ALICE CRISTINA RODRIGUES

ON MULTIPLE DRIVERS PREDICTING ECOSYSTEM FUNCTIONING IN A TROPICAL FOREST

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientadora: Andreza Viana Neri

Coorientador: Pedro Manuel Villa

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Assentimento:

Alice Cristina Rodrigues
Autora

Andreza Viana Neri
Orientadora

Ao meu amado tio Geraldo Donizete Rodrigues, meu eterno Moreno.

Dedico

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"*Sou feliz aqui terra de gigantes, onde bravos índios viviam antes, onde além de ouro e diamantes, tem milhões de estrelas no horizonte" (Almir Sater)*

ABSTRACT

RODRIGUES, Alice Cristina, D.Sc., Universidade Federal de Viçosa, August, 2022. **On multiple drivers predicting ecosystem functioning in a tropical forest.** Advisor: Andreza Viana Neri. Co-adviser: Pedro Manuel Villa.

Understand the relative contribution of different factors that can determine the structure and diversity of forest communities along environmental gradients and secondary succession time has been a relevant theme in contemporary ecology. Recently the impact of these environmental factors (e.g., soils, topography, and climate) on biodiversity-ecosystem function relationship has gained importance in understanding tropical forests. Topographic and edaphic gradients together with climate can influence the distribution of functional traits, and consequently, ecosystem functioning. The study of the secondary succession of tropical forests with an approach based on the relation of functional traits and environmental factors has allowed elucidating emerging patterns of the ecosystem processes, mainly of the production and storage of biomass. Thus, the community weighted mean (CWM) are the diversity metrics to test effects on aboveground biomass. This research will assess how abiotic factors and biotic factors affect the assembly of tree communities and the ecosystem functioning of the forest Atlantic in southeastern Brazil. For this, we will analyze how species richness, composition and dominance can change through edaphic-topographic-climatic gradients and time of succession in permanent plots. For this, the following hypotheses will be tested: (1) The edaphic-topographic factors and the time of succession affect the richness, composition and dominance of the species in terms of their contribution to an ecosystem process (2) the variability climate over time of succession has implications for the classification of leaf phenology groups of tree communities. Finally, (3) we propose that AGB increases with time of succession, but changes depending on environmental variability (soil and topography), and that the variation in biomass can be explained by the functional traits of the species through functional dominance (CWM) in secondary forest communities. To answer these questions, we selected three areas with different topographic conditions located in a fragment in the secondary regeneration stage in Viçosa, MG, Brazil. Each area has permanent plots of 1 ha covering a topographic gradient from the valleys to the plateau. Each permanent plot has 100 subplots of 10m x 10m. Totaling two hectares of forest and 200 subplots. In each subplot, all individuals of the living arboreal species with stem circumference showed a height of 10 cm or greater and a height of 130 cm. For each subplot, three topographic variables (elevation, slope and convexity) were measured and calculated using a total station with the aid of an engineer and surface soil samples with a depth of 0 to 10 cm to determine physical and chemical parameters. The aboveground biomass was calculated for each tree individual sampled in the subplots by an allometric equation. We selected different types of functional traits such as leaf phenology, wood density and tree diameter. Multivariate regression analyzes were performed to classify habitat types according to topographic variables and species composition. In addition, we constructed a series of models to explain the effect of potential predictor variables on the response of species richness, species composition, and ecosystem functioning. We also used machine learning to classify leaf phenology groups under the effect of environmental variables. Our study demonstrated that topographic variability, mainly elevation and convexity, determine soil fertility. These results advance our understanding that context-dependent conditions based on topography and soil properties have a high variability at a fine-scale. Furthermore, we found that different topographic conditions and successional timing affect community composition, richness, abundance and proportion of carbon-dominant species over time. We found that different topographic conditions and stand age change community composition, richness, abundance, and carbon dominant species along the late-secondary stage. This study advances our understanding of the mechanisms that drive carbon stock in tropical forests and supports the 'mass ratio' hypothesis. We observe that evergreen species show higher richness; meanwhile the deciduous species has a greater contribution to aboveground carbon stock. Thus, the leaf phenology groups can affect the relationships between species richness and aboveground carbon stock. For example, deciduous species are key to maintaining higher carbon stock with smaller numbers of species; meanwhile evergreen species are important to maintain a higher species richness. Thus, we presumed that the leaf phenology group's distribution could be responsible for the cobenefits (positive aboveground carbon stock and species richness relationship) in tropical forests. Using random forest, it was observed that the most influential predictor in the classification of functional groups was topography and soil properties. We emphasize that the information generated in this research can be important for the planning of forest restoration activities (passive and active) based on the high variability of environmental variables on a local scale. We also emphasize the relevance of the functional traits approach to understanding the functioning, conservation and management of tropical forests.

Keywords: Biotic and abiotic factors. Cobenefits. Functional diversity. Topographical heterogeneity. Assembly community. Machine learning.

RESUMO

RODRIGUES, Alice Cristina, D.Sc., Universidade Federal de Viçosa, agosto de 2022. **On multiple drivers predicting ecosystem functioning in a tropical forest.** Orientadora: Andreza Viana Neri. Coorientador: Pedro Manuel Villa.

Compreender a contribuição relativa de diferentes fatores que podem determinar a estrutura e a diversidade das comunidades florestais ao longo de gradientes ambientais e tempo de sucessão secundária tem sido um tema relevante na ecologia contemporânea. Recentemente, o impacto desses fatores ambientais (solo, topografia e clima) na relação entre biodiversidade e função do ecossistema (BEF) ganhou importância na compreensão das florestas tropicais. Gradientes topográficos e edáficos juntamente com o clima podem influenciar variações na distribuição de características funcionais e, consequentemente, o funcionamento do ecossistema. O estudo da sucessão secundária de florestas tropicais com uma abordagem baseada na relação de características funcionais e fatores ambientais tem permitido elucidar padrões emergentes dos processos ecossistêmicos, principalmente do armazenamento de carbono. Nesta pesquisa se avaliou como os fatores ambientais e bióticos afetam a montagem de comunidades de árvores e o funcionamento ecossistêmico da Mata Atlântica no sudeste de Brasil. Para isto, analisamos como a riqueza, composição e dominância de espécies mudam através de gradientes edáficos-topográficos-climáticos e tempo de sucessão em parcelas permanentes. Testamos as seguintes hipóteses gerais: (1) Os fatores edáficos-topográficos e o tempo de sucessão afetam a riqueza, composição e dominância das espécies em termos de sua contribuição para um processo ecossistêmico (2) a variabilidade climática ao longo do tempo de sucessão tem implicações na classificação de espécies dos diferentes grupos fenologia foliar das comunidades de árvores. Finalmente, (3) propomos que a AGB incrementa com o tempo de sucessão, mas muda em função da variabilidade ambiental (solo, topografia), e que a variação da biomassa pode ser explicada pela dominância funcional (CWM) nas comunidades de floresta secundária. Para responder a essas questões, selecionamos duas áreas com diferentes condições topográficas localizadas em um fragmento em estágio de regeneração secundária em Viçosa, MG, Brasil. Cada área possui parcelas permanentes de 1-ha cobrindo um gradiente topográfico desde vales a platôs. Cada parcela permanente possui 100 subparcelas de 10 x 10m. Totalizando 2-ha e 200 subparcelas. Em cada subparcela, todos os indivíduos das espécies arbóreas vivas com circunferência à altura do peito (130 cm) maior ou igual a 15 cm foram mensuradas. Foram medidas em cada sub-parcela, três variáveis topográficas (elevação,

declividade e convexidade) usando uma estação total e amostras de solo de superfície em profundidade de 0 a 10 cm para determinar parâmetros químicos. A biomassa acima do solo foi calculada para cada árvore amostrada nas subparcelas utilizando equaçãos alométricas. Selecionamos diferentes tipos de características funcionais como fenologia foliar, densidade da madeira e diâmetro da árvore. Análises de regressão multivariada foram realizadas para classificar os tipos de habitats de acordo com variáveis topográficas e composição de espécies. Além disso, construímos uma série de modelos para explicar o efeito de potenciais variáveis preditoras na resposta da riqueza de espécies, composição de espécies e funcionamento do ecossistêmico. Utilizamos também apredinzagem de máquina para classificar grupos de fenologia foliar sob efeito de variáveis ambientais. Nosso estudo demonstrou que a variabilidade topográfica, principalmente a elevação e a convexidade, determinam a fertilidade do solo. Dessa forma as condições dependentes da topografia e das propriedades do solo têm uma alta variabilidade em escala local, o que pode influenciar as variações nos atributos florestais. Além disso, descobrimos que diferentes condições topográficas e tempo de sucessão afetam a composição da comunidade, riqueza, abundância e proporção de espécies dominantes em carbono ao longo do tempo. Nossos resultados mostraram que os valores de traços funcionais das espécies dominantes em carbono determinam o estoque de carbono acima do solo. Esses resultados avançam nossa compreensão dos mecanismos que impulsionam o estoque de carbono em florestas tropicais e sustentam a hipótese da "razão de massa". Observamos também que as espécies sempre verdes apresentam maior riqueza, enquanto as espécies decíduas têm uma maior contribuição para o estoque de carbono. Assim, os grupos de fenologia foliar podem afetar as relações entre a riqueza de espécies e o estoque de carbono. Por exemplo, as espécies decíduas são fundamentais para manter um maior estoque de carbono com um número menor de espécies; enquanto que as espécies sempre verdes são importantes para manter uma maior riqueza de espécies. Assim, grupos de fenologia foliar podem ser responsáveis pelos cobenefícios (relação positiva entre estoque de carbono e riqueza de espécies) em florestas tropicais. Finalmente, entre os algoritmos de classificação baseados em aprendizado de máquina analisados, random forest foi o melhor modelo de algoritmo. Utilizando random forest, observou-se que o preditor mais influente na classificação dos grupos funcionais foi a topografia e as propriedades do solo. Ressaltamos que as informações geradas nesta pesquisa podem ser importantes para o planejamento das atividades de restauração florestal (passiva e ativa) com base na alta variabilidade das variáveis ambientais em escala

local. Enfatizamos também a relevância da abordagem baseada em traços funcionais para entender o funcionamento, conservação e manejo de florestas tropicais.

Palavras-chave: Fatores bióticos e abióticos. Cobenefícios. Diversidade funcional. Heterogeneidade topográfica. Estruturação de comunidades. Aprendizado de máquina.

SUMÁRIO

INTRODUÇÃO GERAL

Conhecer a contribuição relativa dos diferentes fatores abióticos e bióticos que afetam a estrutura e diversidade das comunidades florestais tem sido um tema relevante na ecologia contemporânea (Chazdon, 2014; Meiners et al., 2015; Villa et al., 2019). Recentemente o impacto de fatores ambientais na relação biodiversidade-função ecossistêmica (BEF) tem ganhado importância para se conhecer melhor o funcionamento das florestas tropicais (Poorter et al., 2015). A análise da relação BEF tem sido muito importante para se entender como a diversidade de espécies (e seus traços funcionais) afetam diferentes funções ecossistêmicas (Poorter et al., 2015). Uma importante função dos ecossistemas de florestas tropicais é a produção de biomassa acima do solo (AGB), uma vez que desempenha um papel fundamental no ciclo global de carbono (Lewis et al., 2015). A AGB varia amplamente entre as florestas devido aos efeitos diferenciais dos fatores ambientais (ex., clima, solo e topografia) e fatores bióticos (ex., diversidade de espécies e traços funcionais) (Ali et al., 2017). Assim, a AGB pode ser determinada tanto pela diversidade de espécies e de seus traços funcionais, quanto pelos efeitos diretos e indiretos de fatores ambientais que podem afetar AGB via efeito sobre a diversidade e traços funcionais (Ali et al., 2017; Poorter et al., 2017). Nesse sentido, o estudo de florestas tropicais com uma abordagem baseada na relação BEF, fatores abióticos e bióticos é uma via promissora para elucidar padrões ainda pouco conhecidos do funcionamento ecossistêmico e da montagem das comunidades vegetais nesses ecossistemas (Prado-Junior et al., 2016; Poorter et al., 2017, van der Sande et al., 2017).

Neste contexto, as florestas secundárias, que regeneram após os distúrbios antropogênicos, abrigam alta biodiversidade e prestam diversas funções ecossistêmicas (Chazdon, 2014). No entanto, as mudanças no uso da terra e no clima são os principais fatores que ameaçam essas florestas (Hubau et al., 2020; Matos et al., 2020). As mudanças climáticas resultam em aumentos na temperatura média global, bem como alterações na frequência e gravidade das secas extremas (Fauset et al., 2012). Por exemplo, várias regiões da América do Sul têm experimentado uma diminuição na precipitação total anual, tornando as florestas tropicais dessa região cada vez mais secas devido à maior intensidade de períodos de baixa precipitação (Gaubert et al., 2019). Esses períodos de estiagem prolongada têm afetado a estrutura, dinâmica e diversidade das comunidades arbóreas (Fauset et al., 2012), causando perda da biodiversidade e comprometendo vários serviços ecossistêmicos (Poorter et al., 2017). Segundo Henrik et al., 2022, florestas que antes não eram consideradas ameaçadas por eventos climáticos extremos estão sendo fortemente afetadas atualmente. Os mesmos autores apontam para a probabilidade de que ocorra ainda um aumento da mortalidade de árvores nos próximos anos. Além dos efeitos climáticos, fatores ambientais tais como solo e topografia também exercem efeitos sobre a estruturação das comunidades arbóreas. Vários estudos mostraram que a topografia interfere na disponibilidade de recursos, desempenhando um papel fundamental na distribuição de espécies em florestas tropicais (Bohlman et al., 2008). Fatores topográficos são bem conhecidos não apenas por determinar um uso diferencial de recursos pelas espécies de árvores (McEwan & Muller, 2006), mas também por moldar gradientes edáficos (ex., nutrientes e umidade do solo) (John et al., 2007). Portanto, os gradientes topográficos e edáficos juntamente com o clima podem influenciar os processos demográficos de crescimento, mortalidade, recrutamento de árvores (Prado-Junior et. al., 2016), e variação na distribuição dos traços funcionais, e consequentemente, o funcionamento desses ecossistemas (Valencia et al., 2009; Poorter et al. 2017).

Nesse sentido, as mudanças climáticas globais podem ter efeitos negativos significativos na dinâmica das florestas tropicais, afetando sua composição e estrutura e causando variações em processos ecossistêmicos (Poorter et al., 2017). Por exemplo, alguns estudos analisando florestais na África e na Amazônia em escala regional mostraram que estão ocorrendo mudanças na riqueza e composição de espécies (Fauset et al., 2012; Esquivel-Muelbert et al., 2019; Aguirre-Gutierrez et al., 2019). Essas comunidades de árvores estão respondendo às mudanças climáticas, ajustando a composição de seus grupos funcionais, por meio de características baseadas na história de vida da planta, como por exemplo, a fenologia das folhas. Assim, comunidades que antes possuíam mais espécies sempre verdes, agora tendem a possuir mais espécies decíduas (Aguirre -Gutierrez et al., 2019).

No que diz respeito às mudanças na composição das características funcionais foliares, essas estão relacionadas à economia de carbono e água da planta sob diferentes condições de disponibilidade hídrica (Aguirre-Gutierrez et al., 2019). Espécies perenes possuem uma estratégia de conservação de recursos para estender sua atividade fotossintética além da estação chuvosa e evitar perdas de água, principalmente durante o período seco, onde há maior déficit hídrico climatológico. Por outro lado, espécies semidecíduas e decíduas apresentam uma estratégia de aquisição de recursos para maximizar o ganho de carbono no curto período de disponibilidade de água (Lusk et al., 2003). Tais mudanças na composição de grupos funcionais em comunidades arbóreas também podem implicar em mudanças em processos-chave do funcionamento do ecossistema (Aguirre-Gutierrez et al., 2019). Por tanto, o aumento na concentração de CO_2 atmosférico, temperaturas, secas extremas e desmatamento devem alterar o funcionamento dos ecossistemas florestais por meio de respostas ecofisiológicas e funcionais das plantas e perda de cobertura florestal nas próximas décadas (Hubau, et al., 2020).

A composição funcional pode afetar as funções ecossistêmicas devido à importância relativa dos traços funcionais de comunidades de árvores em florestas tropicais (Lohbeck et al. 2016; Phillips et al., 2019). Assim, a média ponderada da comunidade (CWM) é uma métrica utilizada para testar os efeitos da variabilidade dos traços funcionais dentro de uma comunidade sobre AGB (Lohbeck et al, 2016; Ali et al., 2017). A CWM quantifica o valor do traço funcional dominante ponderada pelas abundâncias relativas das espécies em uma dada comunidade (Díaz et al. 2007) e é importante para testar a "hipótese da razão de massa" postulando que os processos ecossistêmicos são determinados principalmente pelos traços funcionais das espécies dominantes em uma dada comunidade (Grime, 1998). Neste sentido, tem incrementado as evidências de que a dominância funcional (CWM), afeta fortemente AGB em florestas tropicais (Lohbeck et al, 2016). Além disso, a relação entre AGB e CWM dos traços funcionais das árvores pode sofrer efeitos do tempo de sucessão, do clima e de fatores ambientais (van der Sande et al., 2017).

No entanto, ainda há poucos estudos que avaliem se fatores ambientais tais como o clima, juntamente com o solo e topografia podem influenciar a diversidade, a composição de traços funcionais e a estruturação das comunidades arbóreas, e como todos estes fatores influenciam simultaneamente AGB em florestas sul-americanas, especialmente em florestas secundárias em regeneração da Mata Atlântica. Por esta razão, monitorar as mudanças de comunidades florestais por longos períodos de tempo é essencial para entender os múltiplos processos ecológicos e suas respostas às mudanças climáticas atuais e futuras (Hubau et al., 2020), permitindo assim, avanços no desenvolvimento do conhecimento científico. Segundo Bakker et al. (1996) um método adequado para acompanhar e avaliar as mudanças na composição das espécies e dinâmica da floresta ao longo do tempo é por meio de parcelas permanentes. Essa metodologia permite avaliar a composição e a estrutura florestal e monitorar sua mudança ao longo do tempo (Malhi et al. 2004, Lewis et al. 2015). Permite avaliar também, as consequências para a floresta do aquecimento global e a poluição atmosférica (Bakker et al. 1996). Além disso, a partir dessa metodologia de monitoramento de longo prazo é possível compreender em que extensão fatores como clima e solo determinam a estrutura florestal e afetam AGB (Malhi et al. 2004). Dado que os impactos das mudanças climáticas são maiores em determinadas áreas geográficas do planeta que são mais vulneráveis (IPCC, 2022), a Mata

Atlântica brasileira, que atualmente está reduzida a aproximadamente 11,6% de sua cobertura original (Scarano e Ceotto, 2015), é um ecossistema com alta prioridade para o estudo desses processos.

Neste sentido, utilizando metodologia de parcelas permanentes monitoradas em um fragmento de Mata Atlântica no Município de Viçosa, Minas Gerais, investigamos nessa tese os efeitos do clima, do solo, do tempo de sucessão (*stand age*) e da topografia na diversidade, composição funcional e funcionamento do ecossistema em florestas da Mata Atlântica (Fig. 1).

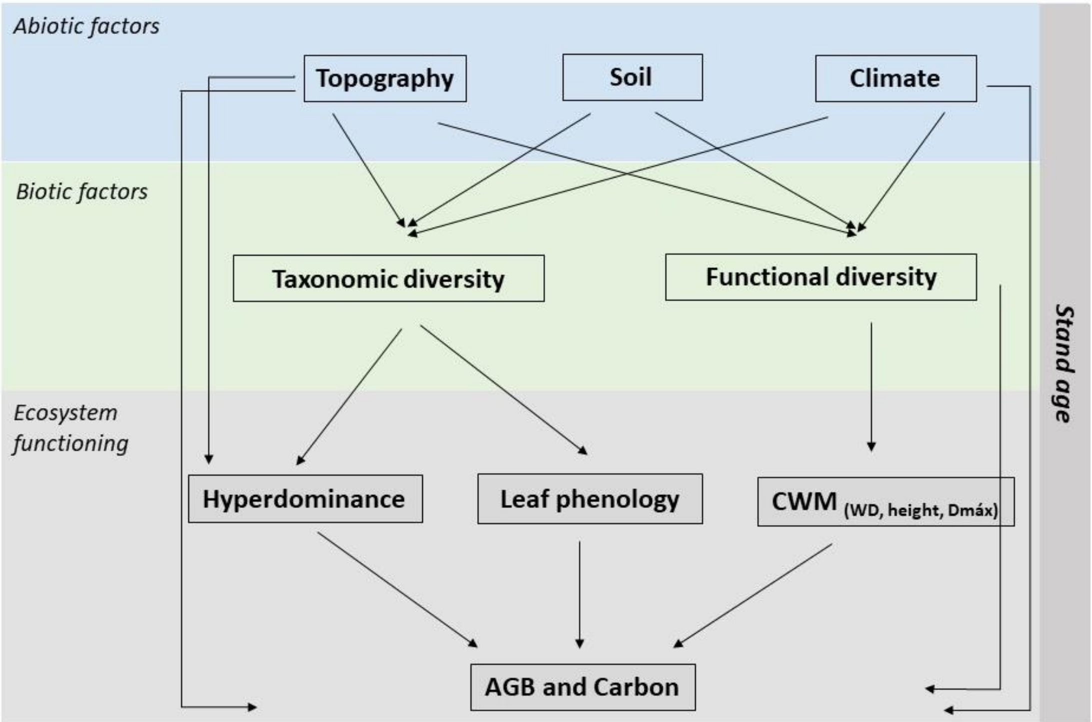

Figura 1: Modelo hipotético para o objetivo geral da pesquisa. Propomos que fatores abióticos (topografia, solo, clima e tempo de sucessão – *stand age*) afetam a diversidade taxonômica e funcional e consequentemente os processos relacionados ao funcionamento ecossistêmico (AGB e carbono) dessa floresta.

Para isso, analisamos como a composição de espécies (taxonômica e funcional) muda através de gradientes climáticos, edáficos e topográficos nessas parcelas permanentes. Além disso, usamos modelos de aprendizado de máquina com dados climáticos (déficit hídrico climatológico), dados do solo (soma de cátions básicos trocáveis e potencial de acidez trocável) dados topográficos (elevação, inclinação e convexidade) durante sucessão secundária (stand age) para prever a classificação de grupos funcionais de fenologia foliar.

As seguintes hipóteses foram testadas:

Capítulo 1: A fertilidade do solo é afetada positivamente pela variabilidade topográfica e atributos florestais com base na premissa de que uma maior variabilidade topográfica e um aumento nos atributos florestais (ou seja, aumento na riqueza, abundância, biomassa) poderiam induzir uma maior incorporação e renovação de nutrientes. Este estudo permitiu investigar se a topografia e os atributos florestais afetam as propriedades do solo associadas à fertilidade como um potencial indicador ecológico para restauração em escala local.

Capítulo 2: As diferentes condições topográficas e tempo de sucessão secundária afetam a composição, riqueza de espécies e abundância da comunidade de árvores. Assim, predizemos que essas mudanças induzem variação na distribuição de AGC entre espécies e famílias dominantes em carbono nas comunidades arbóreas. Além disso, assumimos que as identidades taxonômicas das espécies dominantes governam o estoque de AGC, e não a abundância e riqueza de espécies, devido à importância relativa dos valores de características funcionais de CWM relacionados ao estoque de carbono com base na hipótese da razão de massa. Finalmente, prevemos que a proporção de espécies dominantes em carbono será afetada pela topografia e tempo de sucessão, mas a composição funcional irá governar o estoque AGC.

Capítulo 3: A topografia molda a riqueza de espécies e o estoque de carbono acima do solo entre os grupos de fenologia foliar, bem como os cobenefícios entre carbono e biodiversidade nas comunidades arbóreas. Predizemos que os valores mais altos desses atributos serão encontrados sob maior heterogeneidade topográfica, que é um indicador de partição de nicho e disponibilidade de recursos (por exemplo, Brown et al., 2013; Liu et al., 2018). Além disso, esperamos que os altos valores de características funcionais relacionadas ao estoque de carbono expliquem a dominância de grupos de fenologia foliar, como espécies arbóreas decíduas.

Capítulo 4: Empregamos algoritmos de aprendizado de máquina para prever a associação dos fatores abióticos e stand age na classificação de grupos funcionais de fenologia foliar (perenes, decíduas e semidecíduas). Especificamente, usamos modelos de aprendizado de máquina com dados climáticos (déficit hídrico climatológico, CWD), dados do solo (soma de cátions básicos trocáveis (SB) e potencial de acidez trocável (H + Al)) dados topográficos (elevação, inclinação e convexidade) durante sucessão secundária (stand age) para prever a classificação de grupos funcionais de fenologia foliar.

Capítulo 5: O objetivo desse capítulo foi demostrar uma metodologia de análise e construção de gráficos de distribuição de fatores ambientais e atributos florestais usando o software R. Construímos três tipos de gráficos, 1) tipo *grid*, 2) o tridimensional com contornos de nível e 3) com distribuição das variáveis em *raster*. Descrevemos todas a metodologia envolvida desde a demonstração de como obter as variáveis em campo, passando pela sistematização da planilha de dados, descrição de todos os comandos utilizados nos *scripts* e carregamento dos dados no R até o produto final das análises.

Finalmente, destacamos que entender como e se a relação biodiversidade-função ecossistêmica difere sob diferentes condições climáticas e fatores ambientais é fundamental para identificar espécies-chave para conservar os cobenefícios entre biodiversidade e carbono e vários serviços ecossistêmicos em cenários de mudanças climáticas. Sendo essa abordagem crucial, principalmente sob o desafio global de restaurar florestas degradadas e desmatadas, conservar e aumentar os estoques de carbono florestal e a biodiversidade (Matos et al., 2020).

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CHAPTER 1

Effects of topographic variability and forest attributes on fine-scale soil fertility in late-secondary succession of Atlantic Forest

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Rodrigues, A.C., Villa, P.M., Ferreira-Júnior, W.G., Schaefer, C.E.R.G., Neri, A.V. Effects of topographic variability and forest attributes on fine-scale soil fertility in late-secondary succession of Atlantic Forest. Ecol Process 10, 62 (2021). https://doi.org/10.1186/s13717-021-00333-1

ABSTRACT

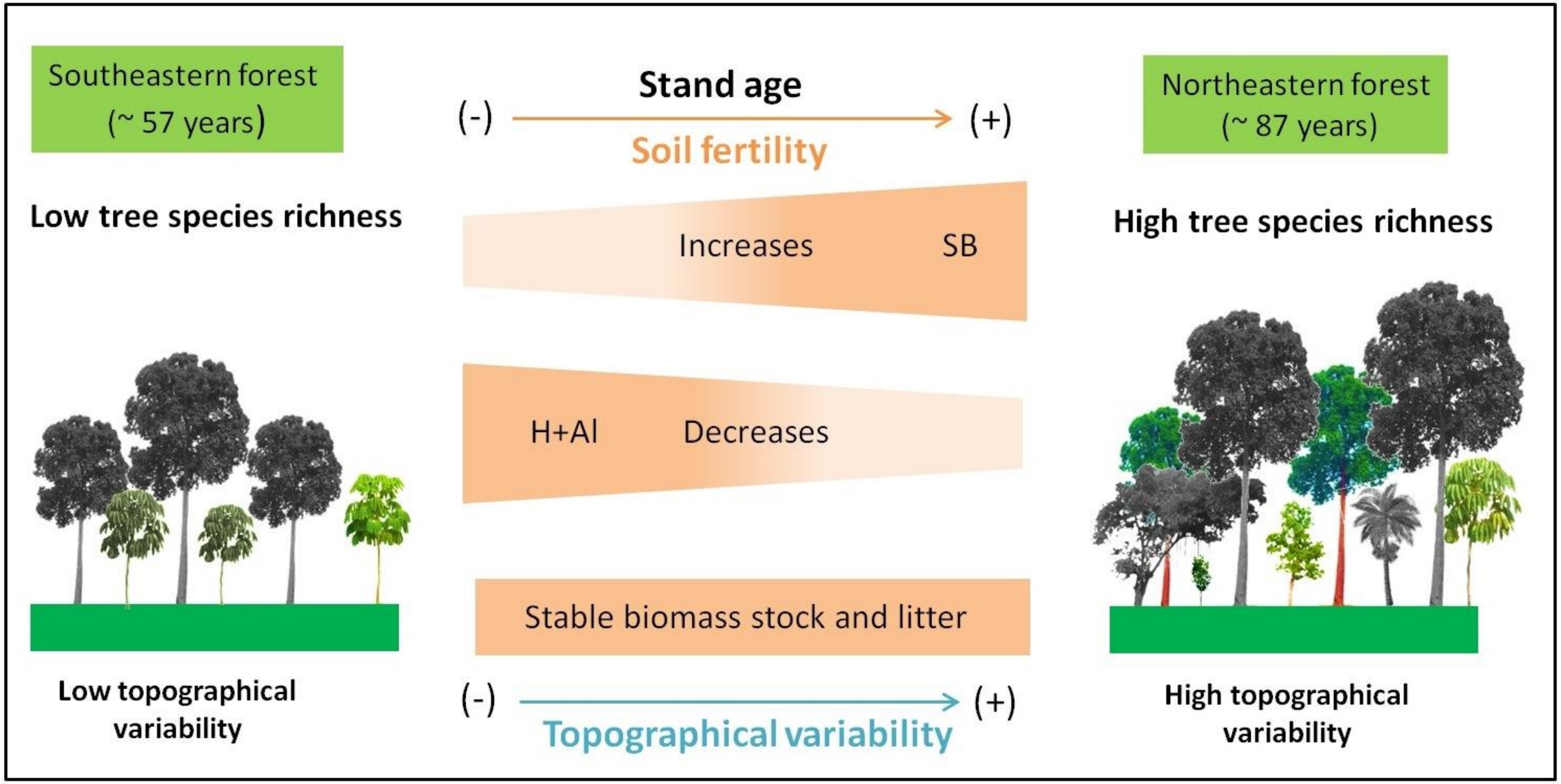
Background: Understanding how soil fertility changes due to topographical conditions and forest attributes is an essential premise for local-scale forest management practices. We evaluated the effects of topographic variables and forest attributes on soil fertility along a local topographical gradient in a Brazilian Atlantic Forest. Thus, we hypothesised that soil fertility is positively affected by topographic variability and forest attributes (structure and diversity). We used tree species richness, composition, and tree abundance and aboveground biomass as forest attributes. We analysed two 1-ha forest patches with contrasting topographical conditions. We used different linear mixed effects models (LMMs) to test the main effects of different forest attributes and topography variables on soil fertility.

Results: The results demonstrated that higher topographic variability determines soil fertility along a fine-scale gradient. The first two axes of the PCA explained near 66.8% of the variation in the soil data, where the first axis (PCA_1) explaining 49.6% of the variation in the soil data and positively correlating with fertility-related soil properties. The second axis (PCA_2) explained 17.2% of the variation in topographical data and positively correlated with convexity (the elevation of a plot minus the average elevation of all immediate neighbour plots) and elevation. Our best models showed that topographic variables (elevation and convexity) are de main predictors that affect fine-scale soil fertility.

Conclusions: Our study demonstrates that the topographic variability, mainly elevation and convexity, determine fine-scale soil fertility in an Atlantic Forests. These results advance our understanding that context-dependent conditions based on topography and soil properties have a high variability at a fine-scale, which can influence variations in forest attributes (i.e., species distribution, diversity and structure of tree communities). In addition, the information generated in this research may be important for planning forest restoration activities (passive and active) based on the high variability of environmental variables on a fine scale.

Keywords: convexity, soil variability, succession, topographical gradient, tropical forests.

Graphical abstract



BACKGROUND

Elucidating the processes that influence plant-soil relationships is one of the most critical issues in forest ecology (Kardol et al. 2013; Ali et al. 2017; Poorter et al. 2017). Most of the studies have focused mainly on the effects of soil properties on tree community diversity and ecosystem functioning (Ali et al. 2017; Rodrigues et al. 2019a; 2019b). Soil properties change along environmental gradients at different spatiotemporal scales (Nettesheim et al. 2015). However, environmental conditions (i.e., climate, topography) and forest attributes (i.e., tree species composition, richness, abundance and biomass) can simultaneously explain chemical soil properties and fertility variability (Baker et al. 2009; Malhi et al. 2009; Laughlin et al. 2015). However, these effects on second-growth tropical forest are still poorly researched.

