roderjan et al. 2002). Devido a essas duas frentes, praticamente não existe um pronuncado déficit hídrico nos dois lados do planalto sul-brasileiro, principalmente se analisarmos apenas os dados médios mensais das últimas décadas. Contudo vale ressaltar que diversos autores já alertaram que os anos extremos, ao invés dos anos situados na média, devem ser os mais significativos em moldar a estrutura, composição e propriedades funcionais dos ecossistemas florestais mais secos e estacionais (Murphy e Lugo 1986; Engelbrecht et al. 2007, 2012). E a significativa proporção de espécies decíduas, faz ao menos se ponderar que se deve ter cautela ao afirmar que eventos de secas nos domínios das florestas estacionais nos subtrópicos, não sejam sequer eventos supra-anuais. O déficit hídrico é um fator chave que delimita os limites do Domínio Atlântico nos subtrópicos, o Chaco, Espinal e os domínios do Pampa são delimitados pela precipitação, onde esta cai o suficiente para originar, pelo menos alguns, meses de seca (Higuchi et al. 2013; Oliveira-Filho et al. 2014).

A distribuição das florestas com Araucaria é provavelmente limitada pelo aumento das temperaturas em direção às altitudes e latitudes menores, onde são substituídas pelas florestas decíduas e sua flora com afinidades relacionadas a ambientes mais quentes e sazonais (Capítulo 2). O fato de várias espécies das florestas deciduais perderem suas folhas durante a estação fria, mesmo em áreas onde não há um significativo déficit hídrico, pode ser nada mais do que uma característica ecológica preservada pelas espécies (Leite e Klein 1990; Marchioretto et al. 2007, Martins 2009). Outro ponto importante a ser considerado é que as florestas estacionais possuem um dossel naturalmente descontínuo, e que também perdem parte das folhas do dossel em determinada época do ano (Inácio & Jarenkow 2008). Desse modo, mesmo indivíduos que estão situados no meio de grandes maciços florestais, bem preservados, estarão sob níveis relativamente altos de radiação luminosa. Situação que não ocorre, naturalmente, em maciços florestais de florestas ombrófilas densas, a não ser do caso da criação de clareiras nesses ambientes. Processo ocasional e isolado tanto espacialmente quanto temporalmente.

Outro ponto a se considerar é que tanto as oscilações de temperaturas diárias quanto ao longo do ano são reduzidas nas regiões próximas à costa, pela rápida troca de massas de ar entre o oceano e o continente, e pelos longos períodos nublados no verão, de modo que as regiões costeiras tipicamente possuem maior estabilidade térmica que as regiões mais continentais, independentes de latitude e altitude (Leite 2002). Desde modo, podemos caracterizar as espécies que estão na costa (Ombrófila Densa), como espécies bem aclimatadas a ambientes constantemente úmidos e sombreadosos, enquanto as espécies de florestas estacionais estão mais aclimatadas a ambientes mais heterogêneos com maiores oscilações (tantos em termos anuais quando diários) em termos de insolação e de umidade.

Dessa maneira, não é de se estranhar que temos diferentes proporções de espécies pioneiras fazendo parte do pool global de espécies em cada formação. Em termos relativos a Floresta Estacional apresenta 36% mais espécies pioneiras que a Floresta Ombrófila Densa (Capítulo 2). Deste modo, considerando que as florestas estacionais, mesmo em situações naturais, estão naturalmente sempre lidando com flutuações microclimáticas em patamares muito superiores aos observados nas áreas interiores dos maciços florestais da Ombrófila Densa, não foi inesperada as florestas estacionais terem apresentado níveis de resiliência à fragmentação muito superiores aos observado nas Florestas Ombrófilas. As florestas com Araucária, apresentam um caráter pioneiro, de avanço sobre áreas previamente ocupadas pelos campos em várias regiões (Behling & Pillar 2007; Duarte et al. 2006, 2007) e também se caracterizam por uma proporção bastante significativa de espécies pioneiras em relação ao seu pool global (36.28%; Capítulo 2). Contudo em florestas mais maduras e antigas, apresentam um dossel fechado e denso, e uma proporção não tão representativa de espécies decíduas comparativamente às florestas estacionais. Desse modo, era esperado que fossem mesmo mais sensíveis que as deciduais quando da abertura de novas bordas (Capítulo 1 e 2). Embora, não tenho sido devidamente testada nessa tese, eu suponho que haja um gradiente de sensibilidade à fragmentação entre as diferentes regiões da floresta com Araucária. Eu suponho que nas regiões em maior contato com a floresta Ombrófila Densa, onde ocorram solos mais profundos e as temperaturas mínimas do mês mais frio mais elevadas, e estas não sejam um fator tão limitante (quanto em locares de maior altitude) eu esperaria encontrar um maior número de espécies adaptadas à sombra do contingente ombrófilo, e desse modo, um maior número de espécies que sofreriam efeitos deletérios com os efeitos de borda e com a criação de novas bordas. E uma situação contrária, na região mais oeste-sudoeste da distribuição da floresta com Araucária, onde esta apresenta uma mescla maior de espécies com a floresta decidual. As possíveis novas perguntas são inúmeras, existem dezenas de novos trabalhos que podem ser elaborados a partir dos resultados obtidos e demonstrados nesta tese.

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6 CONCLUSÃO

Respostas Divergentes à Fragmentação?

O objetivo central dessa tese foi avaliar se as três principais formações florestais do Sul do Brasil, apresentam ou não, distintas respostas à fragmentação florestal e perda de hábitat. Uma pergunta sobre a qual, claramente, não havia nenhum consenso na literatura, e sequer existiam artigos buscando responder diretamente esta questão nos subtrópicos quando iniciei esta tese, situação que perdurou até hoje. Considero que o conjunto de dados, aqui reunidos, sugere fortemente que a resposta seja positiva. Sendo a divergência mais acentuada entre a Floresta Ombrófila Densa e a Floresta Estacional Decidual, sendo esta última mais resiliente que a primeira, e a Floresta Ombrófila Mista apresentando um padrão de resposta intermediário entre as duas.

Próximos passos

Como cada nova resposta costuma sempre gerar umaséria de novas perguntas, pretendo continuar com esta linha de pesquisa no futuro. Pretendo analisar e caracterizar mais detalhamente, os padrões de resposta isoladamente para cada atributo das comunidades, e também analisar detalhamente as respostas das espécies ou de determinados grupos de espécies que compões estas formações. Aqui procuramos responder, primeiramente, se estas formações florestais respondem de maneira diferenciada à fragmentação florestal. Estabelecido este ponto de partida, ainda há muito a ser feito, este foi apenas o começo.

Considero também como um dos “resultados” do doutorado a aquisição desta área, retratada na porção central da foto (8 hectares). Onde, até recentemente, plantavam milho e soja e, a partir de agora voltará, gradualmente, a ser floresta. E no futuro próximo, formará novamente um contínuo florestal com o Parque Estadual do Turvo, com a qual faz divisa.

Crédito da foto Dante Meller. Coordenadas GoogleEarth: Lat - 27.239759º; Lon -53.926056º