The Brazilian Atlantic Forests are one of the most species-rich biomes and threatened tropical forests on the planet (Scarano and Ceotto 2015). Actually, the Atlantic Forests, growth mainly as secondary forest in small remnant patches into the agricultural matrix (Scarano and Ceotto 2015). Second-growth forests that re-growth after disturbance depend on multiple drivers at different spatial scales (i.e., Arroyo-Rodrigues et al. 2015; Poorter et al. 2017). For example, at a regional-scale, climate (i.e., temperature and rainfall) is the predominant factor that determines plant species distribution (Powers et al. 2009; Zhang et al. 2014). On a local-scale, where the climate does not change spatially, abiotic and biotic factors such as soil properties, topographical conditions and forest attributes (i.e., diversity and structure of tree community) increase the relative effects on patterns and process of second-growth forests (Villa et al. 2018a, 2020). Most of the studies assess the effects of topography and soil proprieties on forest attributes, such as diversity, structure and aboveground biomass (Ali et al. 2017; Poorter et al. 2017; Villa et al. 2018a, 2018b). Conversely, few studies have analysed the effect of forest attributes and topography on soil fertility. This information can be essential for the Atlantic

Forest restoration, because the fine scale environmental variability (i.e., topography and soil) determine the selection and spatial distribution of the tree species.

Topography is one of the most relevant factors that influence ecological process in tropical forests (Jucker et al. 2018; Li et al. 2018; Rodrigues et al. 2019a), playing an essential role in determining soil chemistry and fertility patterns (Moeslund et al. 2013; Jucker et al. 2018). Moreover, topography is strongly linked to soil fertility gradients and nutrient availability at the local scale (Balvanera et al. 2011). Thus, topographical variables, such as elevation, slope and convexity, can affect soil properties (Moeslund et al. 2013; Li et al. 2018), including short elevational gradients in a tropical forest (Daws et al. 2002). For example, soils in valleys tend to be wetter and more fertile than those near ridgetops (Gibbons and Newbery 2003; Segura et al. 2003). Furthermore, steeper sites have a higher nutrient output and, therefore, generally have fewer nutrients in the soil available than flatter sites (Balvanera et al. 2011). Thus, differences in the forest attributes can be found in a short topographical gradient (Rodrigues et al. 2019a, 2019b) based on the effects of soil properties variability on tree species distribution (Maestre and Reynolds 2006).

Several researchers demonstrated that forest attributes change along succession (i.e., Chazdon, 2014; Villa et al. 2018a; Poorter et al. 2019), e.g., forest structure and diversity as a function of directional change in forest communities (Campetella et al. 2011). Differences in forest structure and diversity can also affect soil fertility along succession (Kardol et al. 2013; Laughlin et al. 2015). In this sense, it is necessary to quantify the fine-scale biotic and abiotic drivers and their contribution to soil fertility as an ecological indicator that better represents the available soil nutrients for plant growth in tropical forests (Poorter et al. 2017; Ali et al. 2019).

In this context, we evaluated how topographic variables and forest attributes (i.e., structure and diversity of tree communities) affect soil fertility along Atlantic forests, Minas Gerais State, Southeastern Brazil. We evaluate soil-related fertility properties, tree species richness and composition (tree community diversity), abundance and aboveground biomass (tree community structure) as main forest attributes along a topographical gradient. We defined the following research questions: (1) How do soil-related fertility properties change along a topographical gradient? and (2) What is the main effect of forest attributes and topographic variables on soil fertility? We hypothesised that soil fertility is positively affected by topographic variability and forest attributes based on the premise that greater topographic variability and an increase in forest attributes (i.e., increase in richness, abundance, biomass) could induce greater incorporation and turnover of nutrients. This study allowed us to investigate whether topography and forest attributes affect soil properties associated with fertility as a potential ecological indicator for fine-scale restoration.

METHODS AND MATERIALS

Study site

The study was conducted in a Seasonal Atlantic Forest fragment extending over approximately 75 ha at Viçosa, Minas Gerais State, Southeastern Brazil (20º45'14'' S, 42º45'53'' W). According to the Köppen-Geiger classification, the climate is tropical altitude (Cw_b), with a dry season between May and September and a wet season between December and March (Alvares et al. 2014). Mean annual temperature is 21°C and mean annual precipitation 1,270 $mm.yr^{-1}$, with the highest volumes of rain concentrated in December, January and February (Avila-Diaz et al. 2020; UFV 2020). The study area is located at an elevation of 620-820 m.a.s.l., and the relief varies from strongly undulating to mountainous. The site is characterised by two dominant soil classes: a red-yellow alsicose latosol covers hilltops and mountainsides, while a cambic yellow-red podzolic dominates the upper fluvial terraces (Ferreira-Júnior et al. 2007).

The forest fragment was used to cultivate coffee until 1926. With the acquisition of the area by the Universidade Federal Viçosa, it has been protected since then, allowing natural regeneration (Paula et al. 2004) as the main passive restoration strategy. Del Peloso (2012), through temporal analysis via images, observed that, in 1963, the Southeastern patch was entirely on the forest fragment's border, assigning a regeneration age to this patch of approximately 50 years (today ~ 57 years). On the other hand, the Northeastern patch was already part of the fragment's nuclear area. It is possible to suggest, based on the information that the area was abandoned in 1926, that it has been in natural regeneration for approximately 87 years.

Sampling design and forest survey

We analysed two 1-ha forest patches with contrasting topographic conditions, with a difference of approximately 30 years old, a Southeastern patch (~ 57-year-old) and a Northeastern one (~ 87-year-old). Each patch was sub-divided into 100 contiguous subplots of 10 × 10 m to better capture the topography and soil properties at fine scale (van der Sande et al. 2018; Rodrigues et al. 2019b). This experimental design is recommended to explain fine-scale soil variability because can be captured in small plots in a short topographical gradient. Furthermore, soil fertility effects may be weaker at larger spatial scales and plots (van der Sande et al. 2018). All trees having a DBH (diameter at breast height; 1.3 m) greater than or equal to 5.0 cm were inventoried and identified to the species level using specialised literature, through consultation of the VIC Herbarium and by taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxon classification.

Estimation of aboveground biomass

The aboveground biomass of individual tree stems was calculated using a general allometric equation proposed by Chave et al. (2014) based on tree diameter at breast height (DBH, cm), height (H, meters) and species wood density (g cm^{-3}). We used data from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009) to obtain each species' wood density (i.e., Jucker et al. 2018; Ali et al. 2019). The total aboveground biomass per plot was the sum of all trees' aboveground biomass (Ali et al. 2017). The following equation was used:

$$AGB = 0.0673\ (\rho\ \times DBH^2 \times\ H)^{0.976} \qquad \text{Eq. 1}$$

Species-level biomass was calculated as the sum of the biomass values of all individuals from an individual species. Estimation of aboveground biomass was performed using the R package BIOMASS (Réjou-Méchain et al. 2017).

Soil properties

To measure the soil properties associated with fertility within each plot, a composite sample of the topsoil (at 0–10 cm depth) was collected. The samples' soil properties were measured in the Laboratory of Soil Analysis of the Universidade Federal Viçosa, following standard protocols described in Ferreira-Júnior et al. (2007). The following parameters were assessed: exchangeable acidity potential (H + Al, $cmol_c.dm^3$), pH (H_2O), exchangeable potassium (K, $mg.dm^3$), sodium (Na, $mg.dm^3$), calcium (Ca^{2+}, $cmol_c.dm^3$), magnesium (Mg^{2+}, $cmol_c.dm^3$), organic matter (OM, dag.kg), effective cation exchange capacity (CEC, $cmol_c.dm^3$) and percentage of bases saturation (V, %) and soil texture (sand, clay and silt contents).

Measurements of topographical variables

Using a total station, we measured vertical and horizontal angles and linear distances at the four vertices of each of the 200 plots (Kahmen et al. 1988). We calculated three topographic variables (slope, elevation and convexity) in each plot from the values obtained. Elevation was calculated using the mean elevation at each of the four corners of the plot. The slope (measured in degrees) was the mean angular deviation of the horizontal of each of the four triangular planes formed by the connection of three of its edges (Harms 2011). Convexity was determined by subtracting the elevation at the centre of the quadrat from the eight surrounding plots' mean elevation. On edge plots, convexity was calculated as the elevation of the plot of interest minus the mean elevation of the surrounding plots (Lan 2011).

Data analysis

To address the first question, 'how do soil-related fertility properties change along a topographical gradient?' we used a principal component analysis (PCA) on the correlation matrix to describe the topographical and soil gradients between forest patches, reducing the number of redundant variables on the PCA axes. This analysis was preceded by variable standardisation to equalise their contributions on the PCA ordination axes (i.e., Schmitz et al. 2020), using the 'FactoMineR' package (Husson et al. 2018). Thus, we constructed two PCA analyses, a first PCA to represent the fertility and texture gradient due to the high correlation of the variables with the PCA axes. Subsequently, we analysed the Spearman correlation between properties related to fertility and texture with the PCA axes to evaluate the contribution of variables (Fig. S1 from Supplementary Material, SM). We applied a PCA separately for texture because there were no significant relationships with the axes and no significant variation between forests patches (Fig. S2. from SM). Then, we selected the first PCA axes related soil fertility (PCA1f) as a response variable (i.e., Schmitz et al. 2020; Villa et al. 2021). To compare forest attributes, we used the Mann-Whitney U test in the tests for two independent forest patches. However, this test is widely used to test whether or not two independent samples are significantly different (Crawley 2013).

To address the second question, 'what is the main effect of forest attributes and topographic variables on soil fertility?' we used different linear mixed-effects models (LMMs, with random and fixed effects) to test the main effects of different predictors (i.e., topographical variables and forest structure and diversity attributes) on the first PCA axes related soil fertility (PCA1f) as the continuous response variable. The most suitable data distribution and link function was evaluated (Fig. S3. from Supplementary Material), detecting LMM with Gaussian error distribution (Crawley 2013). Based on this, we corroborate a high correlation between PCA1 and other indicators of soil fertility, such as CEC and SB index (Fig. S4 and S5 from SM). To compare the variation of community composition between second-growth forests and old-growth forests patches a non-metric multidimensional scaling (NMDS) analysis was performed using '*metaMDS*' function based on Bray-Curtis dissimilarities (Oksanen et al. 2018). Finally, we extracted the scores on frequency-weighted NMDS axis 1 as proxy of community composition variability (i.e., Schmitz et al. 2020; Villa et al. 2021). All different functions of NMDS are available within the "vegan" package (Oksanen et al. 2018).

The predictors with fixed effects for building the models were grouped into three categories: (i) topographic variables, (ii) forest structure attributes (abundance and aboveground biomass as continuous explanatory variables), and (iii) forest diversity predictors (i.e., species richness and composition) as continuous explanatory variables. We assessed collinearity between selected predictor variables using the Spearman correlation analysis; when two variables were strongly correlated ($r \geq 0.6$), they were included in separate models (Fig. S4. from SM). We tested alternative models with individual effects of predictors and different combinations of predictors with low correlation, and the stand age and plots were considered as a random effect (1 | stand age: plots). All models were calculated using the package 'lme4' (Bates et al. 2019) in the platform R (R-Core-Team 2018).

Finally, we compared the most parsimonious model (null model) with all the ecologically significant combinations of fixed variables based on the multi-model inference approach with the *Dredge* function of the "MuMIn" package (Barton 2017). The general adjustment of all models was using the information-theoretical approach based on the Akaike Information Criterion (AIC) to evaluate the best models (LMMs) tested, considering all models with AIC <2.0 as equally plausible (Burnham and Anderson 2002; Burnham et al. 2011). The predictors' coefficients to interpret parameter estimates on a comparable scale were estimated using the "jtools" package (Long 2020). For graphical illustration, we used the 'ggplot2' package (Hadley 2015).

RESULTS

Differences in soil-related fertility properties and topographical variables

The first two axes of the PCA explained ~ 66.8% of the variation in soil data (Fig. 1). The first axes (PCA_1) explained 49.6% of the variation in soil data and correlated positively with the variability of fertility-related soil properties, such as total exchangeable bases ($R = 0.92$, $p < 0.05$), base saturation index ($R = 0.82$, $p < 0.05$), effective cation exchange capacity ($R = 0.79$, $p < 0.05$) and pH ($R = 0.77$, $p < 0.05$), and negatively with acidity potential ($R = -0.92$, $p < 0.05$) and aluminium saturation index ($R = -0.91$, $p < 0.05$). The second axes (PCA_2) explained 17.2% of the variation in topographical data (Fig. 1) and correlated positively with convexity ($R = 0.72$, $p < 0.05$) and elevation ($R = 0.53$, $p < 0.05$), but did not present a significant correlation with slope (Fig. S1. from ESM).

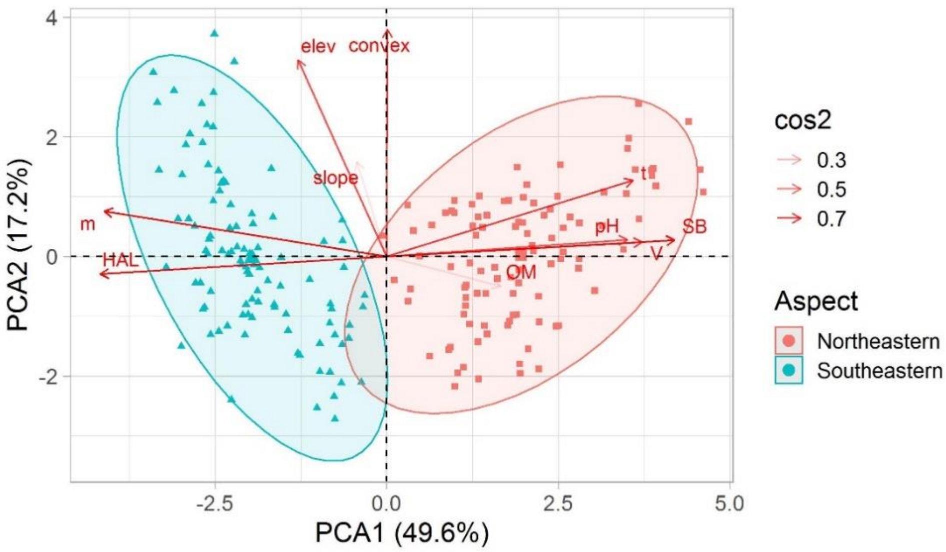


Fig. 1. Principal components analysis (PCA) of the topographic and soil variables of different patches (Northeastern and Southeastern). For analysis, elevation (elev), convexity (convex), slope, exchangeable acidity potential (H + Al), acidity potential index (m), pH (H_2O), organic matter (OM), effective cation exchange capacity (t = CEC), sum of basic exchangeable cations (SB) and base saturation index (V) were included. Cos2 means the relative contribution of the variables represented by the vectors.

Differences in forest attributes

Our results showed differences in forest structure and diversity attributes (i.e. abundance and richness) between patches (Fig. 2A and B), except for aboveground biomass (Fig. 2C). Specifically, tree species richness at the plot scale is higher in a patch of high topographic variability (Northeastern), while the tree abundance increases in the patch of low topographic variability (Southeastern). Despite the high aboveground biomass (AGB) stock variability between plots and patches, the mean values remain close (~150 Mg ha^{-1}) without significant differences (Figure 2C).

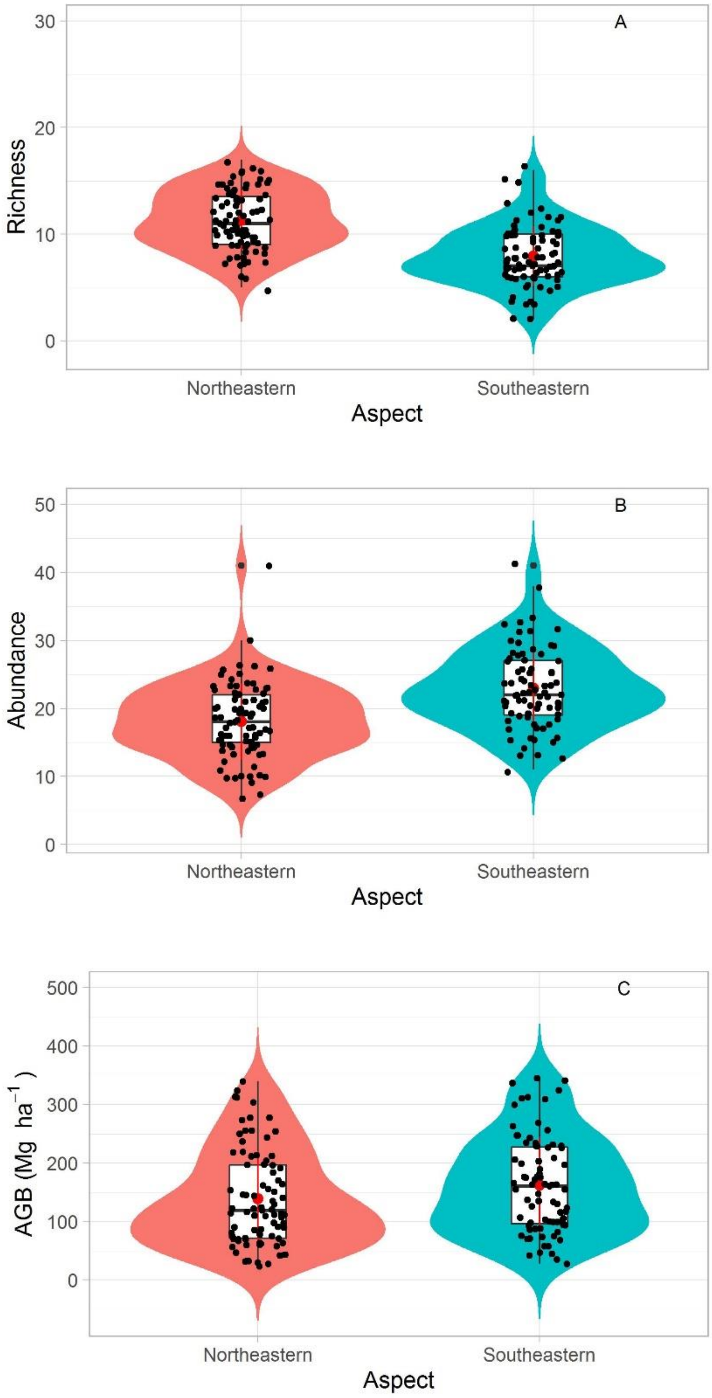


Fig. 2. Differences in tree species richness (A), abundance (B) and AGB, C) between Northeastern and Southeastern patches within two 1-ha plots in the Atlantic Forests, Minas Gerais, Brazil. Each black dot on the graph represents the mean value of the response variable on each plot around the mean the red dot and violins shape represent data variability.

Effects of topographic variables and forest attributes on soil fertility

Our best model selecting topographic variables as main predictors (ΔAICc <2) that explain soil fertility variation. Thus, our results showed that elevation negatively influences soil fertility (LMM: Est. = -0.42, t = -5.6, p <0.001) explaining 60% of the variability (Table 1). Meanwhile, convexity (LMM: Est. = 1.40, z = 9.19, p <0.001) had significant positive on soil fertility. Conversely, the forest attribute predictors had no significant effect on fertility (Table 1, Fig. 3).

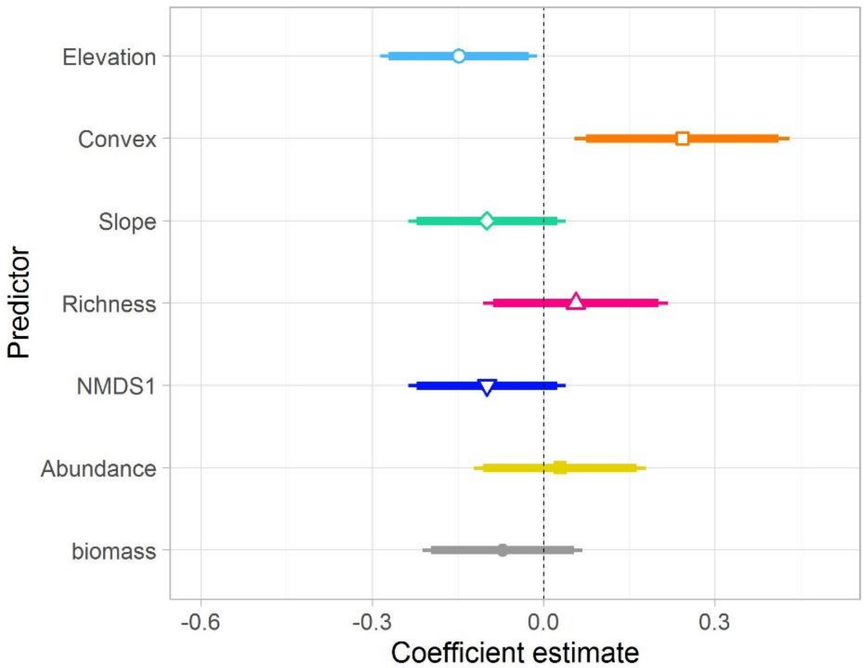


Fig. 3. Standardised regression coefficients of different generalised linear mixed effects models (LMMs, with random and fixed effects) to test the main effects of different predictors (i.e., topographical variables and forest structure and diversity attributes) on PCA1 soil fertility in the Atlantic forest, Minas Gerais, Brazil. Results are presented for the mean distributions. We show the averaged parameter estimates (standardised regression coefficients) of model predictors, the associated 95% confidence intervals and each factor's relative importance, expressed as the percentage of explained variance.

Table 1. Subset of models (linear mixed effect model, lmer) predicting soil fertility (response variable). The result of the information-theoretic-based model selection is indicated. Abbreviations: LogLik, log-likelihood; AICc, Akaike information criterion for small samples; ΔAICc, difference between the AICc of a given model and that of the best model; AICcWt, Akaike weights (based on AIC corrected for small sample sizes). Models that explain significant main effects are indicated (*).

Predictors	**LogLik**	**AICc**	**ΔAICc**	**AICcwt**
~ Elevation	-210.35	433.30	0	0.60*
~ Convexity	-211.47	433.33	0.03	0.25*
~ Slope	-210.49	435.7	2.4	0.13
~Species composition	-212.71	438.0	4.7	0.01
~ Richness	-211.65	438.12	4.82	<0.001
~ Abundance	-212.80	438.4	5.1	<0.001

DISCUSSION

Our results showed that fine scale topographic variables shape soil fertility. Elevation was the best predictor determining soil fertility along a topographical gradient in the studied Atlantic Forests. Moreover, the tested models reveal that convexity also the main predictor that explained soil fertility variation. These results partially demonstrate the hypotheses established in this research, because forest attributes had no significant effect on soil fertility on a fine scale. These results highlight that these topographic variables were considered to establish criteria for fine scale Atlantic Forest restoration and management, mainly to select and manage tree species along topographical gradient.

The first axes (PCA_1) explained 49.6% of the variation in soil data and correlated positively with the variability of soil-related fertility properties, such as total exchangeable bases, base saturation index, exchange capacity effective cation and pH. In several studies, total exchangeable bases were positively correlated with a wide range of soil properties that affect soil fertility, including pH, effective cation exchange capacity, base saturation, organic-matter content and phosphorus availability (i.e., Holmes et al. 2005; Ali et al. 2019; Poorter et al. 2019). Previous studies provide evidence of a stronger relationship between topography and pH (Gibson 1988; Zalatnai and Körmöczi 2004). However, Xia et al. (2015) found that soil properties had higher spatial variability within a 1-ha patch and that the low level of topographic variation within a small area was strongly associated with soil pH but poorly associated with all soil nutrients. Furthermore, changes in pH caused by topographic hydrology may exist (Moeslund et al. 2013). For example, due to gravity and water accumulation in wetland depressions, soil organic matter often accumulates in these low-lying sites, where subsequent decomposition produces a decrease in pH (Courtwright and Findlay 2011). These processes could probably explain our finding that the Northeastern patch, with higher topographic variability (Rodrigues et al. 2019b) being more related to higher pH values. Since this patch has several habitats (high convexity and depressions), this induces organic matter accumulation and, consequently, higher values of properties associated with soil acidity (i.e. acidity potential, aluminium saturation index).

The second axes (PCA_2) explained 17.2% of the topographical variation and correlated negatively with elevation, but there was no significant correlation with convexity and slope. Moreover, our main models explained the significant effects of elevation on fertility-related soil properties, such as the total exchangeable bases that better represent the available soil nutrients for plant growth (Poorter et al. 2017; Ali et al. 2019). In a similar study, soil pH, conductivity, organic matter and macro- and micronutrients along an elevational gradient were significantly correlated with elevation (Grell et al. 2005). On the other hand, in contrast to our findings, Nettesheim et al. (2015) showed that in the Atlantic Forests, even small terrain variations, such as a slight surface change in slope orientation, are sufficient to determine different soil conditions, thereby increasing habitat differentiation.

Our results allow us to presume that topography and soil fertility relationships may be an important factor in local-scale restoration activities. For instance, tree species distributed in valleys along a topographical gradient tend to regenerate faster, presumably because they have higher soil fertility and higher soil nutrient levels than slopes (Griscom and Ashton 2011). Slopes have better-drained soils, and nutrients leach downslope from the ridges and may accumulate in the valleys (Scatena and Lugo 1995), thus increasing tree growth in the valleys (Scholten et al. 2017). We presumed that the Northeastern patch, with a heterogeneous terrain, seems to maximise the influence of topographical conditions on soil fertility. This patch has higher environmental heterogeneity that can be decisive in providing habitats for the establishment of a greater number of tree species (Brown et al. 2013; Rodrigues et al. 2019a). Topography has also been recognised as an important dimension of plants' ecological niches, facilitating species coexistence in tropical forests (Brown et al. 2013). Higher topographic variability and the consequently higher species diversity could be a critical factor in soil fertility feedback. An increase in tree species diversity maintains soil fertility through several mechanisms, such as differences in litter quantity and quality, which can indirectly impact soil microbiota and decomposition processes (Scherer-Lorenzen et al. 2007; Oliveira et al. 2019).

We tested models that reveal that forest attributes had no affect soil fertility. However, in tropical forests, soil properties have a closer relationship with forest attributes (Laughlin et al. 2015). The processes by which diversity influences soil properties are related to litter production and litter quality (Scherer-Lorenzen et al. 2007; Laughlin et al. 2015; Oliveira et al. 2019); differences between soil fertility in different forest gradients are mainly caused by soil litter quality and microbial biomass (Li et al. 2013; Laughlin et al. 2015; Oliveira et al. 2019). However, our study corresponds to a late-secondary forest succession, where there is probably a stabilization of forest attributes and consequently its effects on soil fertility. Therefore, we propose future studies to evaluate soil fertility differences', considering forest attributes during early and late successional stages, since it is expected that the topography will not change over time. Moreover, we suggest evaluating the contribution of species diversity on litter stock and feedback, considering second-growth forest at different successional stages, since the litter composition can affect soil properties such as nutrients and other ecological indicators of soil fertility (Laughlin et al. 2015).

Our results allow to elucidate fine-scale processes to establish specific management plan in forest restoration patches (i.e. natural regeneration, seedling planting). For example, we suggest identifying specific ecological patterns that allow classifying different habitat types and environmental conditions (i.e. topography, soil fertility) to define management strategies within the forest restoration plan (i.e. species selection, site preparation and species distribution). We emphasize that there is usually a tendency to establish the same management methods and techniques within a single forest restoration plan, ignoring the high environmental variability at the landscape and local scale. Thus, we consider that in tropical forests with high topographic variability, it is necessary to define the interest levels of restoration activities and to better evaluate the effects of topographic variables on soil fertility as one main ecological indicator. For the specific case of the Atlantic Forest, which is characterised by its high topographic variability and fragmentation, these premises must be urgently considered to contribute to the successful development and monitoring of current forest restoration projects.

CONCLUSIONS

Our study showed that the topographic variables, elevation and convexity, affected soil fertility in an Atlantic Forests fragment. On the other hand, despite the difference in tree species richness and abundance, forest attributes had no significant effect on soil fertility at a fine-scale. Based on our results the hypotheses can be partially accepted, since some topographical variables has an important effect in the soil attributes. Finally, this study provides valuable information that an assessment of spatial soil variability in forests with high topographic variability must be a premise to optimise resources during management activities. Therefore, our study demonstrates that topographic variability and soil fertility are related it can be extremely important for the development of management plans for fine-scale forest restoration and conservation. For example, for species selection, site preparation and species distribution at fine scale.

Abbreviations

SB: Total exchangeable bases; LMMs: Linear models of mixed effects; Cw_b: Climate is tropical altitude; APG IV: Angiosperm Phylogeny Group IV; DBH: diameter at breast height; H: Height; K: Exchangeable potassium; Na: Sodium; Ca: Calcium; Mg: Magnesium; OM: Organic matter; CEC: effective cation exchange capacity; V: bases saturation; PCA: Principal components analysis; AIC: Akaike Information Criterion; AGB: Aboveground biomass.

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Authors' contributions

ACR and PMV conceptualization, formal analysis, writing-original draft. ACR and WGFJ investigation and data curation. CERGS resources, writing-review. AVN supervision, conceptualization, writing-original draft. All authors contributed to the writing and read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests

Author details

[1] Laboratory of Ecology and Evolution of Plants - LEEP, Departamento de Biologia Vegetal, Programa de Pós-Graduação em Botânica - Universidade Federal de Viçosa, Viçosa, Minas Gerais, CEP: 36570-900, Brazil. [2] Fundación para la Conservación de la Biodiversidad, Mérida, estado Mérida, CEP 5101, Venezuela. [3] Departamento de Engenharia Florestal - Universidade Federal de Viçosa, Viçosa, Minas Gerais, CEP: 36570-900, Brazil. [4] Laboratório de Botânica e Ecologia, Setor de Biologia e Meio Ambiente, Instituto Federal do Sul de Minas Gerais (IFSULDEMINAS) *Campus* Machado, Rodovia Machado - Paraguaçu, km 3, Machado, MG, CEP 37750-000, Brazil. [5] Departamento de Solos, Universidade Federal de Viçosa, Viçosa, MG, CEP: 36570-900, Brazil.

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Supplementary data

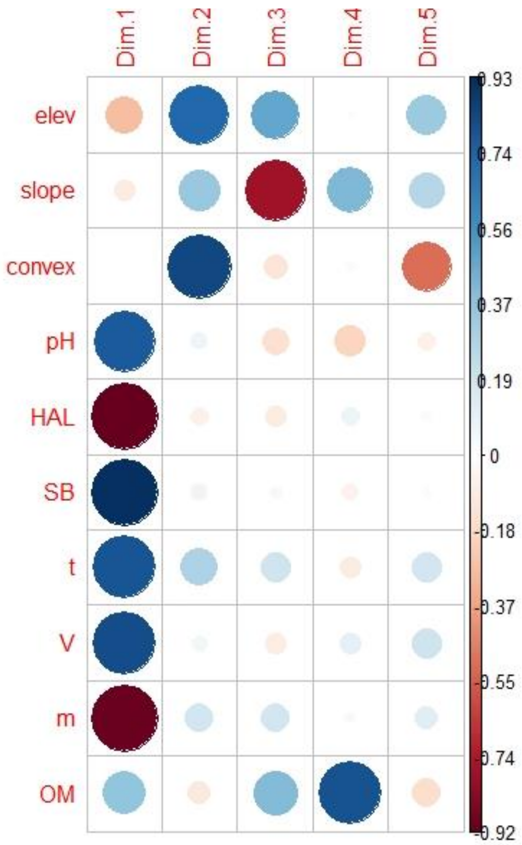

Figure S1. Significance levels are based on Spearman correlation coefficients between soil parameters and principal components of PCA fertility from 200 plots within 2-ha plots in Atlantic Forest, Minas Gerais, Brazil. For analysis, available: elevation (elev), convexity (convex), slope, exchangeable acidity potential (H + Al), aluminum saturation index (m), pH (H_2O), organic matter (OM); effective cation exchange capacity (t = CEC), sum of basic exchangeable cations (SB), bases saturation index (V).

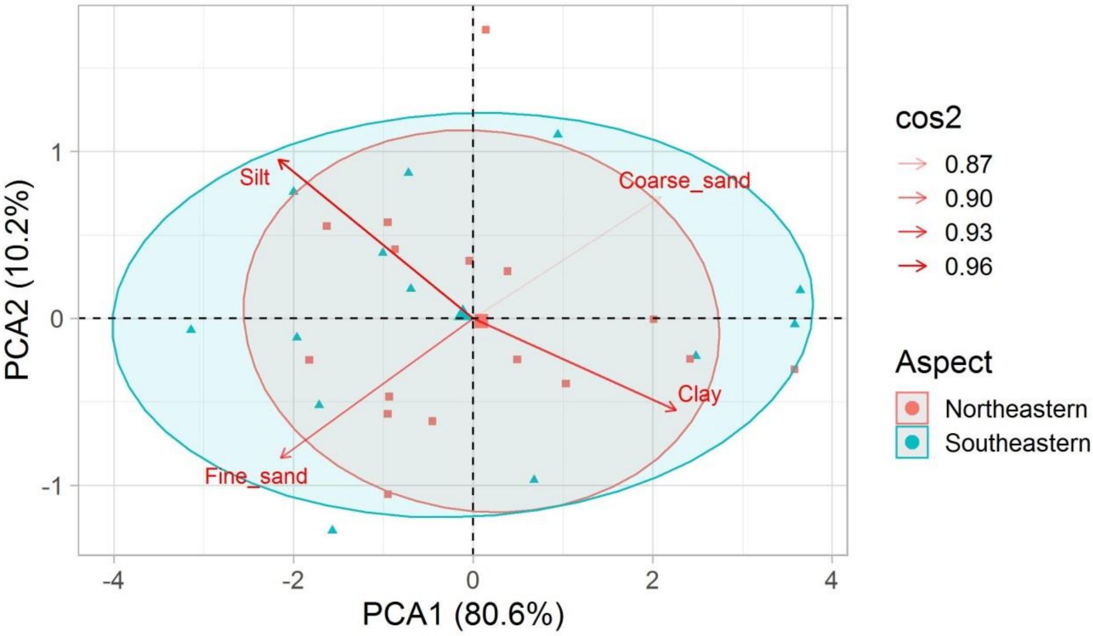

Figure S2. Dimensionality-reduction of physical properties based on Principal Component Analysis (PCA) along topographical gradient. These results showed low variability between forest patches (Northeastern and Southeastern) based on coarse sand (Sand_c), fine sand (Sand_t), clay and silt.

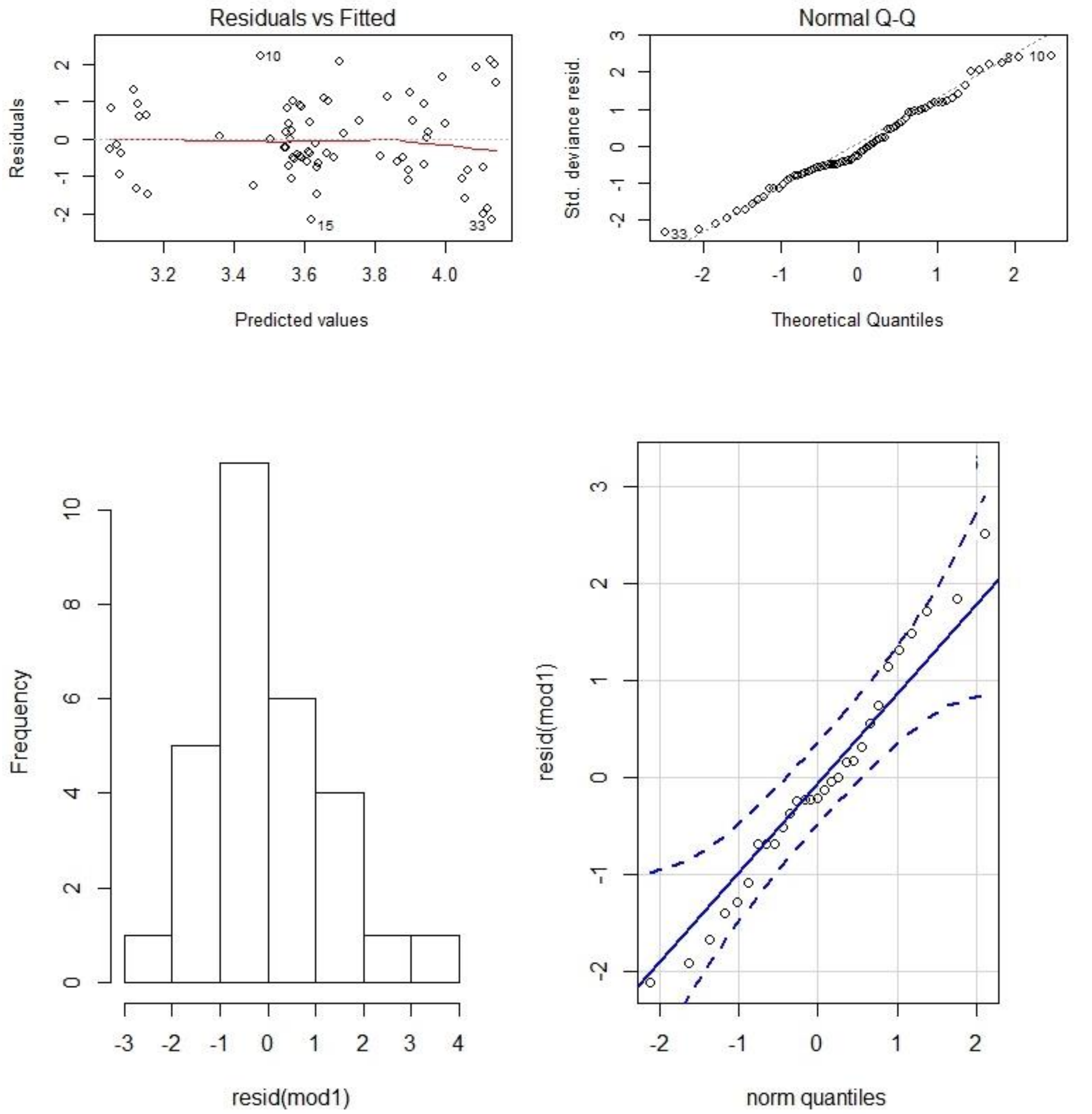

Figure S3. Examples to test the most suitable distribution and link function using histogram and Q-Q considering the bests models with AIC < 2.0 (i.e. mod = Soil fertility ~ Elevation).

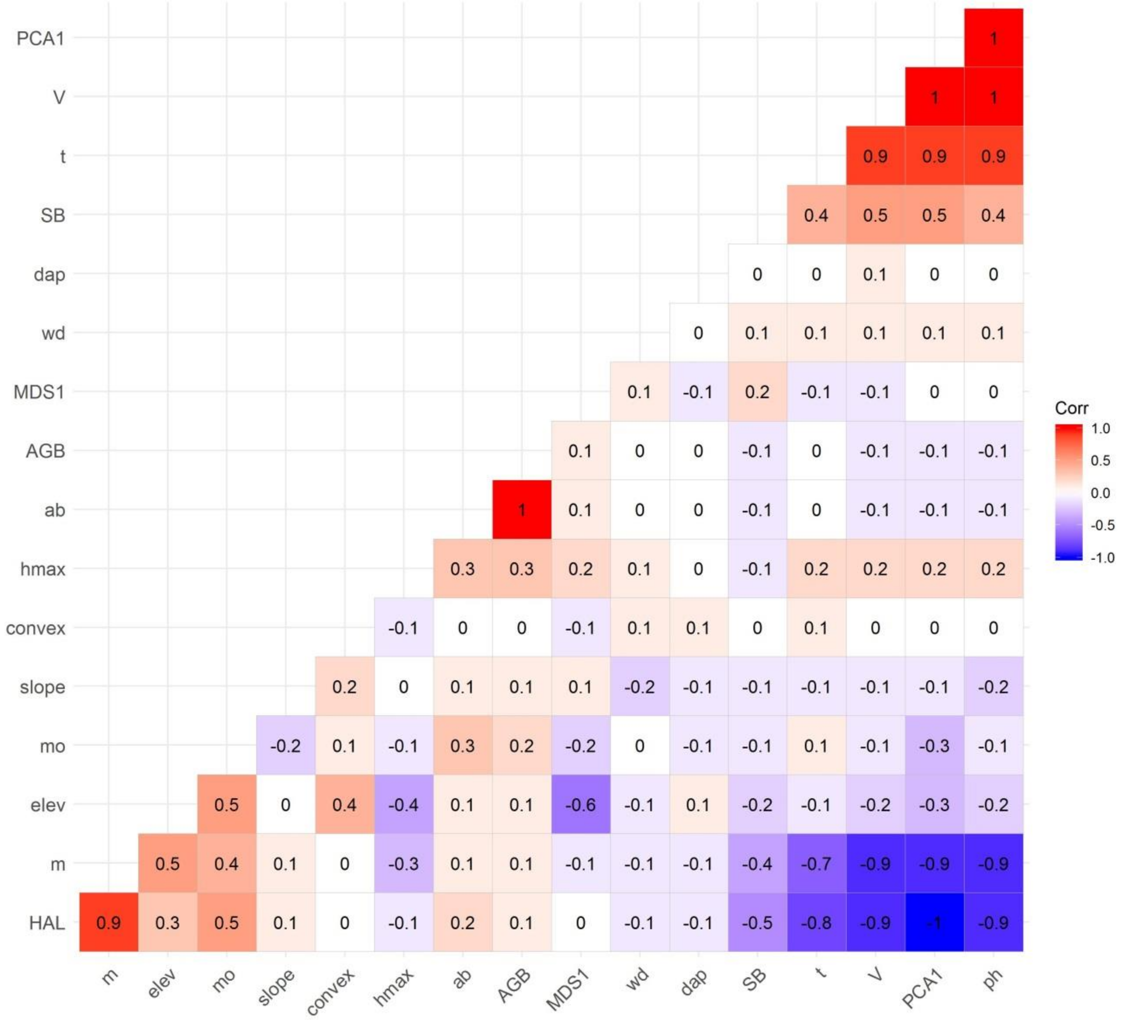

Fig. S4. Spearman correlation among all individual variables measured in 200 plots along forest patches. For analysis topographic variables, chemical properties-related soil texture as PCA1t, and forest attributes were included. The following soil properties are included: soil organic carbon (C), total nitrogen (N), available phosphorus (P), potassium (K+), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe), zinc (Zn), exchangeable acidity ($H^{+}Al$), pH, organic matter (OM) For analysis, available: elevation (elev), convexity (convex), slope, exchangeable acidity potential (H + Al), aluminum saturation index (m), pH (H_2O), organic matter (OM); effective cation exchange capacity (t = CEC), sum of basic exchangeable cations (SB), bases saturation index (V).

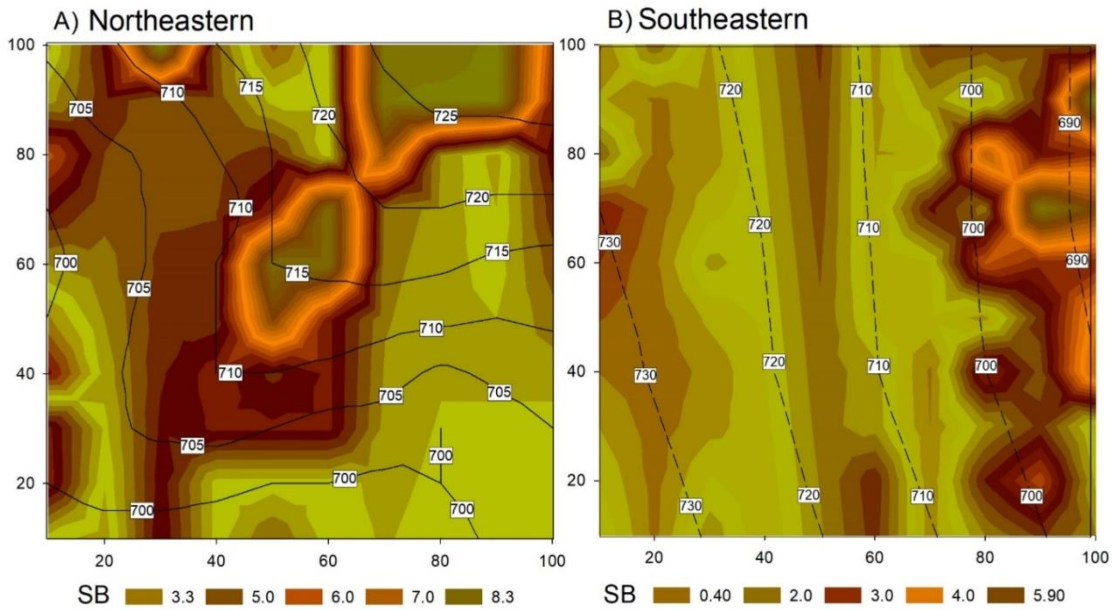

Fig. S5. Kriging maps of the spatial distribution of total exchangeable bases (SB) in relation to elevation - the main predictor of soil fertility along the topographical environmental gradient in each forest patch studied (100 x 100 m). Black lines indicate elevational contours.

CHAPTER 2

Functional composition enhances aboveground carbon stock during tropical late-secondary forest succession

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ABSTRACT

The ‘mass ratio’ hypothesis states that ecosystem functioning is driven by the functional traits of the most dominant species in communities. Thus, we aimed to evaluate i) How topographical conditions and stand age determine changes in tree community composition, richness, abundance, and carbon dominant species, and ii) Assess whether community-weighted mean of functional trait values of carbon dominant species explain aboveground carbon stock. We used community-weighted mean of wood density and maximum stem diameter to evaluate the effect of functional dominance in aboveground carbon stock. We found that different topographic conditions and stand age change community composition, richness, abundance, and carbon dominant species along the late-secondary stage. Our results showed that functional trait values of carbon dominant species determine aboveground carbon stock. Thus, the proportion of carbon dominant species was shaped by topography and stand age, whereas carbon stock by the dominant species' functional traits (wood density and diameter). This study advances our understanding of the mechanisms that drive carbon stock in tropical forests and supports the ‘mass ratio’ hypothesis. We emphasize the relevance of the trait-based approach to understand forest functioning and trait functional composition and taxonomic identity for carbon storage, recovery, and increase in secondary Atlantic Forests.

Keywords: Functional composition, carbon dominant species, Community-weighted mean, topography heterogeneity, stand age, mass ratio hypothesis

INTRODUCTION

Dominant tree species in tropical forests have a fundamental role in maintaining ecosystem functions (i.e., carbon stock), and their relative importance can change along environmental gradients and secondary succession after disturbance (Fauset et al. 2015; Ali et al. 2019; Poulsen et al. 2020; Villa et al. 2020). Dominance has been a widely observed phenomenon where few dominant species explain variation in ecosystem function (Grime 1998). These dominant tree species can determine carbon stock based on the mean values (i.e., functional composition) and variability (i.e., functional diversity) of their functional traits, such as wood density and maximum stem diameter (Grime 1998; Laliberté and Legendre 2010; Ali et al. 2019; Villa et al. 2020). Functional composition and diversity are two complementary components representing the functional property of communities (Grime 1998, Laliberté and Legendre 2010). Aboveground carbon (AGC) stock can be affected by environmental factors, stand age, functional trait composition, and taxonomic identity based on relative abundance and dominance of few species, the carbon dominant (CD) species, that disproportionately store a large amount of carbon (Garnier et al. 2004; Fauset et al. 2015; Ali et al. 2020). Thus, understanding the relationships between functional traits, environmental variability, and AGC stock is important for global climate change mitigation (Lohbeck et al. 2015; Ali et al. 2016; Poorter et al. 2019; Villa et al. 2020a). However, research results on trait-based approaches to evaluate the role of dominant tree species in AGC stock in the second-growth tropical forest that re-growing after disturbance remain unclear.

Based on the 'mass ratio' hypothesis (Grime 1998), dominance pattern is strongly related to functional community-level trait values of the most dominant species (Violle et al. 2007; Ali et al. 2020). This hypothesis states that dominant species in a plant community (those abundant or present some functional traits that account for most of the biomass) contribute most to ecosystem function due to their hard-functional traits (Grime 1998). For example, maximum diameter and wood density are traits that explain ecosystem functions, such as aboveground carbon stock in tropical forests (Ali et al. 2019; Phillips et al. 2019; Rodrigues et al. 2019a; Villa et al. 2020a). However, the relative contributions to ecosystem function can change substantially between species beyond their abundance (Lohbeck et al. 2016; Morlon et al. 2009). Thus, an abundant tree species may not be dominant in AGC stock because it may not have optimal trait values for this ecosystem functioning (Morlon et al. 2009; Rodrigues et al. 2019a).

The functional composition can govern an ecosystem function rather than species richness and abundance due to the relative importance of functional traits of tree communities in tropical forests (Lohbeck et al. 2016; Phillips et al. 2019). One way to access, this is evaluating whether an ecosystem function is associated with dominant trait values (i.e., community-weighted mean, CWM) in the tree community (Garnier et al. 2004). The CWM is an index of functional diversity that weighs species trait values by the relative abundance of the species in a community (Garnier et al. 2007). This index has been used in several studies to evaluate the effect of functional composition on aboveground biomass stock (AGB) (Prado-Junior et al. 2016; Ali et al. 2017; van der Sande et al. 2017a). Under the mass ratio hypothesis, the CWM of several functional traits determines AGB due to the dominance of few tree species in natural second-growth tropical forests (Conti and Díaz 2013; Lohbeck et al. 2016; Villa et al. 2020a).

The relationship between CWM of trait values and AGC is affected by stand age and local environmental conditions (van der Sande et al. 2017b; Villa et al. 2020a). Thus, CWM and AGC stock should reflect abiotic and biotic conditions in tropical forests (van der Sande et al. 2017a). Forest stand age is an important driver of biomass accumulation along forest succession, which can drive carbon stock through its effect on tree diversity, dominance, and functional traits (Ali et al. 2019). On the other hand, environmental factors such as topography can shape resource availability for plant growth, and consequently affect different stand-age forest attributes in tropical forest, i.e., abundance, species richness, community composition, and carbon stock (Guo et al. 2016; Jucker et al. 2018; Rodrigues et al. 2020). Thus, topographical factors (e.g., elevation, slope, and convexity) and stand age can induce variation in the proportion of dominant tree species and biomass (Jucker et al. 2018; Morera-Beita et al. 2019; Villa et al. 2019; Ali et al. 2020). Therefore, the CWM metric can be important for assessing the relationship between the functional traits of (CD) species and AGC stock along forest succession and topography in tropical forests. This information is critical to understanding forest functioning, restoration, conservation and carbon storage enhancement in threatened ecosystems (Kearsley et al. 2019). In this context, we aim to assess how topographical conditions and stand age determine changes in stand forest attributes (i.e., taxonomical, structural and functional attributes) in a Brazilian Atlantic Forest on late-secondary succession. Specifically, we evaluated whether tree species identity and functional trait composition (i.e., wood density and maximum stem diameter) rather than taxonomic and structural attributes (i.e., species richness and composition and abundance) shape aboveground carbon stock along topographical conditions and stand age.

We state the following questions: 1) How do contrasting topographical conditions and stand age determine differences in tree species richness and community composition? 2) What is the carbon dominance and distribution between species and families? 3) What is the relationship between species abundance and CD species along late-secondary succession and contrasting topographical conditions? 4) How do CD species and families change along topographically different stand ages? 5) How do CWM of functional trait values of CD species govern AGC stock in the tree community? We hypothesize that different topographical conditions and late-secondary succession shape change in community composition, species richness, and stem abundance. Thus, we predicted that these changes induce variation in AGC distribution between CD species and families in the tree communities. Secondly, we assume that the taxonomic identities of the dominant species govern AGC stock, and not the abundance and species richness, due to the relative importance of CWM functional trait values related to carbon stock based on the mass ratio hypothesis. Finally, we predict that the proportion of CD species will be affected by topography and stand age, but the functional composition will govern AGC stock.

METHODS

Study area and land-use history

The study was conducted in a Semideciduous Seasonal Atlantic Forest fragment in Minas Gerais, southeast Brazil. Brazilian Atlantic Forests are a hotspot of biodiversity, one of the most species-rich and threatened biomes globally (Scarano and Ceotto 2015). These forests are found mainly as second-growth forests (i.e., forests regenerating, mostly, following anthropogenic disturbance) in small remnant fragments representing less than 12% of the original forest (Scarano and Ceotto 2015).

We studied an Atlantic Forest fragment of approximately 75 ha used for coffee cultivation until 1926; since then, it is in natural regeneration (a passive restoration method). Del Peloso (2012), through the temporal analysis performed through images, observed that, in 1963, the southeastern area of the forest fragment was almost entirely the fragment's border, assigning a regeneration age to this area is ca. 57 years old. On the other hand, the northeastern area of the forest fragment was already part of its nuclear area. Based on the information that this area was abandoned in 1926, it was possible to determine that its natural regeneration is ca. 87 years old.

According to the Köppen-Geiger classification, the study area's climate is tropical altitude (Cw_b), with a dry season between May and September and a wet season between December and March (Alvares et al. 2014). The mean annual temperature is 21°C, and the mean annual precipitation is 1,270 mm, with the highest volumes of rain concentrated in December, January, and February (Avila-Diaz et al. 2020; UFV 2020). The study area is between 620 and 820 m a.s.l., and the relief varies from strongly undulating to mountainous. Two dominant soil classes characterize the site: a red-yellow alsicose latosol covers hilltops; while a cambic yellow-red podzolic dominates the upper fluvial terraces (Ferreira-Júnior et al. 2007).

Vegetation sampling

Two 1-ha permanent plots were established in the forest fragment with contrasting topographical conditions, the southeastern and northeastern patches. The southeastern patch was established in 1984, and five measurements were made in 1984, 1998, 2003, 2011, and 2017, totalizing 33 years of monitoring. On the other hand, the northeastern patch was established in 1993, and four measurements were made in 1993, 2004, 2011, and 2017, totalizing 24 years of monitoring. Each patch was subdivided into 100 subplots of 10 × 10 m to better capture topography's effect on the local-scale. All trees with diameters at breast height (DBH) ≥ 5 cm were inventoried and botanically identified to the species level in both patches and years in each subplot. All individuals were identified using specialized literature, consulting Herbarium, or taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxon classification.

Topographical variables survey

We measured vertical and horizontal angles and linear distances at each 200-10 × 10 m patches at the four vertices utilizing a total station (Kahmen et al. 1988). Thus, we calculate three topographical variables (slope, elevation, and convexity) in each patch (see Rodrigues et al., 2019a).

Estimation of aboveground carbon (AGC)

The AGC stocks estimation was based on allometric equations for forest biomass. The carbon concentration of a tree's different organs is assumed to be approximately 50% of the biomass (Chave et al. 2009). In this study, aboveground biomass (AGB) of trees for each sampled stem was calculated from a combination of variables using the general allometric equation proposed by Chave et al. (2005) as described below, based on just the measured diameter (D) and wood specific density (ρ). According to Chave et al. (2005) diameter and wood density are the most critical parameters necessary to predict the tree biomass accurately. We measured the tree diameter in the field, while the wood specific density (ρ) was extracted from a global database (Chave et al. 2009; Zanne et al. 2010).

$$AGB = exp[-1.803 - 0.976E + 0.976ln(p) + 2.673ln(D) - 0.0299[ln(D)]^2] \quad \text{Eq. 1}$$

The total AGB per patch was the sum of the AGBs of all trees having DBH ≥ 5 cm, which was converted to megagrams per hectare (Mg ha^{-1}) (Ali et al. 2017). Species-level biomass was calculated as the sum of the biomass of all stems from a species. Estimation of aboveground biomass was performed using the R package BIOMASS (Réjou-Méchain et al. 2017).

Quantification of the community-weighted mean of stem traits

The dominant traits in a community can be estimated by the weighted trait mean value in the community (Garnier et al. 2007). Thus, we calculated the functional composition through the

CWM metrics based on two key functional traits for aboveground carbon stock, the wood density (WD) and maximum stem diameter (D_{max}) (Prado-Junior et al. 2016; Villa et al. 2020a). Community-weighted mean was calculated as the mean value of the trait in the community, weighting by species' relative abundance (Garnier et al. 2004). After calculated the CWM values of each functional trait (WD and D_{max}) we separated the tree species into two functional categories: i) carbon dominant species (CD) and ii) carbon non-dominant species (CND). The CD group corresponds to the CWM of functional traits of species that accumulate approximately 50% of the total community AGC stock (i.e., hyperdominant species, see Bastin et al. 2015 and Fauset et al. 2015). On the other hand, the CND group corresponds to the functional traits of different species in the community that contribute little to AGC stock compared to CD species.

We used the relative abundance of species rather than a basal area because it prevents circular redundancy derived from DBH from calculating functional trait and aboveground biomass (Conti and Díaz 2013; Ali et al. 2017). Each species' relative abundance was calculated by dividing the number of individual species from the total species found in each patch and stand age (Conti and Díaz, 2013). We evaluated differences in the CWM of CD traits among stands and between census years using the following equation:

$$CWM\chi = \sum_{i=1}^{S}(pi * ti) \qquad \text{Eq. 2}$$

were CWM_χ is the CWM for trait χ in each subplot, s is the number of species in each southeastern or northeastern patch, p_i is the relative abundance of the *i*th species in each plot and stand age, and t_i is the trait value for the *i*th species. The CWM was calculated for each subplot from the species abundance and functional traits, and was calculated using the 'FD' package (Laliberté and Legendre, 2010).

Data analysis

We evaluated whether topographical conditions determine richness, composition, stem abundance, and CD species during late-secondary succession (questions 1 and 4). Thus, we use the three topographic variables to perform a multivariate regression tree (MRT) analysis (De'ath 2002; Larsen and Speckman 2004) to classify habitat types according to topographical variables as a proxy for topographic heterogeneity in each permanent patch studied (Guo et al. 2016; Wang et al. 2016). MRT is a constrained clustering method that identifies clusters (a group of plots) that are most similar to each other based on a set of predefined values (De'ath, 2002). MRT analysis was performed using the "rpart" package (Therneau et al. 2017). The two study permanent patches have marked differences in the spatial distribution of topographical variables, mainly elevation and convexity (Fig. S.3, Appendix/from Electronic Supplement Material, ESM hereafter). We represented the spatial distribution of habitats from each patch using the "*Field*" package (Nychka et al. 2017). According to the MRT, the southeastern area's permanent patch was less topographically heterogeneous, as determined by the two topographical variables (elevation and slope). Conversely, the permanent patch of the northeastern area was more topographically heterogeneous, determined by the three topographical variables elevation, slope, and convexity (Fig. S.4. from ESM).

We answered our first research question, i.e., whether topography and stand age determine species richness differences, using sampled-based rarefaction and extrapolation curves constructed with the first Hill numbers (Chao et al. 2014). Thus, we assessed species richness differences in each patch and all sampled years (stand ages). Extrapolations were based on presence/absence data (Hill number of order 0 with 100 replicate bootstrapping runs to estimate 95% confidence intervals), up to two the sample size (Colwell et al. 2012), using the "*iNEXT*" package (Hsieh et al. 2016). Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al. 2012).

Furthermore, non-metric multidimensional scaling (NMDS) analysis was performed based on Bray-Curtis dissimilarities (Clarke 1993) to examine species composition differences between patches and patches between different stand ages. We performed the NMDS using the '*metaMDS*' function (Oksanen et al. 2018) and the permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the '*adonis*' routine available within the "*vegan*" package (Oksanen et al. 2018).

We analyzed whether AGC stock was dominant for a small number of species and whether topography and stand age had implications in distributing CD species (questions 2 and 4). We did this by estimating the maximum number of species required to account for approximately 50% of AGC stock in all stand age and patches with different topographical conditions (Rodrigues et al. 2019a). Then, we assessed the number of CD species in each patch with different topographical conditions and stand age sampling. We considered 'CD species' those that represented approximately 50% of the total community AGC in each sampled year. To obtain CD species, all species in our database were ranked by decreasing contribution to the total AGC, based on the definitions adopted by Bastin et al. (2015) and Fauset et al. (2015). To understand the relationship between stem abundance, richness, and composition with CD species during the late-secondary succession and contrasting topographical conditions (question 3), we calculated the contribution of stem abundance to the total AGC in each patch and stand age. Thus, we regressed each species' percentage contribution to the AGC of the whole dataset against their percentage contribution to the number of stems of the whole dataset, following the methods adopted by Fauset et al. (2015). The same methodology was also used to rank the CD families along late-secondary succession. We constructed species and family rank curves (Magurran 2004) based on species-family abundance and distribution (number of species or family per patch and year of sampling). All species and families were ranked from the most to the least abundant to obtain species or family rank curves.

We answered whether dominant species govern AGC stock due to the relative importance of functional trait values compared to other species of tree community (question 5). Thus, we compared the mean AGC between patches and stand age, and CWM of trait values (WD and D_{max}) between categorical functional groups (CD and CND) performing Wilcoxon-tests (non-normally distributed data). Then, we evaluated, for all stand ages and patches with different topographical conditions, the CWM of functional traits WD and D_{max} in two functional categories: i) CD species and ii) CND species. Data were tested for normal distribution with the Shapiro-Wilks test and a Q-Q plot (Crawley 2012).

Finally, we assessed the spatial autocorrelation of the sampling units (subplots) within each patch (northeastern and southeastern) between the main variables used in our study (AGB and species richness) based on distance classes (0 – 12), which correspond to the spatial distance in meters (0-100) between subplots according to the Moran test (based on 9,999 permutations) using the "gstat" package (Pebesma et al., 2017). The spatial autocorrelation tests showed no significant spatial correlation in both patches based on spatial correlograms (Figure S5). All analyses were performed in R version 3.1.2. (R core team, 2019).

RESULTS

Species richness and composition

Species richness differed significantly between the two study patches with different topographical conditions (Fig. 1A). Species richness in the northeastern patch (the more topographically heterogeneous one) was higher than that in the southeastern patch, which is less topographically heterogeneous. Conversely, species richness did not differ significantly between stand ages within each patch. (Fig. 1B). The NMDS revealed that tree species composition varied considerably between patches; and separated the two study patches along the first axis (Fig. 2A). On the other hand, the NMDS during the late-secondary succession revealed no significant differences between stand age in both in both patches (Fig. 2B and C, respectively).

Carbon dominant species and abundance

We found that both patches have CD species, i.e., accounting for approximately 50% of the carbon storage. Only one species (*Anadenanthera peregrina* Speg.) was classified as CD in all stand age in the southeastern patch (Fig. 3). This species presented approximately 3.5% of the total abundance (Tab. 1). On the other hand, three to five species accumulated 50% of the AGC in the northeastern patch (Fig. 3). These species presented together on average, approximately 23.9% of the total abundance (Tab. 1). The top five most dominant species in AGG and abundance are distributed according to their relative contribution (Table 1; data on all species is found in Appendix Table S.1. from ESM).

Shifts of carbon dominant species and families on topographically different stand age

We did not find in the permanent patch of southeastern area shifts in CD species; the only CD species was *Anadenanthera peregrina* regardless of stand age (storing 70.2; 74; 78.9; 83 and 84 Mg ha^{-1} of carbon, respectively in the years 1984, 1998, 2003, 2011 and 2017) (Table 1 and

Fig. S.1 from ESM). The main CD species distribution in the northeastern patch did not change along late-secondary succession. *Anadenanthera peregrina*, *Piptadenia gonoacantha* (Mart.) J.F. Macbr., and *Machaerium stipitatum* Vogel, were the CD species in 1993 (stocking 15,5; 11,3 and 7 Mg ha^{-1} of carbon, respectively); they shared dominance with *Allophylus edulis edulis* (A. St-Hil., A. Juss. & Cambess) Radlk. in 2004 and *Allophylus edulis* and *Trichilia lepidota* Mart. in 2011 and 2017 (Table 1 and Fig. S.1 from ESM). Thus, we observed that different topographical conditions and stand age shape changes in CD species when we evaluate the two patches separately. Still, when assessing each patch, there are no changes in the species identity during the late-secondary succession.

On the other hand, when we analyzed the dominant families, the only carbon dominant family in the southeastern patch was Fabaceae, which accounts for 66.4 to 70.3% of carbon in this late-secondary succession. In the northeastern patch, Fabaceae account for an average of 53% of the carbon stored in 1993 and 2004. In 2011 and 2017, Fabaceae accumulated 48.6% and 45.9% of the total carbon for those years, respectively (Fig. S.2. from ESM). There is a decrease in the proportion of carbon accumulated by the family in late-secondary succession and the different topographical conditions (Data on all families is found in Appendix Table S.2. from ESM).

AGC stock with respect to functional traits and groups

CWM of functional traits WD and D_{max} of the CD species differed significantly from the CND species in most stand age in the patches with different topographical conditions. Nevertheless, CWM of functional trait values WD did not differ in the southeastern patch in the two last sampling periods and CWM of D_{max} in 2017. The highest CWM functional trait values were found for the species that accumulate approximately 50% of the total AGC stock (CD), mainly in the southeastern patch (Fig. 4).

DISCUSSION

We found that topographical conditions and stand age shape changes in community composition, species richness, abundance, and CD species throughout the late-secondary stage. Furthermore, our results showed that the taxonomic identities of the dominant species, and not the species abundance and richness, determine the AGC stock due to the importance of trait values related to carbon stock (WD and D_{max}). In this study, the main novelty was assessing CD and CND species based on CWM functional traits values of WD and D_{max}. Thus, we found that topography and stand age shaped the proportion of CD species. In contrast, AGC stock was driven by the functional composition, expressed in the higher CWM values of conservative functional traits. Moreover, CD species and families do not change along late-secondary succession and topographical conditions when we evaluate each patch separately.

These findings are important for understanding the role of individual species and their traits for ecosystem functioning, which can allow formulating more detailed conservation and restoration plans in highly diverse and threatened ecosystems, such as Atlantic Forest (Scarano and Ceotto 2015; Kearsley et al. 2019). Furthermore, this study highlights the fundamental role of CWM of functional trait values of CD species to estimate AGC stock and the relative importance of functional groups and taxonomic identity in AGC storage in second-growth tropical forests.

Patterns of species richness, abundance, and dominance

We found CD species in both patches, but this dominance pattern is not linked to the species abundance in most stand ages. In the southeastern patch, only *Anadenanthera peregrina* was classified as CD. Besides, this species presented a low stem abundance (on average 58 stems in each stand age) compared to other species, i.e., CND (for example, *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Wess.Boer, presented an average of 544 stems in each stand age evaluated). The same pattern was observed in the northeastern patch, where three to four species accumulated 50% of the AGC. This different proportion pattern in the number of CD can be explained by the different topographic heterogeneity and the stand age differences between patches. Thus, previous studies report that a higher environmental heterogeneity among patches results in a higher probability that some species dominate the plant communities (Hillebrand et al. 2008; Mattsson et al. 2016), explaining the higher number of CD in the northeastern patch, the most topographically heterogeneous.

According to Hillebrand et al. (2008), dominance responds more rapidly to environmental conditions than species richness and might to lead to rapid responses in terms of ecosystem functions. We found that the number of CD is related to the richness of patches. The most species-rich patch has a higher number of CD compared to the less species-rich patch. Thus, the dominance patterns may affect the species richness in different ways, either through evenness that alters the number of species per unit area or because more species are found in patches with higher evenness, i.e., less species dominance (Hillebrand et al. 2008), such as the northeastern patch.

In this sense, the functional composition (i.e., CWM of functional traits of CD) may be more important for tropical forest functioning than species richness and composition (Prado-Junior et al. 2016; Villa et al. 2020a). For example, Fotis et al. (2018) found that traits that drove AGB were strongly associated with two dominant species present at the study site. These authors conclude that higher species richness may dilute the effects of traits that drive AGB accumulation in more dominant species. These results agree with our results, which showed that in the less species-rich patch (southeastern n = 104), there is a smaller CD than the most species-rich patch (northeastern n = 143), which has a high number of CD.

The highest CWM of D_{max} values was found in the southeastern patch, which presents a lower species richness, and showed that the CD are large-sized trees. Furthermore, rather than the topographical condition and stand age, dominant tree species themselves could be limiting the establishment of more species (biotic filter). These large trees limit light, water, and soil nutrients available to other trees, hence driving species richness and diversity (Lohbeck et al. 2018; Ali et al. 2019). In addition, environmental factors, such as topography, can be considered a filter constraining which individuals bearing specific traits can persist in a community (Violle et al. 2007). Different topographical conditions could influence the breadth of functional traits distribution between them, which can affect the ACG stock distribution through the functional composition and categorical functional groups (CD and CND).

Carbon dominant species and Fabaceae family are stable along the late-secondary succession

We did not find changes of CD species and families and CWM of functional traits values during late-secondary succession in both patches. The Fabaceae was the unique carbon dominant family, represented mainly by *Anadenanthera peregrina* (Fabaceae) in all stand ages. These results are consistent with those of Terra et al. (2017), who found that 220 species (5.38%) of all species studied in Minas Gerais state belong to the Fabaceae family. Our results indicated that there was a prolonged late-secondary succession decrease in Fabaceae abundance in the northeastern patch, the oldest one. Consistent with these results, van der Sande et al. (2016) reported that the Fabaceae family has become less abundant in the old-growth forest due to decreased nitrogen limitation and an increase in drought stress, which should be better explored in future research. In this context, ecological theories predict that community stability is due, among other factors, to the persistence of dominant species, as found in our analyses (e.g., Yuan et al. 2019). Meanwhile, other studies suggest that the stabilizing of species richness along succession can only be observed at low dominance (e.g., Hillebrand et al. 2008; Lohbeck et al. 2014). Under high plant dominance, one or few species (as shown in our results) make significant contributions to the biomass or carbon that reduces the stabilizing effect of species richness (Hillebrand et al. 2008).

Functional traits composition shapes the highest AGC stock by carbon dominant species

The results support our hypothesis that species' taxonomic identity is more important than abundance. This is due to the relative importance of CWM of functional trait values that govern ecosystem functioning, i.e., AGC stock. These findings support the approach that ecosystem properties depend more on functional traits than species or abundance (Phillips et al. 2019; Lohbeck et al. 2016). Our results showed that despite the low proportion of dominant species, these present large-sized individuals whith maximum size (expressed as CWM of D_{max}) compared to carbon non-dominant species with smaller-sized individuals. These few dominant species with large-sized individuals could play a more prominent role in AGB stock than those abundant smaller-sized individuals. Previous studies have shown this positive relationship between the maximum stem diameter and CWM of wood density and aboveground biomass, confirming that high aboveground biomass is associated with large-diameter trees (Ali et al. 2019; Rodrigues et al. 2019; Villa et al. 2020a). Moreover, this observed pattern in our study probably explains the more conservative trait values (increasing the community WD with time) and ecosystem functioning stabilization during late-secondary succession (Poorter et al. 2019). This relationship between the CWM of wood density and D_{max} and AGC may explain the importance of slow-growing and shade-tolerant species during late-secondary succession (Poorter et al. 2019, Villa et al. 2020a).

In this sense, large-sized trees have been shown to drive variation in biomass since those store high quantities of carbon in tropical forests (Bastin et al. 2015; Fauset et al. 2015; Poulsen et al. 2020). Despite storing higher amounts of AGC, these trees with high CWM of Dmax values are found in low abundance (Fauset et al. 2015; Rodrigues et al. 2019a). This result showed that the ecosystem functioning is mainly determined by the functional traits of the CD species despite species richness and abundance. Hence, the results found in our research are in agreement with the mass-ratio hypothesis (Grime 1998; Villa et al. 2020a). However, in the northeastern patch, several CD species are also dominant in terms of abundance. Thus, these species can also be considered oligarchs in relation to abundance in this patch. Therefore, here we do not intend to dismiss the importance of abundant species in relation to dominant, as these, together with the dominant species, participate in multiple ecosystem functions and maintain biodiversity (Ali et al. 2019, 2020). This premise is fundamental in programs focused on carbon-diversity cobenefits, especially considering heterogeneity within forests (Matos et al. 2020). In addition, it is extremely relevant to consider our results in forest recovery and conservation programs. Since the anthropogenic disturbances affect tree communities in Atlantic Forests (Matos et al. 2020), changes in species richness and, consequently, relative abundance and dominance, can also affect ecosystems' stability (Hillebrand et al. 2008). These disturbances can have negative effects because the loss of a single dominant species has several negative consequences for forest functioning (Bradford and Murphy 2019).

Our study showed that topographical conditions and stand age shape tree community composition changes, species richness, abundance, and CD species in a second-growth Atlantic Forest. Furthermore, we showed that CWM of functional traits values of WD and D_{max} of CD species determine AGC stock, agreeing with the mass ratio hypothesis. Therefore, our study reveals that both trait functional composition and taxonomic identity across CD species shape AGC stock in our studied forests. We reported a stabilization of the dominant species and families along late-secondary succession, with *A. peregrina* being the main CD species. In addition, we emphasize the relevance of the trait-based approach to understanding forest functioning and trait functional composition, and taxonomic identity (role of key species) for the carbon storage, recovery, and increase of the threatened Atlantic Forest.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHORS' CONTRIBUTION

ACR, PMV and AVN conceived and designed the study. ACR and PMV analysed the data. ACR wrote the manuscript with input from FSC, CEMT, PMV, LPG, JAAMN and AVN. All authors contributed substantially to the writing and revision of the manuscript.

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Southeastern	NºSp.	Species	Ab	%Ab	%Ab.Ac.	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1984	1	*Anadenanthera peregrina* (Ana_per)	68	4.51	4.51	70.22	70.22	50.11	50.11
1984	2	*Casearia ulmifolia* (Cas_ulm)	158	10.47	14.98	13.69	83.91	9.77	59.88
1984	3	*Sorocea bonplandii* (Sor_bon)	328	21.74	36.71	5.86	89.77	4.18	64.07
1984	4	*Anadenanthera colubrina* (Ana_col)	1	0.07	36.78	5.61	95.38	4	68.07
1984	5	*Machaerium nyctitans* (Mac_nyc)	60	3.98	40.76	5.55	100.93	3.96	72.03
1998	1	*Anadenanthera peregrina* (Ana_per)	61	3.44	3.44	74.08	74.08	48.15	48.15
1998	2	*Casearia ulmifolia* (Cas_ulm)	154	8.69	12.13	15.31	89.39	9.95	58.09
1998	3	*Sorocea bonplandii* (Sor_bon)	518	29.23	41.37	9.74	99.13	6.33	64.42
1998	4	*Anadenanthera colubrina* (Ana_col)	3	0.17	41.53	7.27	106.4	4.72	69.15
1998	5	*Dalbergia nigra* (Dal_nig)	13	0.73	42.27	4.79	111.19	3.11	72.26
2003	1	*Anadenanthera peregrina* (Ana_per)	60	3.39	3.39	78.5	78.5	47.03	47.03
2003	2	*Casearia ulmifolia* (Cas_ulm)	144	8.14	11.53	16.7	95.19	10	57.04
2003	3	*Sorocea bonplandii* (Sor_bon)	583	32.94	44.46	12.71	107.9	7.62	64.65
2003	4	*Anadenanthera colubrina* (Ana_col)	5	0.28	44.75	8.26	116.17	4.95	69.6
2003	5	*Apuleia leiocarpa* (Apu_lei)	69	3.9	48.64	5.27	121.43	3.16	72.76
2011	1	*Anadenanthera peregrina* (Ana_per)	51	3.29	3.29	83.1	83.1	51.02	51.02
2011	2	*Sorocea bonplandii* (Sor_bon)	608	39.23	42.52	15.89	98.99	9.76	60.78
2011	3	*Casearia ulmifolia* (Cas_ulm)	104	6.71	49.23	12.27	111.27	7.54	68.32
2011	4	*Anadenanthera colubrina* (Ana_col)	7	0.45	49.68	8.41	119.68	5.16	73.48
2011	5	*Apuleia leiocarpa* (Apu_lei)	58	3.74	53.42	5.1	124.78	3.13	76.61
2017	1	*Anadenanthera peregrina* (Ana_per)	50	3.1	3.1	84.01	84.01	49.36	49.36
2017	2	*Sorocea bonplandii* (Sor_bon)	683	42.37	45.47	18.06	102.07	10.61	59.97
2017	3	*Casearia ulmifolia* (Cas_ulm)	94	5.83	51.3	12.22	114.29	7.18	67.15
2017	4	*Anadenanthera colubrina* (Ana_col)	6	0.37	51.67	8.95	123.24	5.26	72.41
2017	5	*Apuleia leiocarpa* (Apu_lei)	55	3.41	55.09	5.25	128.49	3.09	75.49

Northeastern	NºSp.	Species	Ab	%Ab	%Ab.Ac.	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1993	1	*Anadenanthera peregrina* (Ana_per)	58	5.48	5.48	15.54	15.54	21.6	21.6
1993	2	*Piptadenia gonoacantha* (Pip_gon)	68	6.43	11.91	11.32	26.86	15.73	37.33
1993	3	*Machaerium stipitatum* (Mac_sti)	42	3.97	15.88	7.08	33.95	9.85	47.18
1993	4	*Cedrela fissilis* (Ced_fis)	12	1.13	17.01	3.29	37.23	4.57	51.75
1993	5	*Prunus sellowii* (Pru_sel)	94	8.88	25.9	3.15	40.38	4.37	56.12
2004	1	*Anadenanthera peregrina* (Ana_per)	65	4.8	4.8	18.05	18.05	18.17	18.17
2004	2	*Piptadenia gonoacantha* (Pip_gon)	79	5.83	10.64	16.44	34.48	16.55	34.73
2004	3	*Machaerium stipitatum* (Mac_sti)	53	3.91	14.55	10.34	44.82	10.41	45.14
2004	4	*Allophylus edulis* (All_edu)	44	3.25	17.8	4.71	49.53	4.74	49.88
2004	5	*Trichilia lepidota* (Tri_lep)	101	7.46	25.26	3.77	53.29	3.79	53.68
2011	1	*Anadenanthera peregrina* (Ana_per)	48	3.81	3.81	19.03	19.03	17.53	17.53
2011	2	*Piptadenia gonoacantha* (Pip_gon)	52	4.13	7.94	16.39	35.42	15.1	32.63
2011	3	*Machaerium stipitatum* (Mac_sti)	41	3.25	11.19	10.06	45.47	9.27	41.89
2011	4	*Allophylus edulis* (All_edu)	42	3.33	14.52	6.72	52.19	6.19	48.08
2011	5	*Trichilia lepidota* (Tri_lep)	104	8.25	22.78	4.84	57.03	4.46	52.54
2017	1	*Anadenanthera peregrina* (Ana_per)	61	4.37	4.37	20.41	20.41	17.98	17.98
2017	2	*Piptadenia gonoacantha* (Pip_gon)	43	3.08	7.44	16.58	36.99	14.6	32.58
2017	3	*Allophylus edulis* (All_edu)	43	3.08	10.52	7.73	44.72	6.81	39.38
2017	4	*Machaerium stipitatum* (Mac_sti)	39	2.79	13.31	7.35	52.07	6.48	45.86

2017	5	*Trichilia lepidota* (Tri_lep)	117	8.38	21.69	5.63	57.69	4.95	50.81

Table 1. Top 5 most important species for AGC stock and abundance in the patches for all year's sampling. The carbon dominant species are highlighted.

NºSp. =Species number; Species = abbreviation of each 5 most carbon dominant species; Ab =abundance; %Ab = relative abundance; %Ab.Ac. =accumulated relative abundance; AGC = aboveground carbon; AGC.Ac. = Aboveground carbon accumulated; %AGC = proportion of aboveground carbon; % AGC.Ac. =proportion of aboveground carbon accumulated.

FIGURE LEGENDS

Figure 1. Sample-based rarefaction (solid line) and extrapolation curves (dashed lines) of tree richness for southeastern and northeastern patches (A) and tree richness in all stand age analyzed in the two 1-ha permanent patches (B). Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

Figure 2. Non-metric multidimensional scaling based (NMDS) on species composition (geometric shapes) and study areas (shapes colors) within two 1-ha permanent plots in Atlantic Forest, Minas Gerais, Brazil (A). NMDS on species composition according to stands ages (shapes colors) in the permanents patches of northeastern (B) and southeastern (C).

Figure 3. Cumulative aboveground carbon (AGC) distribution for the permanent plot of southeastern (A) and northeastern (B) patches for carbon dominants species in the Atlantic Forest, Minas Gerais, Brazil. The dashed horizontal red line indicates the limit of species that accumulate approximately 50% of the total carbon in all stands ages.

Figure 4. The relative importance of CWM of the functional traits maximum stem diameter (D_{max}) (A, B) and wood density – WD (C, D) of carbon dominant species (CD) and carbon non-dominant species (CND) in all stand age and patches with different topographic conditions studied. CD corresponds to the CWM of the traits of the species that accumulate approximately 50% of the total AGC stock, while CND corresponds to the CWM of the traits of other species in the community.

FIGURES

Figure 1

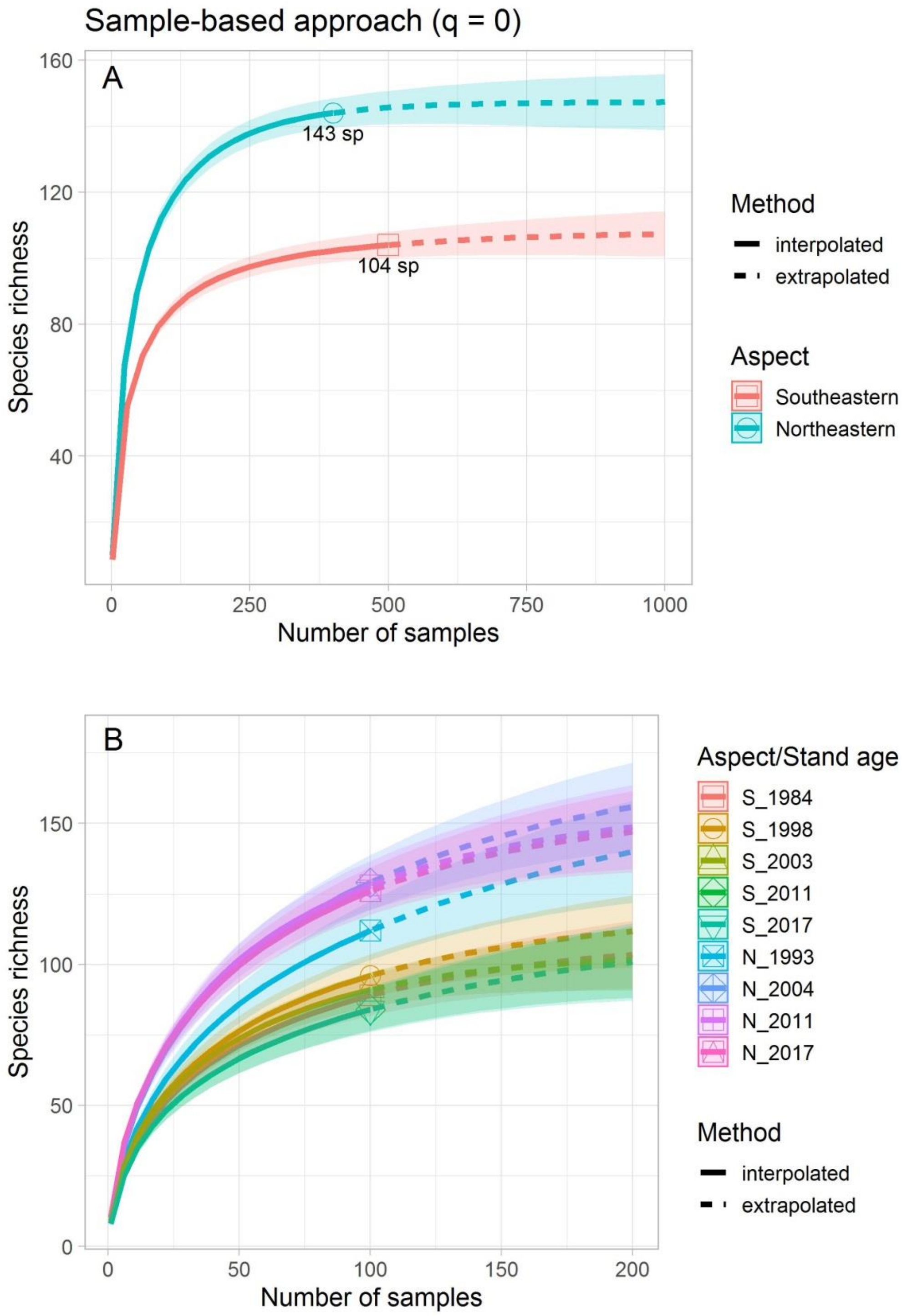
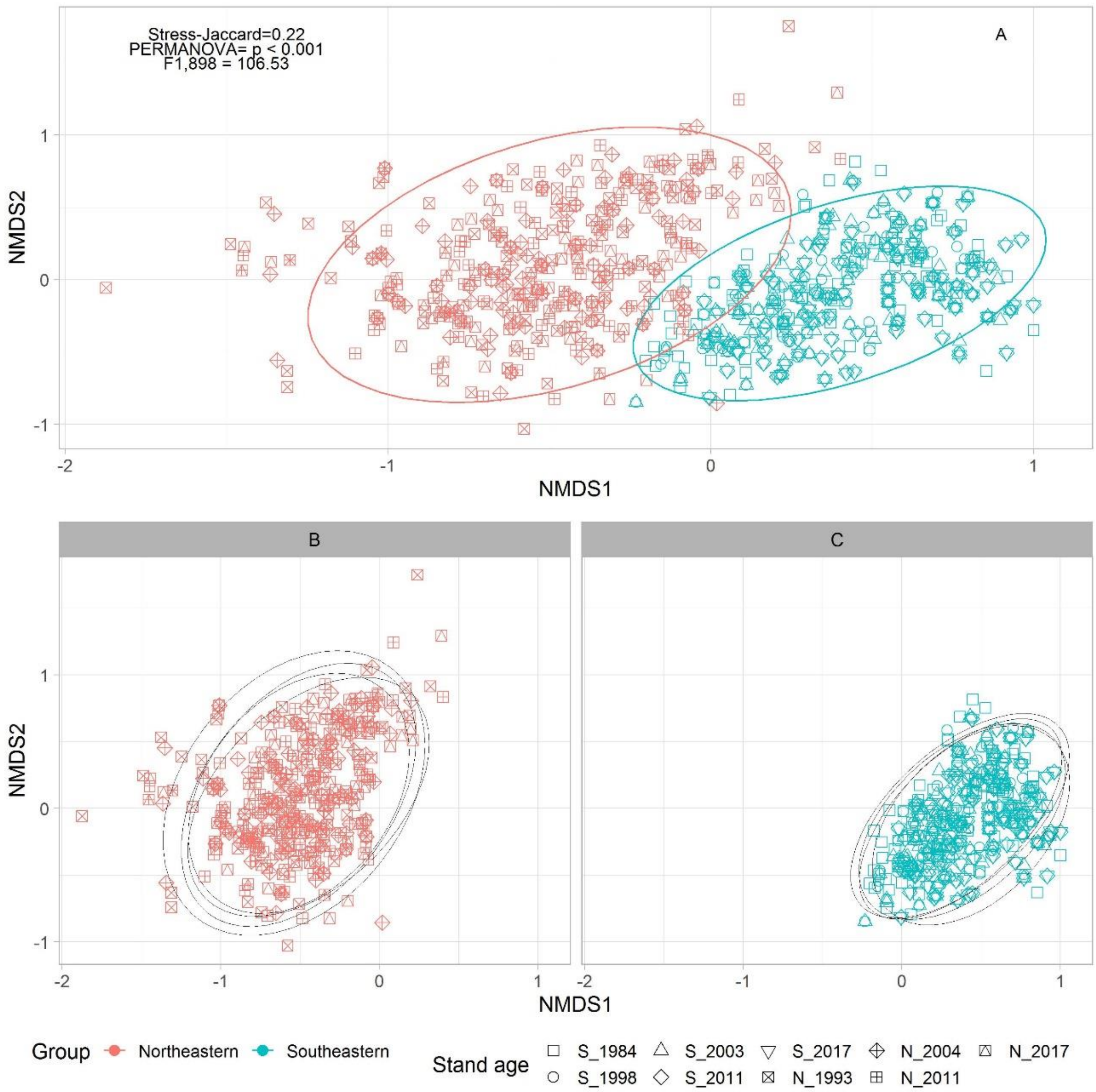


Figure 2



Stress-Jaccard=0.22
PERMANOVA= p < 0.001
F1,898 = 106.53
A
NMDS2
NMDS1
B
C
Group
Northeastern
Southeastern
Stand age
S_1984
S_2003
S_2017
N_2004
N_2017
S_1998
S_2011
N_1993
N_2011

Figure 3

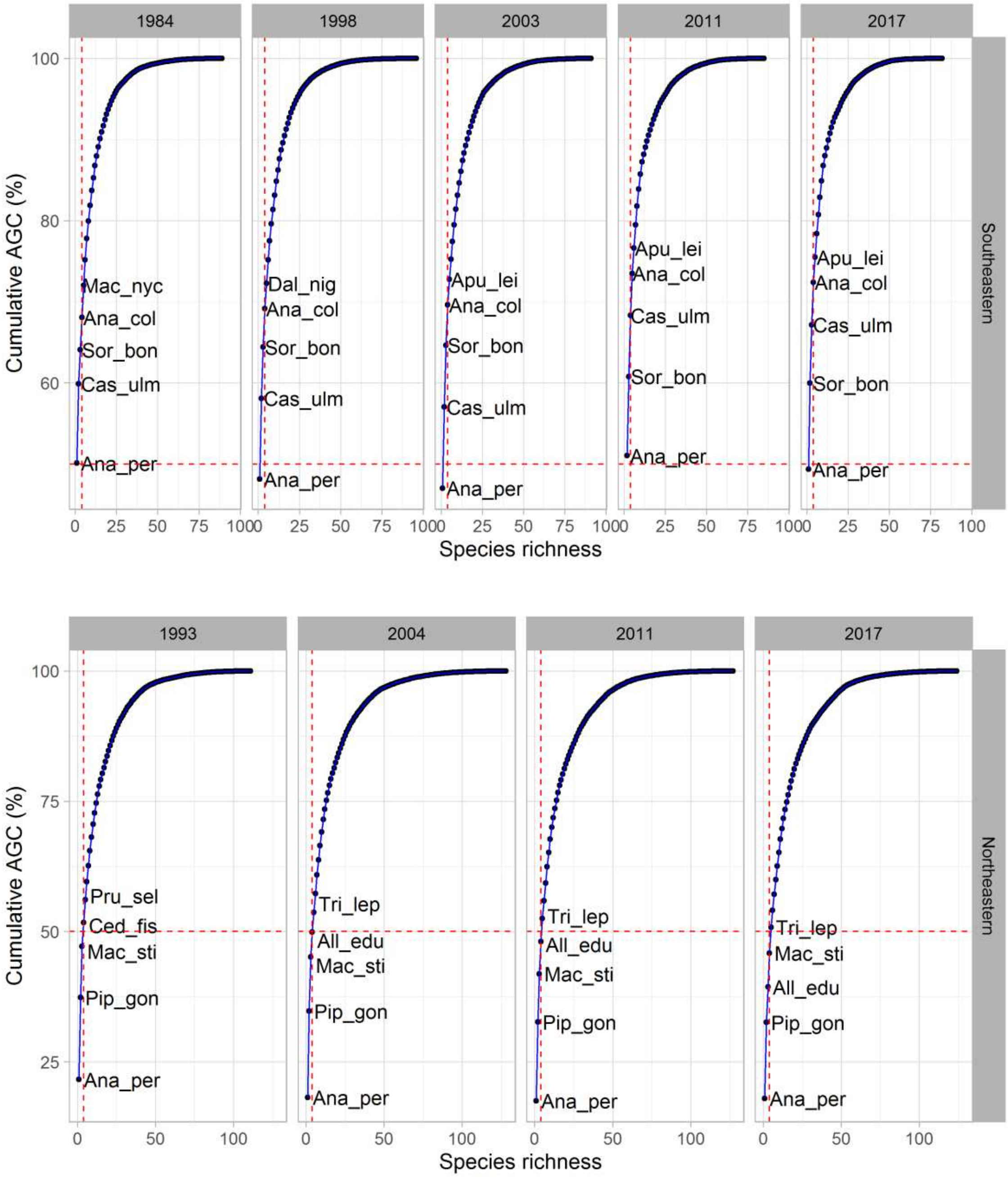
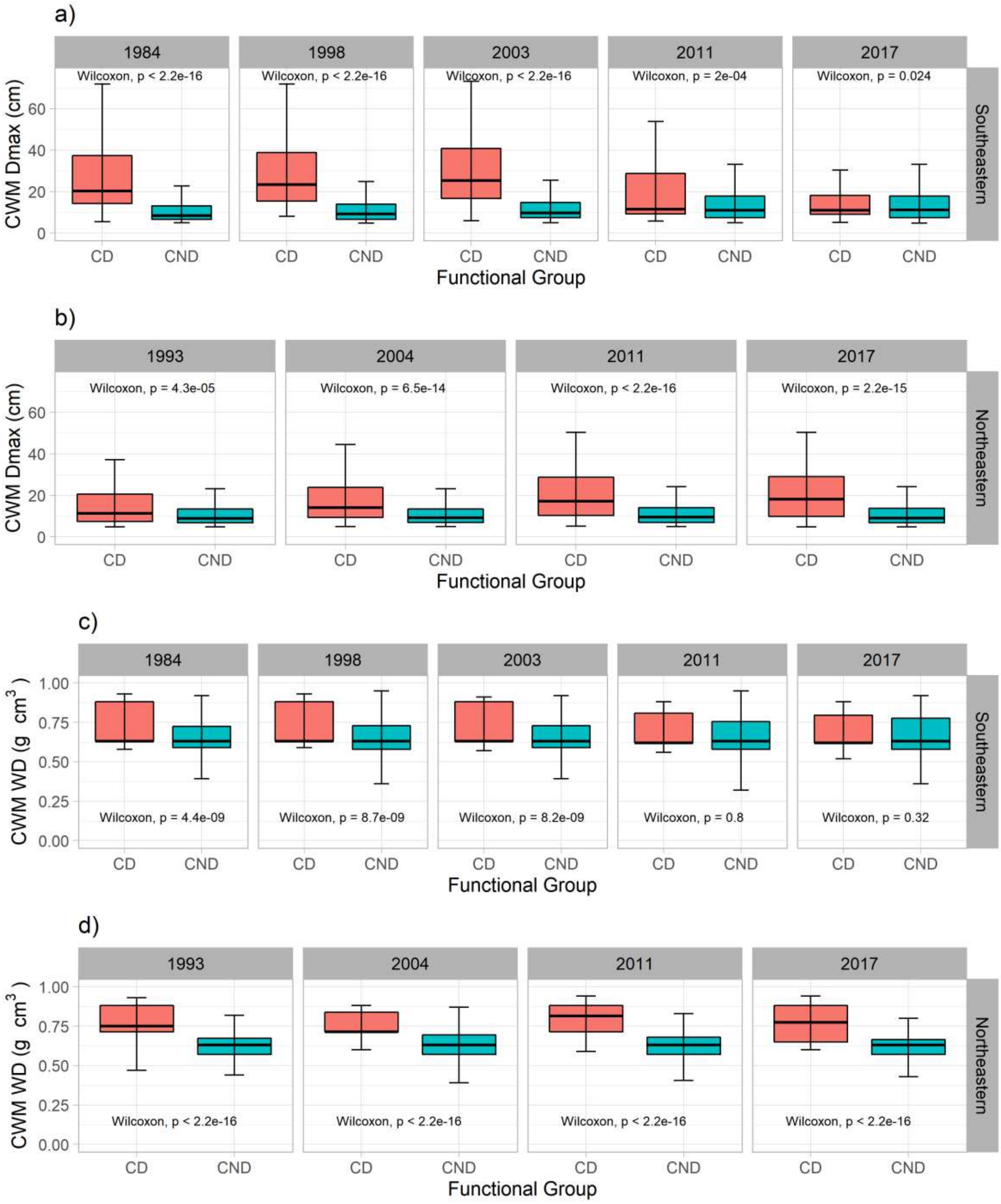

1984
1998
2003
2011
2017
Southeastern
Cumulative AGC (%)
Species richness
Mac_nyc
Ana_col
Sor_bon
Cas_ulm
Ana_per
Dal_nig
Apu_lei
1993
2004
2011
2017
Northeastern
Pru_sel
Ced_fis
Mac_sti
Pip_gon
Tri_lep
All_edu

Figure 4


a)
1984
1998
2003
2011
2017
Wilcoxon, p < 2.2e-16
Wilcoxon, p < 2.2e-16
Wilcoxon, p < 2.2e-16
Wilcoxon, p = 2e-04
Wilcoxon, p = 0.024
CWM Dmax (cm)
Southeastern
CD
CND
Functional Group
b)
1993
2004
2011
2017
Wilcoxon, p = 4.3e-05
Wilcoxon, p = 6.5e-14
Wilcoxon, p < 2.2e-16
Wilcoxon, p = 2.2e-15
CWM Dmax (cm)
Northeastern
CD
CND
Functional Group
c)
1984
1998
2003
2011
2017
Wilcoxon, p = 4.4e-09
Wilcoxon, p = 8.7e-09
Wilcoxon, p = 8.2e-09
Wilcoxon, p = 0.8
Wilcoxon, p = 0.32
CWM WD (g cm^3)
Southeastern
CD
CND
Functional Group
d)
1993
2004
2011
2017
Wilcoxon, p < 2.2e-16
Wilcoxon, p < 2.2e-16
Wilcoxon, p < 2.2e-16
Wilcoxon, p < 2.2e-16
CWM WD (g cm^3)
Northeastern
CD
CND
Functional Group

Supplementary material

Table S.1. Data on all species for aboveground carbon stock (AGC) and abundance in Southeastern and Northeastern patches for all year's sampling.

NºSp. =Species number; Ab =abundance; %Ab = relative abundance; %Ab.Ac. =accumulated relative abundance; AGC = aboveground carbon; AGC.Ac. = Aboveground carbon accumulated; %AGC = proportion of aboveground carbon; % AGC.Ac. =proportion of aboveground carbon accumulated.

Southeastern	NºSp.	Species	Ab	%Ab	%Ab.Ac.	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1984	1	*Anadenanthera peregrina*	68	4.51	4.51	70.22	70.22	50.11	50.11
1984	2	*Casearia ulmifolia*	158	10.47	14.98	13.69	83.91	9.77	59.88
1984	3	*Sorocea bonplandii*	328	21.74	36.71	5.86	89.77	4.18	64.07
1984	4	*Anadenanthera colubrina*	1	0.07	36.78	5.61	95.38	4.00	68.07
1984	5	*Machaerium nyctitans*	60	3.98	40.76	5.55	100.93	3.96	72.03
1984	6	*Dalbergia nigra*	15	0.99	41.75	4.40	105.33	3.14	75.17
1984	7	*Apuleia leiocarpa*	76	5.04	46.79	3.71	109.05	2.65	77.82
1984	8	*Myroxylon peruiferum*	2	0.13	46.92	2.96	112.00	2.11	79.93
1984	9	*Casearia decandra*	17	1.13	48.05	2.70	114.70	1.93	81.86
1984	10	*Peltophorum dubium*	8	0.53	48.58	2.60	117.30	1.85	83.71
1984	11	*Copaifera langsdorffii*	6	0.40	48.97	2.15	119.45	1.53	85.25
1984	12	*Protium warmingiana*	79	5.24	54.21	2.13	121.58	1.52	86.77
1984	13	*Luehea grandiflora*	20	1.33	55.53	1.63	123.22	1.16	87.93
1984	14	*Allophylus edulis*	23	1.52	57.06	1.61	124.82	1.15	89.08
1984	15	*Rollinia sylvatica*	64	4.24	61.30	1.41	126.23	1.00	90.08
1984	16	*Astronium fraxinifolium*	3	0.20	61.50	1.21	127.43	0.86	90.94
1984	17	*Coutarea hexandra*	56	3.71	65.21	1.05	128.48	0.75	91.69
1984	18	*Piptadenia gonoacantha*	65	4.31	69.52	1.03	129.50	0.73	92.42
1984	19	*Casearia arborea*	12	0.80	70.31	0.96	130.46	0.68	93.11
1984	20	*Ocotea odorifera*	10	0.66	70.97	0.81	131.28	0.58	93.69
1984	21	*Trichilia pallida*	126	8.35	79.32	0.81	132.08	0.58	94.26
1984	22	*Cordia sellowiana*	3	0.20	79.52	0.75	132.83	0.53	94.80
1984	23	*Siparuna guianensis*	89	5.90	85.42	0.64	133.47	0.46	95.25
1984	24	*Endlicheria paniculata*	2	0.13	85.55	0.56	134.03	0.40	95.65
1984	25	*Clarisia ilicifolia*	4	0.27	85.82	0.49	134.52	0.35	96.00
1984	26	*Zanthoxylum rhoifolium*	6	0.40	86.22	0.45	134.97	0.32	96.33
1984	27	*Sparattosperma leucanthum*	9	0.60	86.81	0.37	135.35	0.27	96.59
1984	28	*Ceiba speciosa*	7	0.46	87.28	0.32	135.67	0.23	96.82
1984	29	*Prunus sellowii*	8	0.53	87.81	0.32	135.99	0.23	97.05
1984	30	*Seguieria americana*	6	0.40	88.20	0.32	136.31	0.23	97.28
1984	31	*Myrcia sphaerocarpa*	2	0.13	88.34	0.29	136.61	0.21	97.49
1984	32	*Pterocarpus rohrii*	9	0.60	88.93	0.29	136.89	0.20	97.69
1984	33	*Brosimum guianense*	8	0.53	89.46	0.24	137.14	0.17	97.87
1984	34	*Ixora gardneriana*	4	0.27	89.73	0.24	137.38	0.17	98.04
1984	35	*Cecropia pachystachya*	1	0.07	89.79	0.24	137.61	0.17	98.21
1984	36	*Chrysophyllum marginatum*	2	0.13	89.93	0.21	137.82	0.15	98.36
1984	37	*Casearia obliqua*	4	0.27	90.19	0.20	138.02	0.14	98.50
1984	38	*Vitex megapotamica*	4	0.27	90.46	0.16	138.19	0.12	98.62
1984	39	*Zeyheria tuberculosa*	5	0.33	90.79	0.15	138.34	0.11	98.73
1984	40	*Chrysophyllum gonocarpum*	13	0.86	91.65	0.12	138.46	0.09	98.81
1984	41	*Amaioua guianensis*	11	0.73	92.38	0.11	138.57	0.08	98.89
1984	42	*Ocotea pulchella*	1	0.07	92.45	0.11	138.68	0.08	98.97
1984	43	*Guettarda scabra*	5	0.33	92.78	0.10	138.78	0.07	99.04
1984	44	*Licania spicata*	3	0.20	92.98	0.09	138.87	0.06	99.10
1984	45	*Aniba firmula*	1	0.07	93.04	0.09	138.95	0.06	99.17

1984	46	*Eugenia leptoclada*	6	0.40	93.44	0.08	139.03	0.06	99.22
1984	47	*Sapium glandulatum*	2	0.13	93.57	0.08	139.11	0.06	99.28
1984	48	*Carpotroche brasiliensis*	5	0.33	93.90	0.07	139.18	0.05	99.33
1984	49	*Myrciaria axillaris*	11	0.73	94.63	0.07	139.25	0.05	99.38
1984	50	*Eugenia strictopetala*	2	0.13	94.76	0.06	139.31	0.04	99.42
1984	51	*Matayba elaeagnoides*	1	0.07	94.83	0.05	139.36	0.04	99.46
1984	52	*Bathysa meridionalis*	7	0.46	95.29	0.05	139.41	0.04	99.49
1984	53	*Attalea dubia*	3	0.20	95.49	0.05	139.46	0.03	99.53
1984	54	*Cariniana legalis*	1	0.07	95.56	0.05	139.51	0.03	99.56
1984	55	*Jacaranda micrantha*	8	0.53	96.09	0.05	139.55	0.03	99.59
1984	56	*Rheedia gardneriana*	1	0.07	96.16	0.04	139.59	0.03	99.62
1984	57	*Trichilia elegans*	3	0.20	96.36	0.04	139.64	0.03	99.65
1984	58	*Maclura tinctoria*	5	0.33	96.69	0.04	139.68	0.03	99.68
1984	59	*Xylopia sericea*	3	0.20	96.89	0.04	139.72	0.03	99.71
1984	60	*Cordia bullata*	1	0.07	96.95	0.03	139.75	0.02	99.74
1984	61	*Zollernia ilicifolia*	2	0.13	97.08	0.03	139.79	0.02	99.76
1984	62	*Platypodium elegans*	1	0.07	97.15	0.03	139.82	0.02	99.78
1984	63	*Pouteria sp*	3	0.20	97.35	0.03	139.85	0.02	99.81
1984	64	*Mabea longifolia*	2	0.13	97.48	0.03	139.88	0.02	99.83
1984	65	*Aspidosperma olivaceum*	2	0.13	97.61	0.03	139.91	0.02	99.84
1984	66	*Cariniana estrellensis*	2	0.13	97.75	0.02	139.93	0.02	99.86
1984	67	*Cordia silvestris*	3	0.20	97.95	0.02	139.95	0.01	99.87
1984	68	*Qualea jundiahy*	2	0.13	98.08	0.02	139.96	0.01	99.89
1984	69	*Swartzia myrtifolia*	2	0.13	98.21	0.02	139.98	0.01	99.90
1984	70	*Citronella paniculata*	1	0.07	98.28	0.01	139.99	0.01	99.91
1984	71	*Eriotheca candolleana*	4	0.27	98.54	0.01	140.01	0.01	99.92
1984	72	*Lonchocarpus guillemineanus*	2	0.13	98.67	0.01	140.02	0.01	99.93
1984	73	*Picramnia regnelli*	1	0.07	98.74	0.01	140.03	0.01	99.94
1984	74	*Cybistax antisyphilitica*	2	0.13	98.87	0.01	140.04	0.01	99.94
1984	75	*Psychotria vellosiana*	1	0.07	98.94	0.01	140.05	0.01	99.95
1984	76	*Hortia brasiliana*	1	0.07	99.01	0.01	140.06	0.01	99.96
1984	77	*Mollinedia argyrogyna*	1	0.07	99.07	0.01	140.07	0.01	99.96
1984	78	*Ocotea dispersa*	2	0.13	99.20	0.01	140.08	0.01	99.97
1984	79	*Cedrela fissilis*	2	0.13	99.34	0.01	140.08	0.00	99.97
1984	80	*Andira fraxinifolia*	1	0.07	99.40	0.01	140.09	0.00	99.98
1984	81	*Campomanesia xanthocarpa*	1	0.07	99.47	0.01	140.09	0.00	99.98
1984	82	*Maytenus aquifolium*	1	0.07	99.54	0.01	140.10	0.00	99.98
1984	83	*Acacia polyphylla*	1	0.07	99.60	0.01	140.10	0.00	99.99
1984	84	*Tovomitopsis saldanhae*	1	0.07	99.67	0.00	140.11	0.00	99.99
1984	85	*Simira sampaioana*	1	0.07	99.73	0.00	140.11	0.00	99.99
1984	86	*Erythroxylum pelleterianum*	1	0.07	99.80	0.00	140.12	0.00	99.99
1984	87	*Croton floribundus*	1	0.07	99.87	0.00	140.12	0.00	100.00
1984	88	*Persea pyrifolia*	1	0.07	99.93	0.00	140.12	0.00	100.00
1984	89	*Cupania ludowigii*	1	0.07	100.00	0.00	140.12	0.00	100.00
1998	1	*Anadenanthera peregrina*	61	3.44	3.44	74.08	74.08	48.15	48.15
1998	2	*Casearia ulmifolia*	154	8.69	12.13	15.31	89.39	9.95	58.09
1998	3	*Sorocea bonplandii*	518	29.23	41.37	9.74	99.13	6.33	64.42
1998	4	*Anadenanthera colubrina*	3	0.17	41.53	7.27	106.40	4.72	69.15
1998	5	*Dalbergia nigra*	13	0.73	42.27	4.79	111.19	3.11	72.26
1998	6	*Apuleia leiocarpa*	70	3.95	46.22	4.45	115.63	2.89	75.15
1998	7	*Myroxylon peruiferum*	2	0.11	46.33	3.62	119.25	2.35	77.50
1998	8	*Machaerium nyctitans*	54	3.05	49.38	3.21	122.46	2.08	79.59
1998	9	*Copaifera langsdorffii*	6	0.34	49.72	2.76	125.22	1.79	81.38
1998	10	*Protium warmingiana*	102	5.76	55.47	2.72	127.94	1.77	83.15
1998	11	*Casearia decandra*	16	0.90	56.38	2.61	130.55	1.70	84.85
1998	12	*Peltophorum dubium*	6	0.34	56.72	2.15	132.70	1.40	86.24
1998	13	*Allophylus edulis*	25	1.41	58.13	2.12	134.82	1.38	87.62

1998	14	*Piptadenia gonoacantha*	63	3.56	61.68	1.64	136.47	1.07	88.69
1998	15	*Luehea grandiflora*	18	1.02	62.70	1.38	137.85	0.90	89.59
1998	16	*Rollinia sylvatica*	63	3.56	66.25	1.33	139.18	0.87	90.45
1998	17	*Casearia arborea*	18	1.02	67.27	1.24	140.42	0.81	91.26
1998	18	*Coutarea hexandra*	65	3.67	70.94	1.10	141.52	0.71	91.97
1998	19	*Ocotea odorifera*	11	0.62	71.56	1.08	142.60	0.70	92.68
1998	20	*Siparuna guianensis*	108	6.09	77.65	1.02	143.62	0.66	93.34
1998	21	*Cordia sellowiana*	3	0.17	77.82	0.82	144.44	0.53	93.87
1998	22	*Endlicheria paniculata*	2	0.11	77.93	0.76	145.19	0.49	94.36
1998	23	*Trichilia pallida*	126	7.11	85.05	0.73	145.92	0.48	94.83
1998	24	*Ceiba speciosa*	10	0.56	85.61	0.65	146.58	0.42	95.26
1998	25	*Clarisia ilicifolia*	5	0.28	85.89	0.52	147.10	0.34	95.60
1998	26	*Zanthoxylum rhoifolium*	5	0.28	86.17	0.52	147.63	0.34	95.94
1998	27	*Astronium fraxinifolium*	4	0.23	86.40	0.47	148.10	0.31	96.25
1998	28	*Brosimum guianense*	17	0.96	87.36	0.46	148.56	0.30	96.55
1998	29	*Seguieria americana*	6	0.34	87.70	0.39	148.95	0.25	96.80
1998	30	*Pterocarpus rohrii*	8	0.45	88.15	0.37	149.32	0.24	97.05
1998	31	*Myrcia sphaerocarpa*	7	0.40	88.54	0.32	149.65	0.21	97.26
1998	32	*Sparattosperma leucanthum*	9	0.51	89.05	0.32	149.97	0.21	97.46
1998	33	*Casearia obliqua*	4	0.23	89.28	0.28	150.24	0.18	97.64
1998	34	*Chrysophyllum marginatum*	2	0.11	89.39	0.26	150.51	0.17	97.81
1998	35	*Cecropia pachystachya*	1	0.06	89.45	0.24	150.75	0.16	97.97
1998	36	*Prunus sellowii*	4	0.23	89.67	0.21	150.96	0.14	98.11
1998	37	*Plinia glomerata*	17	0.96	90.63	0.19	151.15	0.12	98.23
1998	38	*Vitex megapotamica*	3	0.17	90.80	0.18	151.33	0.11	98.35
1998	39	*Chrysophyllum gonocarpum*	14	0.79	91.59	0.17	151.50	0.11	98.46
1998	40	*Eugenia leptoclada*	8	0.45	92.04	0.16	151.67	0.11	98.57
1998	41	*Ixora gardneriana*	4	0.23	92.27	0.16	151.83	0.10	98.67
1998	42	*Ocotea pulchella*	1	0.06	92.33	0.15	151.98	0.10	98.77
1998	43	*Zeyheria tuberculosa*	2	0.11	92.44	0.13	152.10	0.08	98.85
1998	44	*Myrciaria axillaris*	14	0.79	93.23	0.12	152.22	0.08	98.93
1998	45	*Amaioua guianensis*	11	0.62	93.85	0.12	152.34	0.08	99.01
1998	46	*Zollernia ilicifolia*	2	0.11	93.96	0.12	152.46	0.08	99.08
1998	47	*Guettarda scabra*	4	0.23	94.19	0.12	152.58	0.08	99.16
1998	48	*Licania spicata*	4	0.23	94.41	0.10	152.68	0.07	99.23
1998	49	*Cariniana legalis*	3	0.17	94.58	0.10	152.78	0.06	99.29
1998	50	*Eugenia strictopetala*	3	0.17	94.75	0.08	152.86	0.05	99.34
1998	51	*Carpotroche brasiliensis*	7	0.40	95.15	0.08	152.94	0.05	99.40
1998	52	*Sapium glandulatum*	2	0.11	95.26	0.08	153.02	0.05	99.45
1998	53	*Trichilia elegans*	3	0.17	95.43	0.08	153.09	0.05	99.50
1998	54	*Maytenus aquifolium*	1	0.06	95.49	0.06	153.15	0.04	99.53
1998	55	*Matayba elaeagnoides*	2	0.11	95.60	0.06	153.21	0.04	99.57
1998	56	*Attalea dubia*	3	0.17	95.77	0.06	153.27	0.04	99.61
1998	57	*Jacaranda micrantha*	11	0.62	96.39	0.05	153.33	0.04	99.65
1998	58	*Ocotea dispersa*	4	0.23	96.61	0.04	153.37	0.03	99.67
1998	59	*Aspidosperma olivaceum*	2	0.11	96.73	0.04	153.40	0.02	99.70
1998	60	*Platypodium elegans*	1	0.06	96.78	0.04	153.44	0.02	99.72
1998	61	*Cariniana estrellensis*	2	0.11	96.90	0.03	153.47	0.02	99.74
1998	62	*Picramnia regnelli*	2	0.11	97.01	0.03	153.51	0.02	99.76
1998	63	*Maclura tinctoria*	3	0.17	97.18	0.03	153.54	0.02	99.78
1998	64	*Bathysa meridionalis*	3	0.17	97.35	0.03	153.57	0.02	99.80
1998	65	*Acacia polyphylla*	1	0.06	97.40	0.03	153.60	0.02	99.82
1998	66	*Qualea jundiahy*	2	0.11	97.52	0.02	153.62	0.02	99.84
1998	67	*Cordia silvestris*	3	0.17	97.69	0.02	153.64	0.01	99.85
1998	68	*Eriotheca candolleana*	5	0.28	97.97	0.02	153.66	0.01	99.87
1998	69	*Xylopia sericea*	2	0.11	98.08	0.02	153.68	0.01	99.88
1998	70	*Aniba firmula*	1	0.06	98.14	0.02	153.70	0.01	99.89

1998	71	*Persea pyrifolia*	1	0.06	98.19	0.01	153.71	0.01	99.90
1998	72	*Ocotea indecora*	1	0.06	98.25	0.01	153.72	0.01	99.90
1998	73	*Pouteria sp*	2	0.11	98.36	0.01	153.73	0.01	99.91
1998	74	*Mollinedia argyrogyna*	1	0.06	98.42	0.01	153.75	0.01	99.92
1998	75	*Mabea longifolia*	3	0.17	98.59	0.01	153.76	0.01	99.93
1998	76	*Cybistax antisyphilitica*	2	0.11	98.70	0.01	153.77	0.01	99.93
1998	77	*Hortia brasiliana*	1	0.06	98.76	0.01	153.78	0.01	99.94
1998	78	*Lonchocarpus guillemineanus*	1	0.06	98.81	0.01	153.78	0.01	99.94
1998	79	*Swartzia myrtifolia*	1	0.06	98.87	0.01	153.79	0.01	99.95
1998	80	*Erythroxylum pelleterianum*	2	0.11	98.98	0.01	153.80	0.00	99.95
1998	81	*Andira fraxinifolia*	1	0.06	99.04	0.01	153.81	0.00	99.96
1998	82	*Matayba guianensis*	1	0.06	99.10	0.01	153.81	0.00	99.96
1998	83	*Simira sampaioana*	2	0.11	99.21	0.01	153.82	0.00	99.97
1998	84	*Campomanesia xanthocarpa*	1	0.06	99.27	0.01	153.83	0.00	99.97
1998	85	*Mabea fistulifera*	1	0.06	99.32	0.01	153.83	0.00	99.98
1998	86	*Cupania ludowigii*	1	0.06	99.38	0.01	153.84	0.00	99.98
1998	87	*Inga striata*	1	0.06	99.44	0.00	153.84	0.00	99.98
1998	88	*Guapira opposita*	1	0.06	99.49	0.00	153.85	0.00	99.98
1998	89	*Nectandra lanceolata*	2	0.11	99.60	0.00	153.85	0.00	99.99
1998	90	*Myrcia fallax*	1	0.06	99.66	0.00	153.85	0.00	99.99
1998	91	*Platymiscium pubescens*	1	0.06	99.72	0.00	153.86	0.00	99.99
1998	92	*Croton floribundus*	1	0.06	99.77	0.00	153.86	0.00	99.99
1998	93	*Machaerium brasiliense*	1	0.06	99.83	0.00	153.86	0.00	100.00
1998	94	*Ocotea pubescens*	1	0.06	99.89	0.00	153.87	0.00	100.00
1998	95	*Cedrela fissilis*	1	0.06	99.94	0.00	153.87	0.00	100.00
1998	96	*Psychotria carthagenensis*	1	0.06	100.00	0.00	153.87	0.00	100.00
2003	1	*Anadenanthera peregrina*	60	3.39	3.39	78.50	78.50	47.03	47.03
2003	2	*Casearia ulmifolia*	144	8.14	11.53	16.70	95.19	10.00	57.04
2003	3	*Sorocea bonplandii*	583	32.94	44.46	12.71	107.90	7.62	64.65
2003	4	*Anadenanthera colubrina*	5	0.28	44.75	8.26	116.17	4.95	69.60
2003	5	*Apuleia leiocarpa*	69	3.90	48.64	5.27	121.43	3.16	72.76
2003	6	*Myroxylon peruiferum*	2	0.11	48.76	4.16	125.59	2.49	75.25
2003	7	*Machaerium nyctitans*	52	2.94	51.69	3.62	129.21	2.17	77.42
2003	8	*Dalbergia nigra*	13	0.73	52.43	3.45	132.66	2.07	79.48
2003	9	*Copaifera langsdorffii*	8	0.45	52.88	3.21	135.87	1.93	81.41
2003	10	*Protium warmingiana*	100	5.65	58.53	2.85	138.72	1.71	83.12
2003	11	*Allophylus edulis*	25	1.41	59.94	2.57	141.29	1.54	84.66
2003	12	*Casearia decandra*	17	0.96	60.90	2.35	143.64	1.41	86.07
2003	13	*Peltophorum dubium*	6	0.34	61.24	2.22	145.87	1.33	87.40
2003	14	*Luehea grandiflora*	19	1.07	62.32	1.56	147.43	0.94	88.33
2003	15	*Piptadenia gonoacantha*	44	2.49	64.80	1.52	148.95	0.91	89.25
2003	16	*Ocotea odorifera*	10	0.56	65.37	1.34	150.29	0.80	90.05
2003	17	*Rollinia sylvatica*	49	2.77	68.14	1.33	151.63	0.80	90.85
2003	18	*Casearia arborea*	12	0.68	68.81	1.28	152.90	0.76	91.61
2003	19	*Trichilia pallida*	131	7.40	76.21	1.07	153.97	0.64	92.25
2003	20	*Cordia sellowiana*	3	0.17	76.38	1.00	154.97	0.60	92.85
2003	21	*Siparuna guianensis*	92	5.20	81.58	1.00	155.96	0.60	93.45
2003	22	*Coutarea hexandra*	62	3.50	85.08	0.95	156.91	0.57	94.02
2003	23	*Endlicheria paniculata*	2	0.11	85.20	0.90	157.81	0.54	94.56
2003	24	*Ceiba speciosa*	10	0.56	85.76	0.76	158.57	0.46	95.01
2003	25	*Brosimum guianense*	20	1.13	86.89	0.64	159.22	0.38	95.40
2003	26	*Clarisia ilicifolia*	6	0.34	87.23	0.64	159.85	0.38	95.78
2003	27	*Pterocarpus rohrii*	8	0.45	87.68	0.46	160.31	0.28	96.05
2003	28	*Zanthoxylum rhoifolium*	5	0.28	87.97	0.43	160.74	0.26	96.31
2003	29	*Sparattosperma leucanthum*	9	0.51	88.47	0.40	161.14	0.24	96.55
2003	30	*Chrysophyllum gonocarpum*	14	0.79	89.27	0.35	161.49	0.21	96.76
2003	31	*Seguieria americana*	5	0.28	89.55	0.35	161.84	0.21	96.97

2003	32	*Plinia glomerata*	17	0.96	90.51	0.34	162.18	0.20	97.17
2003	33	*Myrcia sphaerocarpa*	7	0.40	90.90	0.31	162.48	0.19	97.36
2003	34	*Astronium fraxinifolium*	5	0.28	91.19	0.30	162.79	0.18	97.54
2003	35	*Chrysophyllum marginatum*	2	0.11	91.30	0.29	163.08	0.17	97.71
2003	36	*Casearia obliqua*	3	0.17	91.47	0.26	163.34	0.16	97.87
2003	37	*Cecropia pachystachya*	1	0.06	91.53	0.26	163.60	0.16	98.03
2003	38	*Eugenia leptoclada*	10	0.56	92.09	0.24	163.84	0.14	98.17
2003	39	*Prunus sellowii*	2	0.11	92.20	0.23	164.07	0.14	98.31
2003	40	*Ocotea pulchella*	1	0.06	92.26	0.19	164.27	0.12	98.42
2003	41	*Vitex megapotamica*	3	0.17	92.43	0.19	164.45	0.11	98.53
2003	42	*Myrciaria axillaris*	14	0.79	93.22	0.17	164.62	0.10	98.63
2003	43	*Zeyheria tuberculosa*	2	0.11	93.33	0.15	164.77	0.09	98.73
2003	44	*Zollernia ilicifolia*	2	0.11	93.45	0.15	164.92	0.09	98.81
2003	45	*Amaioua guianensis*	11	0.62	94.07	0.14	165.06	0.09	98.90
2003	46	*Cariniana legalis*	3	0.17	94.24	0.14	165.20	0.08	98.98
2003	47	*Licania spicata*	4	0.23	94.46	0.13	165.34	0.08	99.06
2003	48	*Carpotroche brasiliensis*	7	0.40	94.86	0.11	165.44	0.06	99.13
2003	49	*Ixora gardneriana*	3	0.17	95.03	0.11	165.55	0.06	99.19
2003	50	*Trichilia elegans*	3	0.17	95.20	0.11	165.66	0.06	99.26
2003	51	*Eugenia strictopetala*	4	0.23	95.42	0.10	165.76	0.06	99.32
2003	52	*Maytenus aquifolium*	1	0.06	95.48	0.10	165.86	0.06	99.38
2003	53	*Guettarda scabra*	3	0.17	95.65	0.09	165.95	0.06	99.43
2003	54	*Sapium glandulatum*	2	0.11	95.76	0.09	166.04	0.05	99.48
2003	55	*Attalea dubia*	2	0.11	95.88	0.08	166.12	0.05	99.53
2003	56	*Ocotea dispersa*	5	0.28	96.16	0.07	166.19	0.04	99.57
2003	57	*Matayba elaeagnoides*	3	0.17	96.33	0.07	166.26	0.04	99.61
2003	58	*Aspidosperma olivaceum*	2	0.11	96.44	0.05	166.31	0.03	99.65
2003	59	*Cariniana estrellensis*	2	0.11	96.55	0.05	166.36	0.03	99.68
2003	60	*Platypodium elegans*	1	0.06	96.61	0.04	166.40	0.02	99.70
2003	61	*Jacaranda micrantha*	11	0.62	97.23	0.04	166.44	0.02	99.73
2003	62	*Bathysa meridionalis*	3	0.17	97.40	0.04	166.48	0.02	99.75
2003	63	*Qualea jundiahy*	2	0.11	97.51	0.04	166.52	0.02	99.77
2003	64	*Nectandra lanceolata*	1	0.06	97.57	0.04	166.55	0.02	99.79
2003	65	*Cordia silvestris*	3	0.17	97.74	0.03	166.59	0.02	99.81
2003	66	*Mabea longifolia*	3	0.17	97.91	0.02	166.61	0.01	99.83
2003	67	*Eriotheca candolleana*	4	0.23	98.14	0.02	166.63	0.01	99.84
2003	68	*Xylopia sericea*	2	0.11	98.25	0.02	166.66	0.01	99.85
2003	69	*Picramnia regnelli*	2	0.11	98.36	0.02	166.68	0.01	99.87
2003	70	*Aniba firmula*	1	0.06	98.42	0.02	166.70	0.01	99.88
2003	71	*Cybistax antisyphilitica*	3	0.17	98.59	0.02	166.71	0.01	99.89
2003	72	*Ocotea indecora*	1	0.06	98.64	0.02	166.73	0.01	99.90
2003	73	*Swartzia myrtifolia*	2	0.11	98.76	0.02	166.74	0.01	99.91
2003	74	*Simira sampaioana*	3	0.17	98.93	0.01	166.76	0.01	99.92
2003	75	*Maclura tinctoria*	1	0.06	98.98	0.01	166.77	0.01	99.92
2003	76	*Persea pyrifolia*	1	0.06	99.04	0.01	166.78	0.01	99.93
2003	77	*Campomanesia xanthocarpa*	1	0.06	99.10	0.01	166.80	0.01	99.94
2003	78	*Mollinedia argyrogyna*	1	0.06	99.15	0.01	166.81	0.01	99.94
2003	79	*Lonchocarpus guillemineanus*	1	0.06	99.21	0.01	166.82	0.01	99.95
2003	80	*Matayba guianensis*	1	0.06	99.27	0.01	166.83	0.01	99.96
2003	81	*Erythroxylum pelleterianum*	2	0.11	99.38	0.01	166.84	0.01	99.96
2003	82	*Andira fraxinifolia*	1	0.06	99.44	0.01	166.85	0.01	99.97
2003	83	*Cupania ludowigii*	2	0.11	99.55	0.01	166.86	0.00	99.97
2003	84	*Platymiscium pubescens*	1	0.06	99.60	0.01	166.86	0.00	99.98
2003	85	*Myrcia fallax*	1	0.06	99.66	0.01	166.87	0.00	99.98
2003	86	*Acacia polyphylla*	1	0.06	99.72	0.01	166.88	0.00	99.99
2003	87	*Syagrus romanzoffiana*	1	0.06	99.77	0.01	166.88	0.00	99.99
2003	88	*Inga striata*	1	0.06	99.83	0.01	166.89	0.00	99.99

2003	89	*Guapira opposita*	1	0.06	99.89	0.00	166.89	0.00	100.00
2003	90	*Machaerium brasiliense*	1	0.06	99.94	0.00	166.90	0.00	100.00
2003	91	*Psychotria carthagenensis*	1	0.06	100.00	0.00	166.90	0.00	100.00
2011	1	*Anadenanthera peregrina*	51	3.29	3.29	83.10	83.10	51.02	51.02
2011	2	*Sorocea bonplandii*	608	39.23	42.52	15.89	98.99	9.76	60.78
2011	3	*Casearia ulmifolia*	104	6.71	49.23	12.27	111.27	7.54	68.32
2011	4	*Anadenanthera colubrina*	7	0.45	49.68	8.41	119.68	5.16	73.48
2011	6	*Apuleia leiocarpa*	58	3.74	53.42	5.10	124.78	3.13	76.61
2011	7	*Myroxylon peruiferum*	2	0.13	53.55	4.66	129.44	2.86	79.48
2011	8	*Copaifera langsdorffii*	7	0.45	54.00	3.78	133.22	2.32	81.80
2011	9	*Machaerium nyctitans*	48	3.10	57.10	3.42	136.64	2.10	83.90
2011	10	*Allophylus edulis*	22	1.42	58.52	2.96	139.60	1.82	85.72
2011	11	*Protium warmingiana*	99	6.39	64.90	2.50	142.11	1.54	87.26
2011	12	*Dalbergia nigra*	11	0.71	65.61	1.47	143.58	0.90	88.16
2011	13	*Luehea grandiflora*	14	0.90	66.52	1.42	145.00	0.87	89.03
2011	14	*Ocotea odorifera*	9	0.58	67.10	1.26	146.26	0.77	89.81
2011	15	*Casearia decandra*	13	0.84	67.94	1.18	147.44	0.72	90.53
2011	16	*Cordia sellowiana*	3	0.19	68.13	1.08	148.52	0.66	91.19
2011	17	*Rollinia sylvatica*	44	2.84	70.97	1.06	149.57	0.65	91.84
2011	18	*Casearia arborea*	9	0.58	71.55	1.06	150.63	0.65	92.49
2011	19	*Coutarea hexandra*	44	2.84	74.39	0.87	151.50	0.53	93.02
2011	20	*Ceiba speciosa*	9	0.58	74.97	0.85	152.35	0.52	93.54
2011	21	*Piptadenia gonoacantha*	21	1.35	76.32	0.76	153.11	0.47	94.01
2011	22	*Endlicheria paniculata*	2	0.13	76.45	0.75	153.86	0.46	94.47
2011	23	*Clarisia ilicifolia*	7	0.45	76.90	0.65	154.51	0.40	94.87
2011	24	*Trichilia pallida*	92	5.94	82.84	0.55	155.06	0.34	95.21
2011	25	*Pterocarpus rohrii*	5	0.32	83.16	0.54	155.60	0.33	95.54
2011	26	*Sparattosperma leucanthum*	7	0.45	83.61	0.53	156.13	0.33	95.87
2011	27	*Brosimum guianense*	18	1.16	84.77	0.52	156.65	0.32	96.19
2011	28	*Peltophorum dubium*	3	0.19	84.97	0.51	157.16	0.32	96.50
2011	29	*Siparuna guianensis*	54	3.48	88.45	0.47	157.64	0.29	96.79
2011	30	*Astronium fraxinifolium*	5	0.32	88.77	0.38	158.02	0.23	97.02
2011	31	*Plinia glomerata*	21	1.35	90.13	0.36	158.38	0.22	97.25
2011	32	*Chrysophyllum gonocarpum*	12	0.77	90.90	0.33	158.71	0.20	97.45
2011	33	*Chrysophyllum marginatum*	2	0.13	91.03	0.29	159.00	0.18	97.63
2011	34	*Ocotea pulchella*	1	0.06	91.10	0.26	159.25	0.16	97.78
2011	35	*Eugenia leptoclada*	9	0.58	91.68	0.26	159.51	0.16	97.94
2011	36	*Seguieria americana*	5	0.32	92.00	0.25	159.76	0.15	98.09
2011	37	*Prunus sellowii*	1	0.06	92.06	0.24	160.00	0.15	98.24
2011	38	*Zanthoxylum rhoifolium*	4	0.26	92.32	0.23	160.23	0.14	98.38
2011	39	*Cariniana legalis*	3	0.19	92.52	0.22	160.45	0.14	98.52
2011	40	*Casearia obliqua*	1	0.06	92.58	0.19	160.64	0.11	98.63
2011	41	*Myrciaria axillaris*	14	0.90	93.48	0.19	160.82	0.11	98.75
2011	42	*Zeyheria tuberculosa*	1	0.06	93.55	0.16	160.99	0.10	98.85
2011	43	*Licania spicata*	4	0.26	93.81	0.14	161.12	0.09	98.93
2011	44	*Amaioua guianensis*	11	0.71	94.52	0.12	161.25	0.08	99.01
2011	45	*Trichilia elegans*	4	0.26	94.77	0.12	161.37	0.07	99.08
2011	46	*Carpotroche brasiliensis*	6	0.39	95.16	0.12	161.49	0.07	99.16
2011	47	*Eugenia strictopetala*	4	0.26	95.42	0.11	161.60	0.07	99.22
2011	48	*Ixora gardneriana*	1	0.06	95.48	0.11	161.71	0.07	99.29
2011	49	*Guettarda scabra*	3	0.19	95.68	0.10	161.81	0.06	99.35
2011	50	*Maytenus aquifolium*	1	0.06	95.74	0.10	161.91	0.06	99.41
2011	51	*Ocotea dispersa*	4	0.26	96.00	0.09	162.00	0.05	99.47
2011	52	*Zollernia ilicifolia*	3	0.19	96.19	0.08	162.08	0.05	99.52
2011	53	*Aspidosperma olivaceum*	2	0.13	96.32	0.08	162.16	0.05	99.57
2011	54	*Vitex megapotamica*	3	0.19	96.52	0.08	162.24	0.05	99.62
2011	55	*Attalea dubia*	1	0.06	96.58	0.06	162.30	0.04	99.66

2011	56	*Matayba elaeagnoides*	2	0.13	96.71	0.06	162.37	0.04	99.70
2011	57	*Cariniana estrellensis*	2	0.13	96.84	0.05	162.42	0.03	99.73
2011	58	*Qualea jundiahy*	2	0.13	96.97	0.05	162.48	0.03	99.76
2011	59	*Cordia silvestris*	3	0.19	97.16	0.04	162.52	0.03	99.79
2011	60	*Jacaranda micrantha*	8	0.52	97.68	0.03	162.55	0.02	99.81
2011	61	*Aniba firmula*	1	0.06	97.74	0.03	162.58	0.02	99.83
2011	62	*Picramnia regnelli*	2	0.13	97.87	0.03	162.61	0.02	99.84
2011	63	*Ocotea indecora*	1	0.06	97.94	0.03	162.63	0.02	99.86
2011	64	*Myrcia sphaerocarpa*	3	0.19	98.13	0.02	162.66	0.01	99.87
2011	65	*Eriotheca candolleana*	4	0.26	98.39	0.02	162.68	0.01	99.89
2011	66	*Xylopia sericea*	1	0.06	98.45	0.02	162.70	0.01	99.90
2011	67	*Simira sampaioana*	3	0.19	98.65	0.02	162.71	0.01	99.91
2011	68	*Mabea longifolia*	1	0.06	98.71	0.02	162.73	0.01	99.92
2011	69	*Swartzia myrtifolia*	2	0.13	98.84	0.02	162.75	0.01	99.93
2011	70	*Campomanesia xanthocarpa*	1	0.06	98.90	0.02	162.76	0.01	99.94
2011	71	*Cybistax antisyphilitica*	2	0.13	99.03	0.01	162.77	0.01	99.94
2011	72	*Platymiscium pubescens*	1	0.06	99.10	0.01	162.79	0.01	99.95
2011	73	*Mollinedia argyrogyna*	1	0.06	99.16	0.01	162.80	0.01	99.96
2011	74	*Andira fraxinifolia*	1	0.06	99.23	0.01	162.81	0.01	99.97
2011	75	*Cupania ludowigii*	2	0.13	99.35	0.01	162.82	0.01	99.97
2011	76	*Nectandra lanceolata*	1	0.06	99.42	0.01	162.82	0.00	99.98
2011	77	*Syagrus romanzoffiana*	1	0.06	99.48	0.01	162.83	0.00	99.98
2011	78	*Myrcia fallax*	1	0.06	99.55	0.01	162.84	0.00	99.98
2011	79	*Erythroxylum pelleterianum*	1	0.06	99.61	0.00	162.84	0.00	99.99
2011	80	*Eugenia sp.*	1	0.06	99.68	0.00	162.85	0.00	99.99
2011	81	*Machaerium brasiliense*	1	0.06	99.74	0.00	162.85	0.00	99.99
2011	82	*Bathysa meridionalis*	1	0.06	99.81	0.00	162.85	0.00	99.99
2011	83	*Inga striata*	1	0.06	99.87	0.00	162.86	0.00	100.00
2011	84	*Randia spinosa*	1	0.06	99.94	0.00	162.86	0.00	100.00
2011	85	*Psychotria carthagenensis*	1	0.06	100.00	0.00	162.86	0.00	100.00
2017	1	*Anadenanthera peregrina*	50	3.10	3.10	84.01	84.01	49.36	49.36
2017	2	*Sorocea bonplandii*	683	42.37	45.47	18.06	102.07	10.61	59.97
2017	3	*Casearia ulmifolia*	94	5.83	51.30	12.22	114.29	7.18	67.15
2017	4	*Anadenanthera colubrina*	6	0.37	51.67	8.95	123.24	5.26	72.41
2017	5	*Apuleia leiocarpa*	55	3.41	55.09	5.25	128.49	3.09	75.49
2017	6	*Myroxylon peruiferum*	2	0.12	55.21	4.90	133.39	2.88	78.37
2017	7	*Copaifera langsdorffii*	7	0.43	55.65	4.05	137.44	2.38	80.75
2017	8	*Machaerium nyctitans*	50	3.10	58.75	3.63	141.08	2.13	82.89
2017	9	*Protium warmingiana*	100	6.20	64.95	3.40	144.48	2.00	84.89
2017	10	*Allophylus edulis*	21	1.30	66.25	3.25	147.72	1.91	86.79
2017	11	*Plinia glomerata*	34	2.11	68.36	2.01	149.74	1.18	87.98
2017	12	*Luehea grandiflora*	17	1.05	69.42	1.68	151.42	0.99	88.96
2017	13	*Ocotea odorifera*	14	0.87	70.29	1.63	153.05	0.96	89.92
2017	14	*Dalbergia nigra*	11	0.68	70.97	1.41	154.45	0.83	90.75
2017	15	*Casearia decandra*	12	0.74	71.71	1.22	155.67	0.71	91.46
2017	16	*Cordia sellowiana*	3	0.19	71.90	1.14	156.81	0.67	92.13
2017	17	*Ceiba speciosa*	9	0.56	72.46	1.00	157.80	0.59	92.71
2017	18	*Pterocarpus rohrii*	4	0.25	72.70	0.78	158.59	0.46	93.17
2017	19	*Brosimum guianense*	19	1.18	73.88	0.77	159.36	0.45	93.63
2017	20	*Rollinia sylvatica*	37	2.30	76.18	0.77	160.12	0.45	94.08
2017	21	*Siparuna guianensis*	59	3.66	79.84	0.75	160.88	0.44	94.52
2017	22	*Endlicheria paniculata*	2	0.12	79.96	0.75	161.63	0.44	94.96
2017	23	*Casearia arborea*	10	0.62	80.58	0.64	162.27	0.38	95.34
2017	24	*Coutarea hexandra*	33	2.05	82.63	0.61	162.87	0.36	95.69
2017	25	*Clarisia ilicifolia*	6	0.37	83.00	0.56	163.44	0.33	96.02
2017	26	*Trichilia pallida*	91	5.65	88.65	0.55	163.98	0.32	96.35
2017	27	*Sparattosperma leucanthum*	7	0.43	89.08	0.51	164.49	0.30	96.65

2017	28	*Seguieria americana*	5	0.31	89.39	0.48	164.97	0.28	96.93
2017	29	*Astronium fraxinifolium*	5	0.31	89.70	0.42	165.39	0.25	97.17
2017	30	*Chrysophyllum marginatum*	2	0.12	89.83	0.34	165.73	0.20	97.38
2017	31	*Piptadenia gonoacantha*	14	0.87	90.69	0.33	166.07	0.20	97.57
2017	32	*Myrciaria axillaris*	14	0.87	91.56	0.32	166.39	0.19	97.76
2017	33	*Ocotea pulchella*	1	0.06	91.63	0.28	166.67	0.16	97.92
2017	34	*Eugenia leptoclada*	9	0.56	92.18	0.27	166.93	0.16	98.08
2017	35	*Cariniana legalis*	3	0.19	92.37	0.26	167.20	0.15	98.23
2017	36	*Chrysophyllum gonocarpum*	14	0.87	93.24	0.25	167.45	0.15	98.38
2017	37	*Peltophorum dubium*	2	0.12	93.36	0.24	167.68	0.14	98.52
2017	38	*Casearia obliqua*	1	0.06	93.42	0.21	167.89	0.12	98.64
2017	39	*Amaioua guianensis*	14	0.87	94.29	0.21	168.10	0.12	98.76
2017	40	*Zeyheria tuberculosa*	2	0.12	94.42	0.18	168.28	0.11	98.87
2017	41	*Vitex megapotamica*	2	0.12	94.54	0.16	168.44	0.09	98.97
2017	42	*Prunus sellowii*	2	0.12	94.67	0.15	168.59	0.09	99.05
2017	43	*Licania spicata*	4	0.25	94.91	0.14	168.73	0.08	99.14
2017	44	*Zanthoxylum rhoifolium*	3	0.19	95.10	0.13	168.87	0.08	99.22
2017	45	*Aspidosperma olivaceum*	2	0.12	95.22	0.13	169.00	0.08	99.29
2017	46	*Eugenia strictopetala*	4	0.25	95.47	0.12	169.12	0.07	99.36
2017	47	*Trichilia elegans*	3	0.19	95.66	0.12	169.24	0.07	99.43
2017	48	*Ocotea dispersa*	6	0.37	96.03	0.12	169.36	0.07	99.50
2017	49	*Carpotroche brasiliensis*	5	0.31	96.34	0.11	169.47	0.07	99.57
2017	50	*Maytenus aquifolium*	1	0.06	96.40	0.10	169.57	0.06	99.63
2017	51	*Zollernia ilicifolia*	2	0.12	96.53	0.08	169.65	0.05	99.68
2017	52	*Qualea jundiahy*	2	0.12	96.65	0.07	169.72	0.04	99.72
2017	53	*Matayba elaeagnoides*	2	0.12	96.77	0.06	169.78	0.04	99.75
2017	54	*Cordia silvestris*	3	0.19	96.96	0.04	169.82	0.02	99.77
2017	55	*Guettarda scabra*	2	0.12	97.08	0.04	169.85	0.02	99.80
2017	56	*Cariniana estrellensis*	1	0.06	97.15	0.03	169.89	0.02	99.82
2017	57	*Aniba firmula*	1	0.06	97.21	0.03	169.92	0.02	99.83
2017	58	*Inga striata*	1	0.06	97.27	0.03	169.95	0.02	99.85
2017	59	*Jacaranda micrantha*	7	0.43	97.70	0.03	169.98	0.02	99.87
2017	60	*Eriotheca candolleana*	5	0.31	98.01	0.03	170.00	0.02	99.88
2017	61	*Simira sampaioana*	3	0.19	98.20	0.02	170.03	0.01	99.90
2017	62	*Myrcia sphaerocarpa*	2	0.12	98.33	0.02	170.04	0.01	99.91
2017	63	*Campomanesia xanthocarpa*	1	0.06	98.39	0.01	170.06	0.01	99.92
2017	64	*Platymiscium pubescens*	1	0.06	98.45	0.01	170.07	0.01	99.92
2017	65	*Matayba guianensis*	1	0.06	98.51	0.01	170.08	0.01	99.93
2017	66	*Nectandra lanceolata*	1	0.06	98.57	0.01	170.09	0.01	99.94
2017	67	*Cybistax antisyphilitica*	2	0.12	98.70	0.01	170.11	0.01	99.94
2017	68	*Swartzia myrtifolia*	2	0.12	98.82	0.01	170.12	0.01	99.95
2017	69	*Picramnia regnelli*	3	0.19	99.01	0.01	170.13	0.01	99.96
2017	70	*Pouteria sp*	1	0.06	99.07	0.01	170.14	0.01	99.96
2017	71	*Trichilia lepidota*	3	0.19	99.26	0.01	170.15	0.01	99.97
2017	72	*Mollinedia argyrogyna*	1	0.06	99.32	0.01	170.15	0.01	99.97
2017	73	*Syagrus romanzoffiana*	1	0.06	99.38	0.01	170.16	0.01	99.98
2017	74	*Andira fraxinifolia*	1	0.06	99.44	0.01	170.17	0.00	99.98
2017	75	*Cupania ludowigii*	1	0.06	99.50	0.01	170.18	0.00	99.99
2017	76	*Eugenia sp.*	1	0.06	99.57	0.00	170.18	0.00	99.99
2017	77	*Cedrela fissilis*	2	0.12	99.69	0.00	170.19	0.00	99.99
2017	78	*Myr_cau*	1	0.06	99.75	0.00	170.19	0.00	99.99
2017	79	*May_ili*	1	0.06	99.81	0.00	170.19	0.00	100.00
2017	80	*Machaerium brasiliense*	1	0.06	99.88	0.00	170.20	0.00	100.00
2017	81	*Psychotria carthagenensis*	1	0.06	99.94	0.00	170.20	0.00	100.00
2017	82	*Guarea kunthiana*	1	0.06	100.00	0.00	170.20	0.00	100.00
Northeastern	**NºSp.**	***Species***	**Ab**	**%Ab**	**%Ab.Ac.**	**AGC**	**AGC.Ac.**	**%AGC**	**% AGC.Ac.**
1993	1	*Anadenanthera peregrina*	58	5.48	5.48	15.54	15.54	21.60	21.60

1993	2	*Piptadenia gonoacantha*	68	6.43	11.91	11.32	26.86	15.73	37.33
1993	3	*Machaerium stipitatum*	42	3.97	15.88	7.08	33.95	9.85	47.18
1993	4	*Cedrela fissilis*	12	1.13	17.01	3.29	37.23	4.57	51.75
1993	5	*Prunus sellowii*	94	8.88	25.90	3.15	40.38	4.37	56.12
1993	6	*Allophylus edulis*	36	3.40	29.30	2.48	42.86	3.45	59.57
1993	7	*Trichilia lepidota*	77	7.28	36.58	2.22	45.08	3.09	62.66
1993	8	*Luehea grandiflora*	39	3.69	40.26	2.06	47.14	2.86	65.52
1993	9	*Nectandra lanceolata*	29	2.74	43.01	1.88	49.02	2.61	68.13
1993	10	*Ficus enormis*	1	0.09	43.10	1.79	50.80	2.48	70.61
1993	11	*Dalbergia nigra*	34	3.21	46.31	1.55	52.35	2.15	72.76
1993	12	*Maytenus aquifolium*	1	0.09	46.41	1.37	53.72	1.90	74.67
1993	13	*Cariniana legalis*	2	0.19	46.60	1.23	54.95	1.71	76.38
1993	14	*Cariniana estrellensis*	5	0.47	47.07	1.09	56.04	1.51	77.89
1993	15	*Bauhinia forficata*	10	0.95	48.02	0.93	56.97	1.29	79.18
1993	16	*Casearia sylvestris*	2	0.19	48.20	0.83	57.81	1.16	80.34
1993	17	*Xylosma prockia*	36	3.40	51.61	0.81	58.62	1.13	81.47
1993	18	*Guettarda viburnoides*	6	0.57	52.17	0.80	59.42	1.11	82.58
1993	19	*Seguieria americana*	1	0.09	52.27	0.78	60.20	1.09	83.67
1993	20	*Platypodium elegans*	3	0.28	52.55	0.73	60.93	1.01	84.68
1993	21	*Tabernaemontana laeta*	1	0.09	52.65	0.71	61.64	0.98	85.66
1993	22	*Chrysophyllum flexuosum*	45	4.25	56.90	0.71	62.34	0.98	86.65
1993	23	*Endlicheria paniculata*	15	1.42	58.32	0.60	62.95	0.84	87.48
1993	24	*Trichilia pallida*	62	5.86	64.18	0.58	63.52	0.80	88.29
1993	25	*Peltophorum dubium*	5	0.47	64.65	0.53	64.05	0.74	89.02
1993	26	*Apuleia leiocarpa*	8	0.76	65.41	0.46	64.51	0.64	89.66
1993	27	*Campomanesia xanthocarpa*	3	0.28	65.69	0.45	64.97	0.63	90.29
1993	28	*Persea pyrifolia*	3	0.28	65.97	0.43	65.39	0.59	90.88
1993	29	*Maclura tinctoria*	4	0.38	66.35	0.39	65.78	0.54	91.43
1993	30	*Aniba firmula*	6	0.57	66.92	0.38	66.16	0.52	91.95
1993	31	*Cabralea canjerana*	22	2.08	69.00	0.37	66.53	0.51	92.46
1993	32	*Guapira opposita*	35	3.31	72.31	0.36	66.89	0.51	92.97
1993	33	*Cassia ferruginea*	3	0.28	72.59	0.31	67.21	0.44	93.40
1993	34	*Protium warmingiana*	24	2.27	74.86	0.29	67.50	0.41	93.81
1993	35	*Rollinia laurifolia*	4	0.38	75.24	0.28	67.78	0.40	94.20
1993	36	*Ocotea dispersa*	29	2.74	77.98	0.28	68.06	0.38	94.59
1993	37	*Ceiba speciosa*	2	0.19	78.17	0.24	68.30	0.33	94.92
1993	38	*Syagrus romanzoffiana*	8	0.76	78.92	0.23	68.53	0.33	95.25
1993	39	*Zanthoxylum riedelianum*	3	0.28	79.21	0.23	68.76	0.31	95.56
1993	40	*Nectandra rigida*	5	0.47	79.68	0.21	68.96	0.29	95.85
1993	41	*Rollinia sylvatica*	8	0.76	80.43	0.20	69.16	0.28	96.13
1993	42	*Casearia decandra*	15	1.42	81.85	0.19	69.35	0.26	96.38
1993	43	*Coutarea hexandra*	12	1.13	82.99	0.18	69.53	0.25	96.64
1993	44	*Attalea dubia*	3	0.28	83.27	0.15	69.68	0.21	96.85
1993	45	*Siparuna guianensis*	16	1.51	84.78	0.14	69.82	0.19	97.04
1993	46	*Citronella megaphylla*	22	2.08	86.86	0.12	69.94	0.17	97.21
1993	47	*Alchornea glandulosa*	4	0.38	87.24	0.11	70.06	0.15	97.37
1993	48	*Machaerium floridum*	2	0.19	87.43	0.11	70.17	0.15	97.52
1993	49	*Piptadenia paniculata*	2	0.19	87.62	0.09	70.25	0.12	97.64
1993	50	*Cryptocarya moschata*	2	0.19	87.81	0.08	70.34	0.12	97.76
1993	51	*Myrcia fallax*	4	0.38	88.19	0.08	70.42	0.11	97.87
1993	52	*Cryptocarya sp.*	1	0.09	88.28	0.08	70.50	0.11	97.98
1993	53	*Plinia glomerata*	5	0.47	88.75	0.08	70.57	0.11	98.08
1993	54	*Croton floribundus*	2	0.19	88.94	0.06	70.63	0.09	98.17
1993	55	*Platymiscium pubescens*	1	0.09	89.04	0.06	70.70	0.08	98.25
1993	56	*Citronella paniculata*	6	0.57	89.60	0.06	70.75	0.08	98.34
1993	57	*Eugenia sp.1*	1	0.09	89.70	0.05	70.81	0.08	98.41
1993	58	*Sapium glandulatum*	5	0.47	90.17	0.05	70.86	0.07	98.49

1993	59	*Symplocos pubescens*	1	0.09	90.26	0.05	70.92	0.07	98.56
1993	60	*Newtonia contorta*	3	0.28	90.55	0.05	70.97	0.07	98.63
1993	61	*Mabea fistulifera*	7	0.66	91.21	0.05	71.02	0.07	98.70
1993	62	*Cecropia sp.*	2	0.19	91.40	0.05	71.07	0.07	98.77
1993	63	*Amaioua guianensis*	6	0.57	91.97	0.05	71.11	0.07	98.84
1993	64	*Pithecellobium langsdorffii*	4	0.38	92.34	0.05	71.16	0.07	98.90
1993	65	*Casearia gossypiosperma*	1	0.09	92.44	0.05	71.21	0.06	98.97
1993	66	*Himatanthus phagedaenicus*	2	0.19	92.63	0.04	71.25	0.06	99.02
1993	67	*Zanthoxylum rhoifolium*	3	0.28	92.91	0.04	71.29	0.06	99.08
1993	68	*Guarea macrophylla*	3	0.28	93.19	0.04	71.33	0.05	99.13
1993	69	*Persea sp.*	1	0.09	93.29	0.04	71.36	0.05	99.19
1993	70	*Sorocea bonplandii*	8	0.76	94.05	0.04	71.40	0.05	99.24
1993	71	*Erythroxylum pelleterianum*	5	0.47	94.52	0.03	71.43	0.05	99.28
1993	72	*Allophylus sericeus*	1	0.09	94.61	0.03	71.46	0.04	99.32
1993	73	*Cordia bullata*	2	0.19	94.80	0.03	71.49	0.04	99.36
1993	74	*Casearia ulmifolia*	2	0.19	94.99	0.03	71.52	0.04	99.40
1993	75	*Annona cacans*	1	0.09	95.09	0.03	71.55	0.04	99.44
1993	76	*Vernonia diffusa*	2	0.19	95.27	0.03	71.58	0.04	99.48
1993	77	*Guarea kunthiana*	3	0.28	95.56	0.03	71.60	0.04	99.51
1993	78	*Trichilia elegans*	2	0.19	95.75	0.03	71.63	0.03	99.55
1993	79	*Rheedia gardneriana*	2	0.19	95.94	0.02	71.65	0.03	99.58
1993	80	*Albizia polycephala*	1	0.09	96.03	0.02	71.68	0.03	99.62
1993	81	*Randia spinosa*	1	0.09	96.12	0.02	71.69	0.03	99.64
1993	82	*Marlierea teuscheriana*	3	0.28	96.41	0.02	71.71	0.03	99.67
1993	83	*Jacaranda macrantha*	4	0.38	96.79	0.02	71.73	0.03	99.69
1993	84	*Guapira hirsuta*	3	0.28	97.07	0.02	71.75	0.02	99.72
1993	85	*Nectandra mollis*	1	0.09	97.16	0.02	71.77	0.02	99.74
1993	86	*Matayba elaeagnoides*	1	0.09	97.26	0.02	71.78	0.02	99.76
1993	87	*Allophylus semidentatus*	1	0.09	97.35	0.02	71.80	0.02	99.79
1993	88	*Inga affinis*	1	0.09	97.45	0.02	71.81	0.02	99.81
1993	89	*Mabea brasiliensis*	1	0.09	97.54	0.01	71.82	0.02	99.82
1993	90	*Eugenia sp.*	1	0.09	97.64	0.01	71.84	0.02	99.84
1993	91	*Eugenia leptoclada*	2	0.19	97.83	0.01	71.85	0.01	99.86
1993	92	*Rollinia sericea*	3	0.28	98.11	0.01	71.86	0.01	99.87
1993	93	*Pseudobombax grandiflorum*	2	0.19	98.30	0.01	71.87	0.01	99.88
1993	94	*Guatteria villosissima*	1	0.09	98.39	0.01	71.88	0.01	99.90
1993	95	*Carpotroche brasiliensis*	1	0.09	98.49	0.01	71.88	0.01	99.91
1993	96	*Swartzia myrtifolia*	1	0.09	98.58	0.01	71.89	0.01	99.92
1993	97	*Machaerium nyctitans*	1	0.09	98.68	0.01	71.90	0.01	99.93
1993	98	*Miconia cinnamomifolia*	1	0.09	98.77	0.01	71.90	0.01	99.93
1993	99	*Dictyoloma incanescens*	1	0.09	98.87	0.01	71.91	0.01	99.94
1993	100	*Lacistema pubescens*	1	0.09	98.96	0.01	71.91	0.01	99.95
1993	101	*Celtis iguanaea*	1	0.09	99.05	0.00	71.92	0.01	99.96
1993	102	*Tapirira guianensis*	1	0.09	99.15	0.00	71.92	0.01	99.96
1993	103	*Casearia arborea*	1	0.09	99.24	0.00	71.93	0.01	99.97
1993	104	*Miconia hymenonervia*	1	0.09	99.34	0.00	71.93	0.01	99.97
1993	105	*Machaerium brasiliense*	1	0.09	99.43	0.00	71.94	0.01	99.98
1993	106	*Guatteria australis*	1	0.09	99.53	0.00	71.94	0.00	99.98
1993	107	*Eugenia strictopetala*	1	0.09	99.62	0.00	71.94	0.00	99.99
1993	108	*Myrciaria axillaris*	1	0.09	99.72	0.00	71.94	0.00	99.99
1993	109	*Inga marginata*	1	0.09	99.81	0.00	71.95	0.00	99.99
1993	110	*Guatteria nigrescens*	1	0.09	99.91	0.00	71.95	0.00	100.00
1993	111	*Brunfelsia uniflora*	1	0.09	100.00	0.00	71.95	0.00	100.00
2004	1	*Anadenanthera peregrina*	65	4.80	4.80	18.05	18.05	18.17	18.17
2004	2	*Piptadenia gonoacantha*	79	5.83	10.64	16.44	34.48	16.55	34.73
2004	3	*Machaerium stipitatum*	53	3.91	14.55	10.34	44.82	10.41	45.14
2004	4	*Allophylus edulis*	44	3.25	17.80	4.71	49.53	4.74	49.88

2004	5	*Trichilia lepidota*	101	7.46	25.26	3.77	53.29	3.79	53.68
2004	6	*Prunus sellowii*	113	8.35	33.60	3.58	56.87	3.60	57.28
2004	7	*Cedrela fissilis*	14	1.03	34.64	3.54	60.41	3.56	60.84
2004	8	*Maytenus aquifolium*	1	0.07	34.71	2.90	63.31	2.92	63.76
2004	9	*Luehea grandiflora*	40	2.95	37.67	2.73	66.04	2.75	66.51
2004	10	*Nectandra lanceolata*	36	2.66	40.32	2.59	68.63	2.61	69.12
2004	11	*Ficus enormis*	1	0.07	40.40	2.36	70.99	2.38	71.50
2004	12	*Dalbergia nigra*	46	3.40	43.80	1.93	72.92	1.95	73.45
2004	13	*Cariniana legalis*	2	0.15	43.94	1.72	74.64	1.73	75.18
2004	14	*Apuleia leiocarpa*	10	0.74	44.68	1.44	76.08	1.45	76.62
2004	15	*Cariniana estrellensis*	5	0.37	45.05	1.42	77.50	1.43	78.05
2004	16	*Xylosma prockia*	45	3.32	48.38	1.20	78.69	1.21	79.26
2004	17	*Casearia sylvestris*	3	0.22	48.60	1.14	79.84	1.15	80.41
2004	18	*Trichilia pallida*	82	6.06	54.65	0.99	80.82	1.00	81.40
2004	19	*Tabernaemontana laeta*	2	0.15	54.80	0.98	81.81	0.99	82.39
2004	20	*Chrysophyllum flexuosum*	58	4.28	59.08	0.97	82.77	0.97	83.37
2004	21	*Bauhinia forficata*	9	0.66	59.75	0.90	83.68	0.91	84.28
2004	22	*Guettarda viburnoides*	6	0.44	60.19	0.90	84.58	0.91	85.18
2004	23	*Persea pyrifolia*	4	0.30	60.49	0.84	85.42	0.84	86.03
2004	24	*Seguieria americana*	2	0.15	60.64	0.80	86.22	0.81	86.84
2004	25	*Platypodium elegans*	3	0.22	60.86	0.73	86.95	0.73	87.57
2004	26	*Endlicheria paniculata*	19	1.40	62.26	0.70	87.64	0.70	88.27
2004	27	*Guapira opposita*	44	3.25	65.51	0.64	88.28	0.64	88.91
2004	28	*Peltophorum dubium*	7	0.52	66.03	0.55	88.83	0.56	89.47
2004	29	*Cabralea canjerana*	26	1.92	67.95	0.55	89.39	0.56	90.03
2004	30	*Syagrus romanzoffiana*	12	0.89	68.83	0.49	89.88	0.50	90.52
2004	31	*Protium warmingiana*	27	1.99	70.83	0.49	90.37	0.50	91.02
2004	32	*Maclura tinctoria*	4	0.30	71.12	0.43	90.80	0.44	91.45
2004	33	*Ocotea dispersa*	34	2.51	73.63	0.41	91.22	0.42	91.87
2004	34	*Aniba firmula*	8	0.59	74.22	0.41	91.63	0.41	92.28
2004	35	*Cassia ferruginea*	5	0.37	74.59	0.40	92.03	0.40	92.69
2004	36	*Casearia decandra*	23	1.70	76.29	0.38	92.40	0.38	93.06
2004	37	*Rollinia laurifolia*	5	0.37	76.66	0.37	92.78	0.38	93.44
2004	38	*Campomanesia xanthocarpa*	5	0.37	77.03	0.36	93.13	0.36	93.80
2004	39	*Ceiba speciosa*	4	0.30	77.33	0.32	93.45	0.32	94.12
2004	40	*Zanthoxylum riedelianum*	3	0.22	77.55	0.31	93.76	0.31	94.43
2004	41	*Nectandra rigida*	7	0.52	78.06	0.30	94.06	0.30	94.73
2004	42	*Siparuna guianensis*	27	1.99	80.06	0.30	94.36	0.30	95.04
2004	43	*Senna multijuga*	1	0.07	80.13	0.30	94.66	0.30	95.33
2004	44	*Citronella megaphylla*	31	2.29	82.42	0.26	94.92	0.26	95.60
2004	45	*Coutarea hexandra*	14	1.03	83.46	0.25	95.17	0.25	95.85
2004	46	*Rollinia sylvatica*	8	0.59	84.05	0.23	95.39	0.23	96.08
2004	47	*Cryptocarya moschata*	2	0.15	84.19	0.23	95.62	0.23	96.31
2004	48	*Plinia glomerata*	12	0.89	85.08	0.20	95.82	0.20	96.51
2004	49	*Attalea dubia*	3	0.22	85.30	0.16	95.98	0.16	96.67
2004	50	*Myrcia fallax*	5	0.37	85.67	0.13	96.11	0.14	96.80
2004	51	*Alchornea glandulosa*	4	0.30	85.97	0.13	96.25	0.13	96.93
2004	52	*Croton floribundus*	2	0.15	86.12	0.13	96.37	0.13	97.06
2004	53	*Annona cacans*	5	0.37	86.48	0.12	96.50	0.13	97.19
2004	54	*Machaerium floridum*	2	0.15	86.63	0.12	96.61	0.12	97.30
2004	55	*Anadenanthera colubrina*	2	0.15	86.78	0.11	96.73	0.11	97.42
2004	56	*Vernonia diffusa*	2	0.15	86.93	0.11	96.84	0.11	97.53
2004	57	*Amaioua guianensis*	10	0.74	87.67	0.10	96.94	0.10	97.63
2004	58	*Piptadenia paniculata*	4	0.30	87.96	0.10	97.04	0.10	97.73
2004	59	*Sapium glandulatum*	5	0.37	88.33	0.10	97.14	0.10	97.84
2004	60	*Casearia gossypiosperma*	1	0.07	88.40	0.10	97.24	0.10	97.94
2004	61	*Cecropia glaziovi*	1	0.07	88.48	0.09	97.33	0.09	98.03

2004	62	*Sorocea bonplandii*	16	1.18	89.66	0.08	97.42	0.08	98.12
2004	63	*Solanum pseudoquina*	2	0.15	89.81	0.08	97.50	0.08	98.20
2004	64	*Citronella paniculata*	7	0.52	90.32	0.08	97.58	0.08	98.28
2004	65	*Cryptocarya sp.*	1	0.07	90.40	0.08	97.66	0.08	98.36
2004	66	*Allophylus sericeus*	2	0.15	90.55	0.08	97.74	0.08	98.44
2004	67	*Mabea fistulifera*	7	0.52	91.06	0.08	97.82	0.08	98.52
2004	68	*Platymiscium pubescens*	1	0.07	91.14	0.08	97.89	0.08	98.59
2004	69	*Guarea macrophylla*	4	0.30	91.43	0.07	97.96	0.07	98.66
2004	70	*Eugenia sp.1*	1	0.07	91.51	0.06	98.02	0.06	98.72
2004	71	*Zanthoxylum rhoifolium*	3	0.22	91.73	0.06	98.08	0.06	98.78
2004	72	*Guarea kunthiana*	6	0.44	92.17	0.06	98.14	0.06	98.84
2004	73	*Symplocos pubescens*	1	0.07	92.25	0.06	98.20	0.06	98.90
2004	74	*Trichilia elegans*	3	0.22	92.47	0.06	98.25	0.06	98.96
2004	75	*Erythroxylum pelleterianum*	8	0.59	93.06	0.05	98.30	0.05	99.01
2004	76	*Newtonia contorta*	3	0.22	93.28	0.05	98.36	0.05	99.06
2004	77	*Pithecellobium langsdorffii*	4	0.30	93.57	0.05	98.41	0.05	99.11
2004	78	*Himatanthus phagedaenicus*	2	0.15	93.72	0.04	98.45	0.04	99.16
2004	79	*Jacaranda macrantha*	5	0.37	94.09	0.04	98.49	0.04	99.20
2004	80	*Sparattosperma leucanthum*	2	0.15	94.24	0.04	98.54	0.04	99.24
2004	81	*Marlierea teuscheriana*	5	0.37	94.61	0.04	98.58	0.04	99.28
2004	82	*Casearia ulmifolia*	2	0.15	94.76	0.04	98.62	0.04	99.32
2004	83	*Persea sp.*	1	0.07	94.83	0.04	98.66	0.04	99.36
2004	84	*Rheedia gardneriana*	2	0.15	94.98	0.04	98.69	0.04	99.40
2004	85	*Guapira hirsuta*	5	0.37	95.35	0.04	98.73	0.04	99.44
2004	86	*Cordia bullata*	3	0.22	95.57	0.03	98.76	0.03	99.47
2004	87	*Cecropia sp.*	1	0.07	95.64	0.03	98.80	0.03	99.50
2004	88	*Pseudobombax grandiflorum*	4	0.30	95.94	0.03	98.83	0.03	99.54
2004	89	*Albizia polycephala*	1	0.07	96.01	0.03	98.86	0.03	99.56
2004	90	*Miconia hymenonervia*	3	0.22	96.23	0.03	98.89	0.03	99.59
2004	91	*Randia spinosa*	1	0.07	96.31	0.03	98.91	0.03	99.62
2004	92	*Eugenia strictopetala*	4	0.30	96.60	0.02	98.94	0.02	99.64
2004	93	*Matayba elaeagnoides*	2	0.15	96.75	0.02	98.96	0.02	99.67
2004	94	*Inga affinis*	2	0.15	96.90	0.02	98.98	0.02	99.69
2004	95	*Allophylus semidentatus*	1	0.07	96.97	0.02	99.00	0.02	99.71
2004	96	*Aegiphila sellowiana*	1	0.07	97.05	0.02	99.02	0.02	99.73
2004	97	*Mabea brasiliensis*	1	0.07	97.12	0.02	99.04	0.02	99.75
2004	98	*Nectandra mollis*	1	0.07	97.19	0.02	99.05	0.02	99.76
2004	99	*Eugenia sp.*	1	0.07	97.27	0.02	99.07	0.02	99.78
2004	100	*Eugenia leptoclada*	2	0.15	97.42	0.02	99.08	0.02	99.79
2004	101	*Rollinia sericea*	3	0.22	97.64	0.02	99.10	0.02	99.81
2004	102	*Machaerium nyctitans*	2	0.15	97.78	0.01	99.11	0.01	99.82
2004	103	*Guatteria nigrescens*	3	0.22	98.01	0.01	99.13	0.01	99.84
2004	104	*Guatteria villosissima*	2	0.15	98.15	0.01	99.14	0.01	99.85
2004	105	*Bathysa cuspidata*	1	0.07	98.23	0.01	99.15	0.01	99.86
2004	106	*Chrysophyllum gonocarpum*	1	0.07	98.30	0.01	99.16	0.01	99.87
2004	107	*Swartzia myrtifolia*	1	0.07	98.38	0.01	99.17	0.01	99.88
2004	108	*Trema micrantha*	1	0.07	98.45	0.01	99.18	0.01	99.89
2004	109	*Ocotea odorifera*	1	0.07	98.52	0.01	99.19	0.01	99.90
2004	110	*Carpotroche brasiliensis*	1	0.07	98.60	0.01	99.20	0.01	99.91
2004	111	*Casearia arborea*	1	0.07	98.67	0.01	99.21	0.01	99.92
2004	112	*Lacistema pubescens*	1	0.07	98.74	0.01	99.22	0.01	99.93
2004	113	*Acacia glomerosa*	1	0.07	98.82	0.01	99.22	0.01	99.93
2004	114	*Tapirira guianensis*	1	0.07	98.89	0.01	99.23	0.01	99.94
2004	115	*Dictyoloma incanescens*	1	0.07	98.97	0.01	99.23	0.01	99.94
2004	116	*Miconia cinnamomifolia*	1	0.07	99.04	0.01	99.24	0.01	99.95
2004	117	*Piptocarpha macropoda*	1	0.07	99.11	0.01	99.25	0.01	99.96
2004	118	*Myrciaria axillaris*	1	0.07	99.19	0.01	99.25	0.01	99.96

2004	119	*Psychotria myriantha*	2	0.15	99.34	0.01	99.26	0.01	99.97
2004	120	*Machaerium brasiliense*	1	0.07	99.41	0.01	99.26	0.01	99.97
2004	121	*Celtis iguanaea*	1	0.07	99.48	0.00	99.27	0.01	99.98
2004	122	*Licania spicata*	1	0.07	99.56	0.00	99.27	0.00	99.98
2004	123	*Clarisia ilicifolia*	1	0.07	99.63	0.00	99.28	0.00	99.99
2004	124	*Guatteria australis*	1	0.07	99.70	0.00	99.28	0.00	99.99
2004	125	*Inga marginata*	1	0.07	99.78	0.00	99.28	0.00	99.99
2004	126	*Ocotea teleiandra*	1	0.07	99.85	0.00	99.28	0.00	100.00
2004	127	*Ocotea sp.*	1	0.07	99.93	0.00	99.29	0.00	100.00
2004	128	*Brunfelsia uniflora*	1	0.07	100.00	0.00	99.29	0.00	100.00
2011	1	*Anadenanthera peregrina*	48	3.81	3.81	19.03	19.03	17.53	17.53
2011	2	*Piptadenia gonoacantha*	52	4.13	7.94	16.39	35.42	15.10	32.63
2011	3	*Machaerium stipitatum*	41	3.25	11.19	10.06	45.47	9.27	41.89
2011	4	*Allophylus edulis*	42	3.33	14.52	6.72	52.19	6.19	48.08
2011	5	*Trichilia lepidota*	104	8.25	22.78	4.84	57.03	4.46	52.54
2011	6	*Cedrela fissilis*	12	0.95	23.73	3.68	60.71	3.39	55.93
2011	7	*Ficus enormis*	1	0.08	23.81	3.64	64.36	3.36	59.29
2011	8	*Nectandra lanceolata*	31	2.46	26.27	3.45	67.80	3.17	62.46
2011	9	*Luehea grandiflora*	33	2.62	28.89	2.93	70.74	2.70	65.17
2011	10	*Maytenus aquifolium*	1	0.08	28.97	2.76	73.50	2.54	67.71
2011	11	*Cariniana legalis*	2	0.16	29.13	2.50	76.00	2.30	70.01
2011	12	*Dalbergia nigra*	46	3.65	32.78	1.99	77.98	1.83	71.84
2011	13	*Prunus sellowii*	70	5.56	38.33	1.89	79.87	1.74	73.58
2011	14	*Cariniana estrellensis*	5	0.40	38.73	1.75	81.62	1.61	75.19
2011	15	*Apuleia leiocarpa*	10	0.79	39.52	1.59	83.20	1.46	76.65
2011	16	*Xylosma prockia*	44	3.49	43.02	1.48	84.68	1.36	78.01
2011	17	*Chrysophyllum flexuosum*	71	5.63	48.65	1.20	85.88	1.10	79.12
2011	18	*Persea pyrifolia*	3	0.24	48.89	1.15	87.03	1.06	80.17
2011	19	*Tabernaemontana laeta*	2	0.16	49.05	1.12	88.15	1.04	81.21
2011	20	*Guettarda viburnoides*	6	0.48	49.52	1.04	89.19	0.96	82.17
2011	21	*Trichilia pallida*	75	5.95	55.48	0.88	90.07	0.81	82.98
2011	22	*Bauhinia forficata*	6	0.48	55.95	0.87	90.95	0.81	83.78
2011	23	*Seguieria americana*	2	0.16	56.11	0.84	91.79	0.78	84.56
2011	24	*Protium warmingiana*	35	2.78	58.89	0.80	92.59	0.74	85.30
2011	25	*Endlicheria paniculata*	14	1.11	60.00	0.79	93.38	0.73	86.02
2011	26	*Platypodium elegans*	3	0.24	60.24	0.79	94.16	0.72	86.75
2011	27	*Casearia sylvestris*	3	0.24	60.48	0.76	94.92	0.70	87.45
2011	28	*Guapira opposita*	42	3.33	63.81	0.73	95.65	0.67	88.12
2011	29	*Campomanesia xanthocarpa*	5	0.40	64.21	0.66	96.32	0.61	88.73
2011	30	*Cabralea canjerana*	23	1.83	66.03	0.63	96.95	0.58	89.31
2011	31	*Peltophorum dubium*	5	0.40	66.43	0.56	97.51	0.52	89.83
2011	32	*Syagrus romanzoffiana*	11	0.87	67.30	0.55	98.06	0.51	90.34
2011	33	*Aniba firmula*	7	0.56	67.86	0.52	98.58	0.48	90.82
2011	34	*Ocotea dispersa*	33	2.62	70.48	0.50	99.08	0.46	91.28
2011	35	*Rollinia laurifolia*	5	0.40	70.87	0.43	99.51	0.40	91.68
2011	36	*Persea americana*	2	0.16	71.03	0.41	99.92	0.38	92.05
2011	37	*Senna multijuga*	1	0.08	71.11	0.40	100.32	0.37	92.42
2011	38	*Ceiba speciosa*	5	0.40	71.51	0.40	100.72	0.37	92.79
2011	39	*Rollinia sylvatica*	12	0.95	72.46	0.38	101.10	0.35	93.14
2011	40	*Casearia decandra*	17	1.35	73.81	0.37	101.47	0.34	93.48
2011	41	*Citronella megaphylla*	34	2.70	76.51	0.36	101.83	0.34	93.81
2011	42	*Zanthoxylum riedelianum*	4	0.32	76.83	0.36	102.19	0.33	94.14
2011	43	*Maclura tinctoria*	3	0.24	77.06	0.35	102.54	0.33	94.47
2011	44	*Coutarea hexandra*	13	1.03	78.10	0.34	102.88	0.31	94.78
2011	45	*Cassia ferruginea*	3	0.24	78.33	0.34	103.22	0.31	95.09
2011	46	*Cryptocarya moschata*	2	0.16	78.49	0.33	103.55	0.31	95.40
2011	47	*Cecropia glaziovi*	3	0.24	78.73	0.30	103.85	0.28	95.67

2011	48	*Anadenanthera colubrina*	7	0.56	79.29	0.27	104.12	0.25	95.92
2011	49	*Siparuna guianensis*	28	2.22	81.51	0.23	104.35	0.21	96.13
2011	50	*Plinia glomerata*	11	0.87	82.38	0.23	104.57	0.21	96.34
2011	51	*Croton floribundus*	2	0.16	82.54	0.22	104.79	0.20	96.54
2011	52	*Nectandra rigida*	6	0.48	83.02	0.20	104.99	0.18	96.72
2011	53	*Vernonia diffusa*	8	0.63	83.65	0.19	105.18	0.18	96.90
2011	54	*Annona cacans*	6	0.48	84.13	0.19	105.37	0.17	97.07
2011	55	*Guarea macrophylla*	5	0.40	84.52	0.17	105.54	0.16	97.23
2011	56	*Myrcia fallax*	5	0.40	84.92	0.16	105.70	0.15	97.38
2011	57	*Sorocea bonplandii*	21	1.67	86.59	0.16	105.86	0.14	97.52
2011	58	*Solanum pseudoquina*	2	0.16	86.75	0.15	106.01	0.14	97.66
2011	59	*Amaioua guianensis*	12	0.95	87.70	0.15	106.16	0.14	97.80
2011	60	*Sapium glandulatum*	3	0.24	87.94	0.14	106.30	0.13	97.93
2011	61	*Machaerium floridum*	2	0.16	88.10	0.13	106.43	0.12	98.05
2011	62	*Piptadenia paniculata*	6	0.48	88.57	0.13	106.56	0.12	98.17
2011	63	*Casearia gossypiosperma*	1	0.08	88.65	0.11	106.67	0.10	98.27
2011	64	*Citronella paniculata*	7	0.56	89.21	0.11	106.78	0.10	98.37
2011	65	*Alchornea glandulosa*	3	0.24	89.44	0.10	106.88	0.09	98.46
2011	66	*Platymiscium pubescens*	1	0.08	89.52	0.10	106.97	0.09	98.55
2011	67	*Cryptocarya sp.*	1	0.08	89.60	0.08	107.06	0.08	98.63
2011	68	*Trichilia elegans*	2	0.16	89.76	0.08	107.14	0.07	98.70
2011	69	*Eugenia sp.1*	1	0.08	89.84	0.07	107.21	0.06	98.76
2011	70	*Guarea kunthiana*	6	0.48	90.32	0.07	107.27	0.06	98.83
2011	71	*Sparattosperma leucanthum*	2	0.16	90.48	0.06	107.34	0.06	98.89
2011	72	*Newtonia contorta*	3	0.24	90.71	0.06	107.40	0.05	98.94
2011	73	*Rheedia gardneriana*	4	0.32	91.03	0.06	107.45	0.05	98.99
2011	74	*Guapira hirsuta*	7	0.56	91.59	0.06	107.51	0.05	99.04
2011	75	*Jacaranda macrantha*	6	0.48	92.06	0.06	107.57	0.05	99.10
2011	76	*Pseudobombax grandiflorum*	4	0.32	92.38	0.05	107.62	0.05	99.15
2011	77	*Marlierea teuscheriana*	7	0.56	92.94	0.05	107.67	0.05	99.20
2011	78	*Himatanthus phagedaenicus*	2	0.16	93.10	0.05	107.73	0.05	99.24
2011	79	*Allophylus sericeus*	1	0.08	93.17	0.05	107.78	0.05	99.29
2011	80	*Pithecellobium langsdorffii*	3	0.24	93.41	0.04	107.82	0.04	99.33
2011	81	*Casearia ulmifolia*	1	0.08	93.49	0.04	107.86	0.04	99.37
2011	82	*Cordia bullata*	2	0.16	93.65	0.04	107.91	0.04	99.41
2011	83	*Matayba elaeagnoides*	4	0.32	93.97	0.04	107.95	0.04	99.44
2011	84	*Eugenia strictopetala*	4	0.32	94.29	0.04	107.98	0.04	99.48
2011	85	*Randia spinosa*	1	0.08	94.37	0.03	108.02	0.03	99.51
2011	86	*Chrysophyllum gonocarpum*	1	0.08	94.44	0.03	108.05	0.03	99.54
2011	87	*Zanthoxylum rhoifolium*	2	0.16	94.60	0.03	108.08	0.03	99.57
2011	88	*Miconia hymenonervia*	6	0.48	95.08	0.03	108.11	0.03	99.60
2011	89	*Albizia polycephala*	1	0.08	95.16	0.03	108.15	0.03	99.63
2011	90	*Inga affinis*	4	0.32	95.48	0.03	108.18	0.03	99.66
2011	91	*Allophylus semidentatus*	1	0.08	95.56	0.03	108.20	0.03	99.68
2011	92	*Mabea fistulifera*	3	0.24	95.79	0.02	108.23	0.02	99.71
2011	93	*Erythroxylum pelleterianum*	3	0.24	96.03	0.02	108.25	0.02	99.73
2011	94	*Rollinia sericea*	3	0.24	96.27	0.02	108.27	0.02	99.74
2011	95	*Eugenia sp.*	1	0.08	96.35	0.02	108.29	0.02	99.76
2011	96	*Swartzia myrtifolia*	1	0.08	96.43	0.02	108.31	0.02	99.78
2011	97	*Eugenia leptoclada*	2	0.16	96.59	0.02	108.32	0.01	99.79
2011	98	*Guatteria villosissima*	2	0.16	96.75	0.02	108.34	0.01	99.81
2011	99	*Guatteria nigrescens*	3	0.24	96.98	0.01	108.35	0.01	99.82
2011	100	*Ocotea odorifera*	1	0.08	97.06	0.01	108.37	0.01	99.83
2011	101	*Machaerium nyctitans*	2	0.16	97.22	0.01	108.38	0.01	99.85
2011	102	*Bathysa cuspidata*	1	0.08	97.30	0.01	108.39	0.01	99.86
2011	103	*Lacistema pubescens*	1	0.08	97.38	0.01	108.41	0.01	99.87
2011	104	*Psychotria myriantha*	4	0.32	97.70	0.01	108.42	0.01	99.88

2011	105	*Inga marginata*	3	0.24	97.94	0.01	108.43	0.01	99.89
2011	106	*Carpotroche brasiliensis*	1	0.08	98.02	0.01	108.43	0.01	99.90
2011	107	*Casearia arborea*	1	0.08	98.10	0.01	108.44	0.01	99.90
2011	108	*Machaerium brasiliense*	1	0.08	98.17	0.01	108.45	0.01	99.91
2011	109	*Miconia cinnamomifolia*	1	0.08	98.25	0.01	108.46	0.01	99.92
2011	110	*Ocotea pubescens*	2	0.16	98.41	0.01	108.47	0.01	99.93
2011	111	*Clarisia ilicifolia*	2	0.16	98.57	0.01	108.48	0.01	99.93
2011	112	*Ocotea teleiandra*	2	0.16	98.73	0.01	108.48	0.01	99.94
2011	113	*Myrciaria axillaris*	1	0.08	98.81	0.01	108.49	0.01	99.95
2011	114	*Tapirira guianensis*	1	0.08	98.89	0.01	108.50	0.01	99.95
2011	115	*Dictyoloma incanescens*	1	0.08	98.97	0.01	108.50	0.01	99.96
2011	116	*Licania spicata*	1	0.08	99.05	0.01	108.51	0.01	99.97
2011	117	*Copaifera langsdorffii*	2	0.16	99.21	0.01	108.52	0.01	99.97
2011	118	*Guatteria australis*	1	0.08	99.29	0.00	108.52	0.00	99.97
2011	119	*Siparuna reginae*	1	0.08	99.37	0.00	108.52	0.00	99.98
2011	120	*Myrcia sp.*	1	0.08	99.44	0.00	108.53	0.00	99.98
2011	121	*Mollinedia schottiana*	1	0.08	99.52	0.00	108.53	0.00	99.98
2011	122	*Euterpe edulis*	1	0.08	99.60	0.00	108.54	0.00	99.99
2011	123	*Picramnia regnelli*	1	0.08	99.68	0.00	108.54	0.00	99.99
2011	124	*Eugenia sp.2*	1	0.08	99.76	0.00	108.54	0.00	99.99
2011	125	*Persea sp.*	1	0.08	99.84	0.00	108.54	0.00	100.00
2011	126	*Psychotria vellosiana*	1	0.08	99.92	0.00	108.55	0.00	100.00
2011	127	*Psychotria vellosiana*	1	0.08	100.00	0.00	108.55	0.00	100.00
2017	1	*Anadenanthera peregrina*	61	4.37	4.37	20.41	20.41	17.98	17.98
2017	2	*Piptadenia gonoacantha*	43	3.08	7.44	16.58	36.99	14.60	32.58
2017	3	*Allophylus edulis*	43	3.08	10.52	7.73	44.72	6.81	39.38
2017	4	*Machaerium stipitatum*	39	2.79	13.31	7.35	52.07	6.48	45.86
2017	5	*Trichilia lepidota*	117	8.38	21.69	5.63	57.69	4.95	50.81
2017	6	*Cedrela fissilis*	15	1.07	22.76	3.67	61.37	3.24	54.05
2017	7	*Nectandra lanceolata*	28	2.00	24.77	3.53	64.90	3.11	57.16
2017	8	*Cariniana legalis*	2	0.14	24.91	3.17	68.07	2.79	59.95
2017	9	*Maytenus aquifolium*	1	0.07	24.98	2.98	71.05	2.63	62.58
2017	10	*Ficus enormis*	1	0.07	25.05	2.94	74.00	2.59	65.17
2017	11	*Luehea grandiflora*	32	2.29	27.34	2.93	76.92	2.58	67.75
2017	12	*Dalbergia nigra*	46	3.29	30.64	2.29	79.22	2.02	69.77
2017	13	*Prunus sellowii*	69	4.94	35.58	2.17	81.38	1.91	71.68
2017	14	*Cariniana estrellensis*	6	0.43	36.01	1.94	83.32	1.71	73.39
2017	15	*Persea pyrifolia*	3	0.21	36.22	1.65	84.97	1.45	74.84
2017	16	*Apuleia leiocarpa*	9	0.64	36.86	1.58	86.55	1.39	76.23
2017	17	*Xylosma prockia*	47	3.36	40.23	1.53	88.08	1.35	77.58
2017	18	*Chrysophyllum flexuosum*	95	6.80	47.03	1.48	89.57	1.31	78.88
2017	19	*Casearia sylvestris*	3	0.21	47.24	1.35	90.92	1.19	80.07
2017	20	*Guettarda viburnoides*	6	0.43	47.67	1.23	92.15	1.08	81.16
2017	21	*Tabernaemontana laeta*	2	0.14	47.82	1.18	93.33	1.04	82.20
2017	22	*Protium warmingiana*	38	2.72	50.54	1.06	94.39	0.94	83.13
2017	23	*Endlicheria paniculata*	14	1.00	51.54	1.00	95.39	0.88	84.01
2017	24	*Bauhinia forficata*	5	0.36	51.90	0.88	96.27	0.78	84.79
2017	25	*Seguieria americana*	2	0.14	52.04	0.85	97.12	0.75	85.53
2017	26	*Trichilia pallida*	75	5.37	57.41	0.82	97.94	0.72	86.25
2017	27	*Nectandra rigida*	6	0.43	57.84	0.81	98.75	0.71	86.97
2017	28	*Guapira opposita*	43	3.08	60.92	0.80	99.54	0.70	87.67
2017	29	*Platypodium elegans*	3	0.21	61.13	0.79	100.33	0.69	88.36
2017	30	*Cabralea canjerana*	20	1.43	62.56	0.68	101.01	0.59	88.96
2017	31	*Syagrus romanzoffiana*	12	0.86	63.42	0.62	101.63	0.55	89.50
2017	32	*Ocotea dispersa*	39	2.79	66.21	0.51	102.14	0.45	89.95
2017	33	*Peltophorum dubium*	5	0.36	66.57	0.50	102.64	0.44	90.39
2017	34	*Aniba firmula*	5	0.36	66.93	0.50	103.13	0.44	90.83

2017	35	*Citronella megaphylla*	48	3.44	70.37	0.49	103.62	0.43	91.26
2017	36	*Persea americana*	2	0.14	70.51	0.48	104.10	0.42	91.68
2017	37	*Senna multijuga*	1	0.07	70.58	0.45	104.55	0.40	92.08
2017	38	*Rollinia laurifolia*	5	0.36	70.94	0.44	104.99	0.39	92.47
2017	39	*Ceiba speciosa*	6	0.43	71.37	0.43	105.42	0.38	92.84
2017	40	*Cecropia glaziovi*	9	0.64	72.01	0.41	105.83	0.36	93.21
2017	41	*Casearia decandra*	15	1.07	73.09	0.41	106.24	0.36	93.57
2017	42	*Campomanesia xanthocarpa*	5	0.36	73.44	0.39	106.63	0.34	93.91
2017	43	*Rollinia sylvatica*	15	1.07	74.52	0.38	107.02	0.34	94.25
2017	44	*Coutarea hexandra*	14	1.00	75.52	0.38	107.40	0.34	94.59
2017	45	*Siparuna guianensis*	53	3.79	79.31	0.38	107.78	0.33	94.92
2017	46	*Cryptocarya moschata*	2	0.14	79.46	0.36	108.13	0.31	95.23
2017	47	*Anadenanthera colubrina*	5	0.36	79.81	0.35	108.48	0.31	95.54
2017	48	*Cassia ferruginea*	2	0.14	79.96	0.34	108.82	0.30	95.84
2017	49	*Maclura tinctoria*	3	0.21	80.17	0.34	109.16	0.30	96.14
2017	50	*Annona cacans*	7	0.50	80.67	0.31	109.47	0.28	96.41
2017	51	*Plinia glomerata*	25	1.79	82.46	0.29	109.76	0.25	96.67
2017	52	*Sorocea bonplandii*	45	3.22	85.68	0.28	110.04	0.25	96.91
2017	53	*Croton floribundus*	3	0.21	85.90	0.22	110.25	0.19	97.10
2017	54	*Amaioua guianensis*	16	1.15	87.04	0.20	110.46	0.18	97.28
2017	55	*Guarea macrophylla*	5	0.36	87.40	0.18	110.64	0.16	97.44
2017	56	*Myrcia fallax*	4	0.29	87.69	0.16	110.80	0.14	97.59
2017	57	*Piptadenia paniculata*	7	0.50	88.19	0.15	110.96	0.14	97.72
2017	58	*Solanum pseudoquina*	1	0.07	88.26	0.14	111.09	0.12	97.84
2017	59	*Machaerium floridum*	5	0.36	88.62	0.13	111.22	0.11	97.95
2017	60	*Casearia gossypiosperma*	1	0.07	88.69	0.12	111.34	0.11	98.06
2017	61	*Sapium glandulatum*	3	0.21	88.90	0.12	111.47	0.11	98.17
2017	62	*Trichilia elegans*	3	0.21	89.12	0.11	111.57	0.09	98.27
2017	63	*Platymiscium pubescens*	1	0.07	89.19	0.11	111.68	0.09	98.36
2017	64	*Rheedia gardneriana*	7	0.50	89.69	0.10	111.78	0.08	98.44
2017	65	*Citronella paniculata*	7	0.50	90.19	0.09	111.87	0.08	98.52
2017	66	*Cryptocarya sp.*	1	0.07	90.26	0.09	111.95	0.07	98.60
2017	67	*Newtonia contorta*	3	0.21	90.48	0.08	112.03	0.07	98.67
2017	68	*Guarea kunthiana*	8	0.57	91.05	0.08	112.11	0.07	98.74
2017	69	*Marlierea teuscheriana*	6	0.43	91.48	0.07	112.18	0.06	98.80
2017	70	*Eugenia sp.1*	1	0.07	91.55	0.07	112.25	0.06	98.86
2017	71	*Allophylus sericeus*	1	0.07	91.62	0.07	112.32	0.06	98.92
2017	72	*Himatanthus phagedaenicus*	2	0.14	91.77	0.06	112.38	0.06	98.98
2017	73	*Sparattosperma leucanthum*	2	0.14	91.91	0.06	112.44	0.05	99.03
2017	74	*Pseudobombax grandiflorum*	4	0.29	92.20	0.06	112.50	0.05	99.08
2017	75	*Cordia bullata*	3	0.21	92.41	0.06	112.56	0.05	99.13
2017	76	*Matayba elaeagnoides*	5	0.36	92.77	0.06	112.61	0.05	99.18
2017	77	*Randia spinosa*	1	0.07	92.84	0.05	112.67	0.05	99.23
2017	78	*Jacaranda macrantha*	5	0.36	93.20	0.05	112.72	0.04	99.27
2017	79	*Chrysophyllum gonocarpum*	1	0.07	93.27	0.05	112.77	0.04	99.32
2017	80	*Eugenia strictopetala*	4	0.29	93.56	0.05	112.81	0.04	99.36
2017	81	*Albizia polycephala*	1	0.07	93.63	0.04	112.85	0.03	99.39
2017	82	*Allophylus semidentatus*	1	0.07	93.70	0.04	112.89	0.03	99.42
2017	83	*Guapira hirsuta*	5	0.36	94.06	0.03	112.92	0.03	99.45
2017	84	*Psychotria myriantha*	11	0.79	94.85	0.03	112.95	0.03	99.48
2017	85	*Carpotroche brasiliensis*	2	0.14	94.99	0.03	112.98	0.03	99.51
2017	86	*Vernonia diffusa*	5	0.36	95.35	0.03	113.01	0.03	99.53
2017	87	*Inga affinis*	3	0.21	95.56	0.03	113.04	0.03	99.56
2017	88	*Mabea fistulifera*	3	0.21	95.78	0.03	113.07	0.02	99.58
2017	89	*Swartzia myrtifolia*	1	0.07	95.85	0.03	113.10	0.02	99.61
2017	90	*Zanthoxylum rhoifolium*	1	0.07	95.92	0.03	113.12	0.02	99.63
2017	91	*Eugenia sp.*	1	0.07	95.99	0.03	113.15	0.02	99.65

2017	92	*Rollinia sericea*	4	0.29	96.28	0.02	113.17	0.02	99.67
2017	93	*Alchornea glandulosa*	1	0.07	96.35	0.02	113.20	0.02	99.70
2017	94	*Erythroxylum pelleterianum*	3	0.21	96.56	0.02	113.22	0.02	99.72
2017	95	*Pithecellobium langsdorffii*	2	0.14	96.71	0.02	113.24	0.02	99.74
2017	96	*Miconia hymenonervia*	4	0.29	96.99	0.02	113.26	0.02	99.75
2017	97	*Guatteria villosissima*	2	0.14	97.14	0.02	113.29	0.02	99.77
2017	98	*Zanthoxylum riedelianum*	1	0.07	97.21	0.02	113.31	0.02	99.79
2017	99	*Ocotea odorifera*	1	0.07	97.28	0.02	113.33	0.02	99.81
2017	100	*Ocotea pubescens*	2	0.14	97.42	0.02	113.35	0.02	99.83
2017	101	*Guatteria nigrescens*	3	0.21	97.64	0.02	113.36	0.01	99.84
2017	102	*Inga marginata*	4	0.29	97.92	0.01	113.38	0.01	99.85
2017	103	*Lacistema pubescens*	1	0.07	98.00	0.01	113.39	0.01	99.86
2017	104	*Machaerium nyctitans*	2	0.14	98.14	0.01	113.40	0.01	99.88
2017	105	*Euterpe edulis*	1	0.07	98.21	0.01	113.42	0.01	99.89
2017	106	*Seguieria langsdorffii*	2	0.14	98.35	0.01	113.43	0.01	99.90
2017	107	*Bathysa cuspidata*	1	0.07	98.43	0.01	113.44	0.01	99.91
2017	108	*Casearia arborea*	1	0.07	98.50	0.01	113.46	0.01	99.92
2017	109	*Clarisia ilicifolia*	3	0.21	98.71	0.01	113.47	0.01	99.93
2017	110	*Machaerium brasiliense*	1	0.07	98.78	0.01	113.48	0.01	99.94
2017	111	*Copaifera langsdorffii*	3	0.21	99.00	0.01	113.48	0.01	99.95
2017	112	*Psychotria vellosiana*	1	0.07	99.07	0.01	113.49	0.01	99.95
2017	113	*Eugenia leptoclada*	1	0.07	99.14	0.01	113.50	0.01	99.96
2017	114	*Tapirira guianensis*	1	0.07	99.21	0.01	113.51	0.01	99.97
2017	115	*Picramnia regnelli*	2	0.14	99.36	0.01	113.51	0.00	99.97
2017	116	*Mollinedia schottiana*	1	0.07	99.43	0.00	113.52	0.00	99.98
2017	117	*Ocotea teleiandra*	1	0.07	99.50	0.00	113.52	0.00	99.98
2017	118	*Myrcia sp.*	1	0.07	99.57	0.00	113.53	0.00	99.98
2017	119	*Brunfelsia uniflora*	1	0.07	99.64	0.00	113.53	0.00	99.99
2017	120	*Psychotria sessilis*	1	0.07	99.71	0.00	113.53	0.00	99.99
2017	121	*Persea sp.*	1	0.07	99.79	0.00	113.54	0.00	99.99
2017	122	*Eugenia sp.2*	1	0.07	99.86	0.00	113.54	0.00	100.00
2017	123	*Randia armata*	1	0.07	99.93	0.00	113.54	0.00	100.00
2017	124	*Eriotheca candolleana*	1	0.07	100.00	0.00	113.54	0.00	100.00

Table S.2. Data on all families for aboveground carbon stock (AGC) in Southeastern and Northeastern patches for all years sampling.

AGC = aboveground carbon; AGC.Ac. = Aboveground carbon accumulated; %AGC = proportion of aboveground carbon; % AGC.Ac. =proportion of aboveground carbon accumulated.

Southeastern	Family	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1984	Fabaceae	98.62	98.62	70.38	70.38
1984	Salicaceae	17.55	116.17	12.52	82.90
1984	Moraceae	6.63	122.80	4.74	87.64
1984	Burseraceae	2.13	124.94	1.52	89.16
1984	Malvaceae	1.97	126.91	1.41	90.57
1984	Sapindaceae	1.66	128.57	1.18	91.75
1984	Lauraceae	1.58	130.15	1.13	92.88
1984	Rubiaceae	1.56	131.71	1.12	94.00
1984	Annonaceae	1.44	133.15	1.03	95.03
1984	Anacardiaceae	1.21	134.36	0.86	95.89
1984	Meliaceae	0.86	135.22	0.61	96.50
1984	Boraginaceae	0.80	136.02	0.57	97.07
1984	Siparunaceae	0.64	136.66	0.46	97.53
1984	Bignoniaceae	0.58	137.24	0.42	97.94
1984	Myrtaceae	0.51	137.75	0.36	98.30
1984	Rutaceae	0.46	138.21	0.33	98.63
1984	Sapotaceae	0.36	138.57	0.26	98.89
1984	Rosaceae	0.32	138.89	0.23	99.12
1984	Phytolaccaceae	0.32	139.21	0.23	99.35
1984	Urticaceae	0.24	139.44	0.17	99.52
1984	Lamiaceae	0.16	139.61	0.12	99.63
1984	Euphorbiaceae	0.11	139.72	0.08	99.71
1984	Chrysobalanaceae	0.09	139.80	0.06	99.77
1984	Achariaceae	0.07	139.87	0.05	99.82
1984	Clusiaceae	0.05	139.92	0.03	99.86
1984	Arecaceae	0.05	139.97	0.03	99.89
1984	Lecythidaceae	0.05	140.02	0.03	99.92
1984	Apocynaceae	0.03	140.04	0.02	99.94
1984	Lecythidaceae	0.02	140.06	0.02	99.96
1984	Vochysiaceae	0.02	140.08	0.01	99.97
1984	Cardiopteridaceae	0.01	140.09	0.01	99.98
1984	Picramniaceae	0.01	140.11	0.01	99.99
1984	Monimiaceae	0.01	140.11	0.01	99.99
1984	Celastraceae	0.01	140.12	0.00	100.00
1984	Erythroxylaceae	0.00	140.12	0.00	100.00
1998	Fabaceae	104.56	104.56	67.95	67.95
1998	Salicaceae	19.44	124.00	12.63	80.58
1998	Moraceae	10.76	134.75	6.99	87.58
1998	Burseraceae	2.72	137.47	1.77	89.34
1998	Sapindaceae	2.19	139.66	1.42	90.77

1998	Lauraceae	2.07	141.74	1.35	92.12
1998	Malvaceae	2.06	143.79	1.34	93.45
1998	Rubiaceae	1.53	145.33	1.00	94.45
1998	Annonaceae	1.35	146.68	0.88	95.32
1998	Siparunaceae	1.02	147.69	0.66	95.99
1998	Myrtaceae	0.90	148.59	0.58	96.57
1998	Boraginaceae	0.84	149.43	0.55	97.11
1998	Meliaceae	0.81	150.24	0.53	97.64
1998	Rutaceae	0.53	150.77	0.35	97.99
1998	Bignoniaceae	0.51	151.28	0.33	98.32
1998	Anacardiaceae	0.47	151.75	0.31	98.62
1998	Sapotaceae	0.45	152.20	0.29	98.91
1998	Phytolaccaceae	0.39	152.59	0.25	99.17
1998	Urticaceae	0.24	152.84	0.16	99.33
1998	Rosaceae	0.21	153.05	0.14	99.47
1998	Lamiaceae	0.18	153.23	0.11	99.58
1998	Chrysobalanaceae	0.10	153.33	0.07	99.65
1998	Euphorbiaceae	0.10	153.43	0.06	99.71
1998	Lecythidaceae	0.10	153.52	0.06	99.77
1998	Achariaceae	0.08	153.60	0.05	99.83
1998	Celastraceae	0.06	153.66	0.04	99.87
1998	Arecaceae	0.06	153.72	0.04	99.90
1998	Apocynaceae	0.04	153.76	0.02	99.93
1998	Lecythidaceae	0.03	153.79	0.02	99.95
1998	Picramniaceae	0.03	153.82	0.02	99.97
1998	Vochysiaceae	0.02	153.85	0.02	99.98
1998	Monimiaceae	0.01	153.86	0.01	99.99
1998	Erythroxylaceae	0.01	153.87	0.00	100.00
1998	Nyctaginaceae	0.00	153.87	0.00	100.00
2003	Fabaceae	110.92	110.92	66.46	66.46
2003	Salicaceae	20.59	131.51	12.34	78.79
2003	Moraceae	14.00	145.51	8.39	87.18
2003	Burseraceae	2.85	148.36	1.71	88.89
2003	Sapindaceae	2.65	151.01	1.59	90.48
2003	Lauraceae	2.59	153.60	1.55	92.03
2003	Malvaceae	2.35	155.95	1.41	93.44
2003	Annonaceae	1.36	157.31	0.81	94.25
2003	Rubiaceae	1.35	158.66	0.81	95.06
2003	Myrtaceae	1.17	159.83	0.70	95.77
2003	Meliaceae	1.17	161.01	0.70	96.47
2003	Boraginaceae	1.03	162.03	0.62	97.08
2003	Siparunaceae	1.00	163.03	0.60	97.68
2003	Sapotaceae	0.64	163.67	0.38	98.06
2003	Bignoniaceae	0.61	164.28	0.37	98.43
2003	Rutaceae	0.43	164.71	0.26	98.69
2003	Phytolaccaceae	0.35	165.05	0.21	98.89

2003	Anacardiaceae	0.30	165.36	0.18	99.08
2003	Urticaceae	0.26	165.62	0.16	99.23
2003	Rosaceae	0.23	165.85	0.14	99.37
2003	Lamiaceae	0.19	166.04	0.11	99.48
2003	Lecythidaceae	0.14	166.18	0.08	99.57
2003	Chrysobalanaceae	0.13	166.31	0.08	99.65
2003	Euphorbiaceae	0.11	166.42	0.07	99.71
2003	Achariaceae	0.11	166.53	0.06	99.78
2003	Celastraceae	0.10	166.63	0.06	99.84
2003	Arecaceae	0.08	166.71	0.05	99.89
2003	Apocynaceae	0.05	166.77	0.03	99.92
2003	Lecythidaceae	0.05	166.82	0.03	99.95
2003	Vochysiaceae	0.04	166.85	0.02	99.97
2003	Picramniaceae	0.02	166.87	0.01	99.98
2003	Monimiaceae	0.01	166.88	0.01	99.99
2003	Erythroxylaceae	0.01	166.89	0.01	100.00
2003	Nyctaginaceae	0.00	166.90	0.00	100.00
2011	Fabaceae	111.89	111.89	68.70	68.70
2011	Moraceae	17.06	128.95	10.48	79.18
2011	Salicaceae	14.69	143.64	9.02	88.20
2011	Sapindaceae	3.04	146.68	1.86	90.06
2011	Burseraceae	2.50	149.18	1.54	91.60
2011	Lauraceae	2.42	151.60	1.49	93.09
2011	Malvaceae	2.29	153.89	1.41	94.49
2011	Rubiaceae	1.23	155.13	0.76	95.25
2011	Boraginaceae	1.12	156.24	0.69	95.94
2011	Annonaceae	1.08	157.32	0.66	96.60
2011	Myrtaceae	0.96	158.28	0.59	97.19
2011	Bignoniaceae	0.74	159.02	0.45	97.64
2011	Meliaceae	0.67	159.69	0.41	98.05
2011	Sapotaceae	0.62	160.31	0.38	98.43
2011	Siparunaceae	0.47	160.78	0.29	98.72
2011	Anacardiaceae	0.38	161.16	0.23	98.96
2011	Phytolaccaceae	0.25	161.41	0.15	99.11
2011	Rosaceae	0.24	161.65	0.15	99.26
2011	Rutaceae	0.23	161.88	0.14	99.40
2011	Lecythidaceae	0.22	162.11	0.14	99.53
2011	Chrysobalanaceae	0.14	162.24	0.09	99.62
2011	Achariaceae	0.12	162.36	0.07	99.69
2011	Celastraceae	0.10	162.46	0.06	99.75
2011	Apocynaceae	0.08	162.54	0.05	99.80
2011	Lamiaceae	0.08	162.62	0.05	99.85
2011	Arecaceae	0.07	162.69	0.04	99.90
2011	Lecythidaceae	0.05	162.75	0.03	99.93
2011	Vochysiaceae	0.05	162.80	0.03	99.96
2011	Picramniaceae	0.03	162.83	0.02	99.98

2011	Euphorbiaceae	0.02	162.85	0.01	99.99
2011	Monimiaceae	0.01	162.86	0.01	100.00
2011	Erythroxylaceae	0.00	162.86	0.00	100.00
2017	Fabaceae	113.70	113.70	66.80	66.80
2017	Moraceae	19.39	133.09	11.39	78.20
2017	Salicaceae	14.28	147.38	8.39	86.59
2017	Burseraceae	3.40	150.78	2.00	88.59
2017	Sapindaceae	3.32	154.10	1.95	90.54
2017	Lauraceae	2.82	156.92	1.65	92.20
2017	Myrtaceae	2.76	159.68	1.62	93.82
2017	Malvaceae	2.70	162.39	1.59	95.41
2017	Boraginaceae	1.18	163.56	0.69	96.10
2017	Rubiaceae	0.87	164.44	0.51	96.61
2017	Annonaceae	0.77	165.20	0.45	97.06
2017	Siparunaceae	0.75	165.96	0.44	97.51
2017	Bignoniaceae	0.73	166.69	0.43	97.94
2017	Meliaceae	0.68	167.37	0.40	98.34
2017	Sapotaceae	0.60	167.97	0.35	98.69
2017	Phytolaccaceae	0.48	168.45	0.28	98.97
2017	Anacardiaceae	0.42	168.87	0.25	99.22
2017	Lecythidaceae	0.26	169.14	0.15	99.37
2017	Lamiaceae	0.16	169.30	0.09	99.47
2017	Rosaceae	0.15	169.44	0.09	99.55
2017	Chrysobalanaceae	0.14	169.59	0.08	99.64
2017	Rutaceae	0.13	169.72	0.08	99.72
2017	Apocynaceae	0.13	169.85	0.08	99.79
2017	Achariaceae	0.11	169.96	0.07	99.86
2017	Celastraceae	0.11	170.07	0.06	99.92
2017	Vochysiaceae	0.07	170.14	0.04	99.96
2017	Lecythidaceae	0.03	170.17	0.02	99.98
2017	Picramniaceae	0.01	170.18	0.01	99.99
2017	Monimiaceae	0.01	170.19	0.01	99.99
2017	Arecaceae	0.01	170.20	0.01	100.00
Northeastern	**Family**	**AGC**	**AGC.Ac.**	**%AGC**	**% AGC.Ac.**
1993	Fabaceae	38.87	38.87	54.02	54.02
1993	Meliaceae	6.54	45.41	9.10	63.12
1993	Lauraceae	3.98	49.40	5.54	68.65
1993	Rosaceae	3.15	52.54	4.37	73.03
1993	Sapindaceae	2.54	55.09	3.53	76.56
1993	Malvaceae	2.31	57.39	3.20	79.76
1993	Moraceae	2.21	59.61	3.08	82.84
1993	Salicaceae	1.91	61.52	2.65	85.50
1993	Celastraceae	1.37	62.88	1.90	87.40
1993	Lecythidaceae	1.23	64.12	1.71	89.11
1993	Lecythidaceae	1.09	65.20	1.51	90.62
1993	Rubiaceae	1.05	66.26	1.46	92.08

1993	Phytolaccaceae	0.78	67.04	1.09	93.17
1993	Apocynaceae	0.75	67.79	1.04	94.21
1993	Sapotaceae	0.71	68.49	0.98	95.20
1993	Myrtaceae	0.66	69.15	0.92	96.11
1993	Annonaceae	0.54	69.69	0.75	96.86
1993	Arecaceae	0.39	70.08	0.54	97.40
1993	Nyctaginaceae	0.38	70.46	0.53	97.93
1993	Burseraceae	0.29	70.75	0.41	98.33
1993	Euphorbiaceae	0.29	71.04	0.40	98.73
1993	Rutaceae	0.27	71.31	0.38	99.11
1993	Cardiopteridaceae	0.18	71.49	0.25	99.36
1993	Siparunaceae	0.14	71.63	0.19	99.55
1993	Myrtaceae1	0.05	71.68	0.08	99.63
1993	Symplocaceae	0.05	71.74	0.07	99.70
1993	Urticaceae	0.05	71.79	0.07	99.77
1993	Erythroxylaceae	0.03	71.82	0.05	99.82
1993	Boraginaceae	0.03	71.85	0.04	99.86
1993	Asteraceae	0.03	71.87	0.04	99.89
1993	Clusiaceae	0.02	71.90	0.03	99.93
1993	Bignoniaceae	0.02	71.92	0.03	99.95
1993	Melastomataceae	0.01	71.93	0.01	99.97
1993	Achariaceae	0.01	71.94	0.01	99.98
1993	Lacistemataceae	0.01	71.94	0.01	99.98
1993	Ulmaceae	0.00	71.94	0.01	99.99
1993	Anacardiaceae	0.00	71.95	0.01	100.00
1993	Solanaceae	0.00	71.95	0.00	100.00
2004	Fabaceae	51.66	51.66	52.03	52.03
2004	Meliaceae	9.03	60.69	9.09	61.13
2004	Lauraceae	5.63	66.32	5.67	66.79
2004	Sapindaceae	4.83	71.15	4.86	71.66
2004	Rosaceae	3.58	74.72	3.60	75.26
2004	Malvaceae	3.08	77.80	3.10	78.36
2004	Celastraceae	2.90	80.70	2.92	81.28
2004	Moraceae	2.88	83.59	2.90	84.18
2004	Salicaceae	2.86	86.45	2.88	87.07
2004	Lecythidaceae	1.72	88.17	1.73	88.80
2004	Lecythidaceae	1.42	89.58	1.43	90.22
2004	Rubiaceae	1.30	90.88	1.31	91.53
2004	Apocynaceae	1.03	91.91	1.03	92.57
2004	Sapotaceae	0.98	92.89	0.98	93.55
2004	Phytolaccaceae	0.80	93.69	0.81	94.36
2004	Myrtaceae	0.79	94.48	0.80	95.16
2004	Annonaceae	0.77	95.25	0.77	95.93
2004	Nyctaginaceae	0.68	95.93	0.68	96.62
2004	Arecaceae	0.65	96.58	0.66	97.27
2004	Burseraceae	0.49	97.07	0.50	97.77

2004	Euphorbiaceae	0.45	97.53	0.46	98.22
2004	Rutaceae	0.38	97.90	0.38	98.60
2004	Cardiopteridaceae	0.34	98.24	0.34	98.95
2004	Siparunaceae	0.30	98.54	0.30	99.25
2004	Urticaceae	0.13	98.67	0.13	99.38
2004	Asteraceae	0.12	98.78	0.12	99.49
2004	Bignoniaceae	0.08	98.87	0.09	99.58
2004	Solanaceae	0.08	98.95	0.08	99.66
2004	Myrtaceae1	0.06	99.01	0.06	99.72
2004	Symplocaceae	0.06	99.07	0.06	99.78
2004	Erythroxylaceae	0.05	99.12	0.05	99.83
2004	Clusiaceae	0.04	99.16	0.04	99.87
2004	Boraginaceae	0.03	99.19	0.03	99.90
2004	Melastomataceae	0.03	99.23	0.03	99.94
2004	Lamiaceae	0.02	99.25	0.02	99.96
2004	Cannabaceae	0.01	99.26	0.01	99.97
2004	Achariaceae	0.01	99.27	0.01	99.98
2004	Lacistemataceae	0.01	99.27	0.01	99.98
2004	Anacardiaceae	0.01	99.28	0.01	99.99
2004	Ulmaceae	0.00	99.28	0.01	100.00
2004	Chrysobalanaceae	0.00	99.29	0.00	100.00
2011	Fabaceae	52.85	52.85	48.69	48.69
2011	Meliaceae	10.35	63.20	9.54	58.22
2011	Lauraceae	7.05	70.25	6.50	64.72
2011	Sapindaceae	6.83	77.09	6.30	71.02
2011	Moraceae	4.16	81.25	3.84	74.85
2011	Malvaceae	3.39	84.64	3.12	77.97
2011	Salicaceae	2.76	87.40	2.55	80.52
2011	Celastraceae	2.76	90.16	2.54	83.06
2011	Lecythidaceae	2.50	92.66	2.30	85.37
2011	Rosaceae	1.89	94.55	1.74	87.11
2011	Lecythidaceae	1.75	96.30	1.61	88.72
2011	Rubiaceae	1.59	97.89	1.47	90.18
2011	Sapotaceae	1.23	99.12	1.13	91.32
2011	Myrtaceae	1.19	100.31	1.09	92.41
2011	Apocynaceae	1.18	101.49	1.08	93.50
2011	Annonaceae	1.05	102.54	0.97	94.47
2011	Phytolaccaceae	0.84	103.39	0.78	95.24
2011	Burseraceae	0.80	104.18	0.74	95.98
2011	Nyctaginaceae	0.79	104.97	0.73	96.71
2011	Arecaceae	0.55	105.52	0.51	97.21
2011	Euphorbiaceae	0.48	106.00	0.44	97.65
2011	Cardiopteridaceae	0.47	106.47	0.43	98.09
2011	Luaraceae	0.41	106.88	0.38	98.47
2011	Rutaceae	0.39	107.28	0.36	98.83
2011	Urticaceae	0.30	107.58	0.28	99.10

2011	Siparunaceae	0.23	107.81	0.21	99.32
2011	Asteraceae	0.19	108.00	0.18	99.50
2011	Solanaceae	0.15	108.15	0.14	99.64
2011	Bignoniaceae	0.12	108.27	0.11	99.75
2011	Myrtaceae1	0.07	108.34	0.06	99.81
2011	Clusiaceae	0.06	108.40	0.05	99.87
2011	Boraginaceae	0.04	108.44	0.04	99.90
2011	Melastomataceae	0.04	108.48	0.04	99.94
2011	Erythroxylaceae	0.02	108.51	0.02	99.96
2011	Lacistemataceae	0.01	108.52	0.01	99.97
2011	Achariaceae	0.01	108.53	0.01	99.98
2011	Anacardiaceae	0.01	108.53	0.01	99.99
2011	Chrysobalanaceae	0.01	108.54	0.01	99.99
2011	Monimiaceae	0.00	108.54	0.00	99.99
2011	Picramniaceae	0.00	108.55	0.00	100.00
2011	Myrtaceae2	0.00	108.55	0.00	100.00
2017	Fabaceae	52.15	52.15	45.93	45.93
2017	Meliaceae	11.16	63.31	9.83	55.76
2017	Lauraceae	8.48	71.80	7.47	63.23
2017	Sapindaceae	7.88	79.68	6.94	70.18
2017	Moraceae	3.57	83.25	3.14	73.32
2017	Salicaceae	3.43	86.68	3.03	76.34
2017	Malvaceae	3.41	90.10	3.01	79.35
2017	Lecythidaceae	3.17	93.27	2.79	82.14
2017	Celastraceae	2.98	96.25	2.63	84.77
2017	Rosaceae	2.17	98.42	1.91	86.68
2017	Lecythidaceae	1.94	100.36	1.71	88.39
2017	Rubiaceae	1.93	102.29	1.70	90.09
2017	Sapotaceae	1.53	103.82	1.35	91.44
2017	Apocynaceae	1.25	105.07	1.10	92.53
2017	Annonaceae	1.20	106.26	1.05	93.59
2017	Burseraceae	1.06	107.32	0.94	94.52
2017	Myrtaceae	0.99	108.31	0.87	95.39
2017	Phytolaccaceae	0.86	109.18	0.76	96.15
2017	Nyctaginaceae	0.83	110.01	0.73	96.89
2017	Arecaceae	0.63	110.64	0.56	97.45
2017	Cardiopteridaceae	0.58	111.22	0.51	97.96
2017	Luaraceae	0.48	111.70	0.42	98.38
2017	Urticaceae	0.41	112.12	0.36	98.74
2017	Euphorbiaceae	0.39	112.51	0.34	99.09
2017	Siparunaceae	0.38	112.88	0.33	99.42
2017	Solanaceae	0.14	113.02	0.12	99.54
2017	Bignoniaceae	0.11	113.13	0.10	99.64
2017	Clusiaceae	0.10	113.23	0.08	99.72
2017	Myrtaceae1	0.07	113.30	0.06	99.79
2017	Boraginaceae	0.06	113.35	0.05	99.83

2017	Rutaceae	0.05	113.40	0.04	99.88
2017	Achariaceae	0.03	113.43	0.03	99.90
2017	Asteraceae	0.03	113.46	0.03	99.93
2017	Erythroxylaceae	0.02	113.49	0.02	99.95
2017	Melastomataceae	0.02	113.51	0.02	99.97
2017	Lacistemataceae	0.01	113.52	0.01	99.98
2017	Anacardiaceae	0.01	113.53	0.01	99.99
2017	Picramniaceae	0.01	113.54	0.00	99.99
2017	Monimiaceae	0.00	113.54	0.00	100.00
2017	Myrtaceae2	0.00	113.54	0.00	100.00

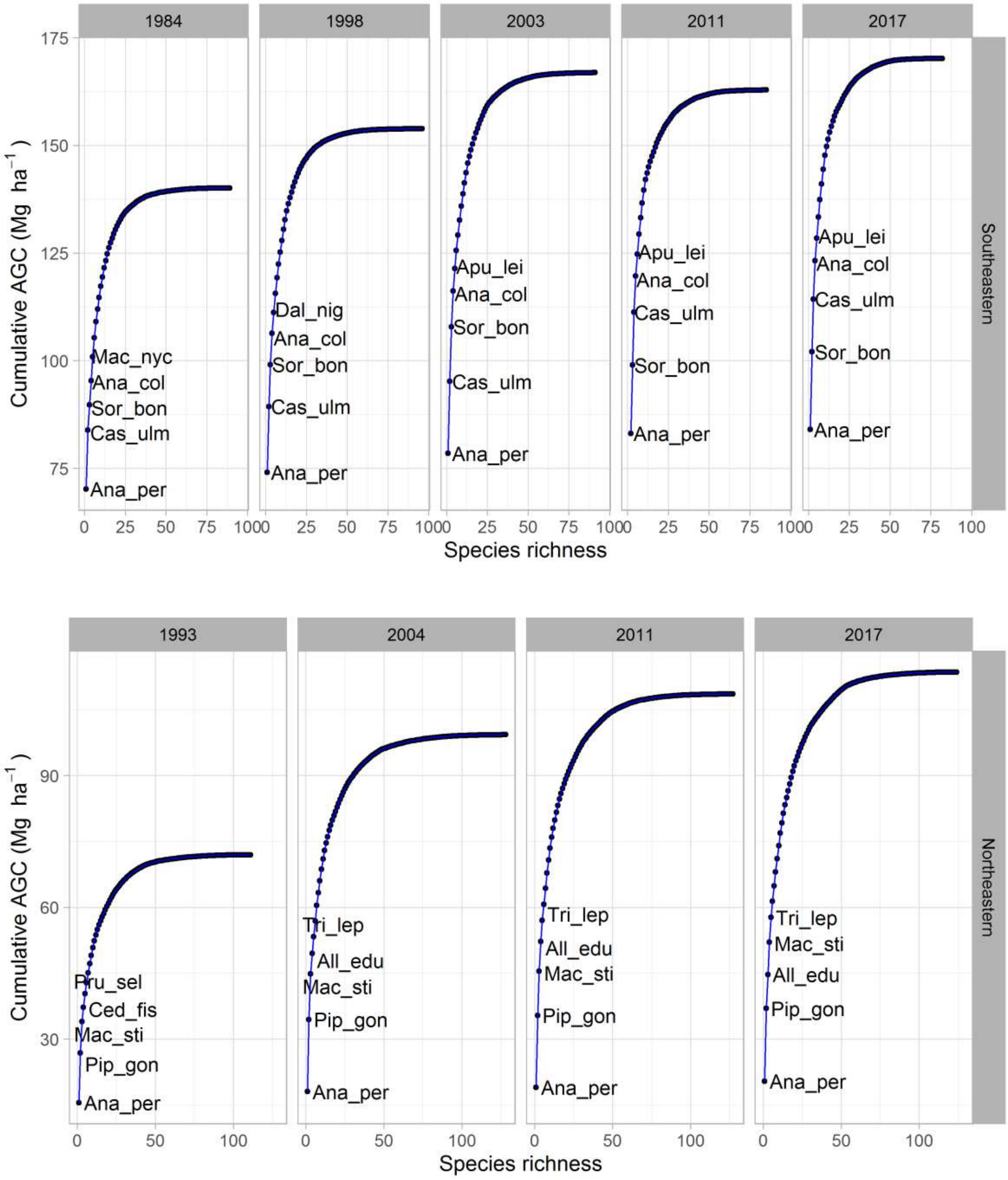


Fig. S.1. Aboveground carbon distribution (AGC) in all stands ages in Southeastern (A) and Northeastern (B) patches for carbon dominants species in Atlantic forest, Minas Gerais, Brazil.

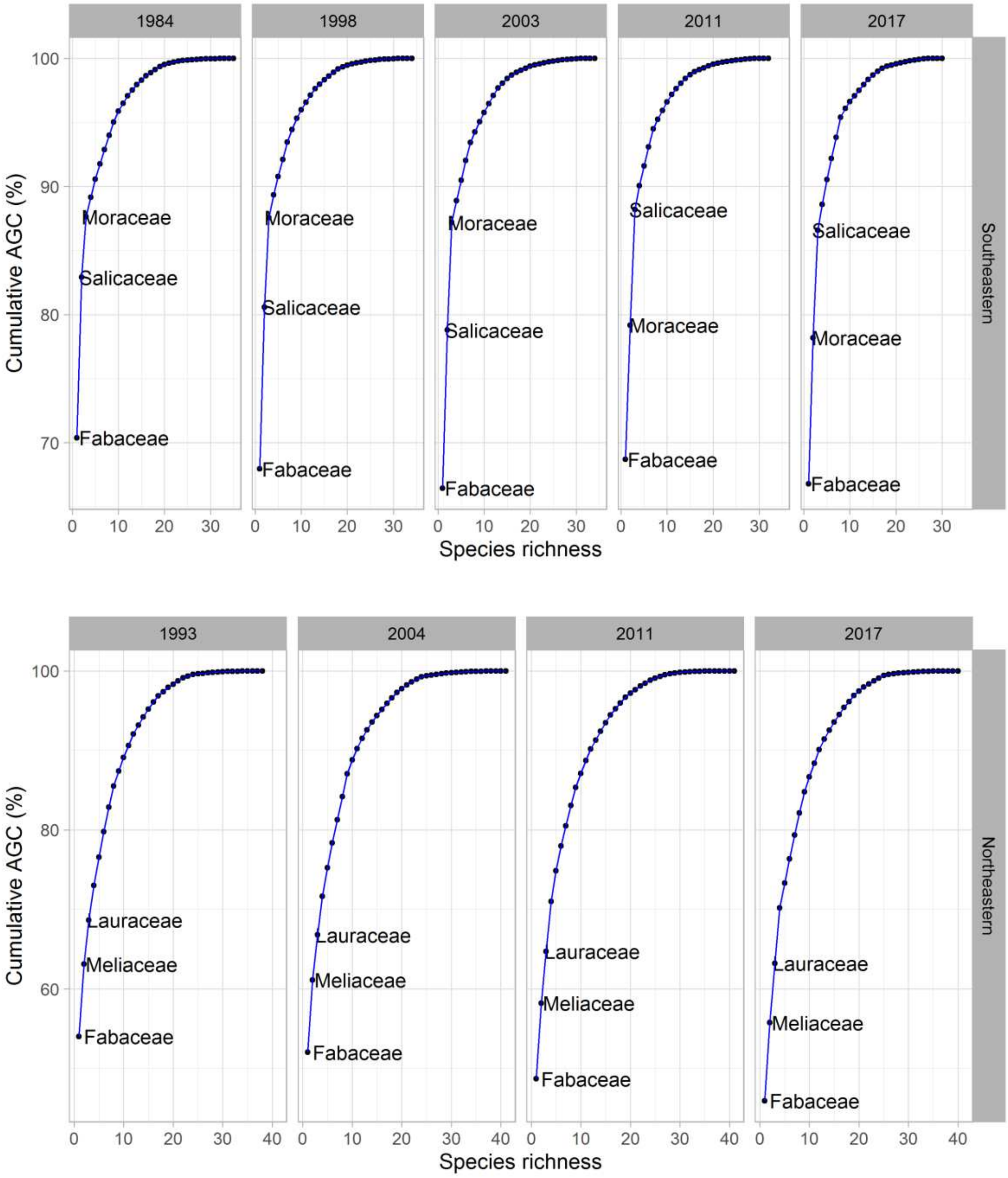


Fig. S.2. Cumulative aboveground carbon (AGC) distribution for the permanent plot of Southeastern (A) and Northeastern (B) patches for carbon dominants families in Atlantic forest, Minas Gerais, Brazil.

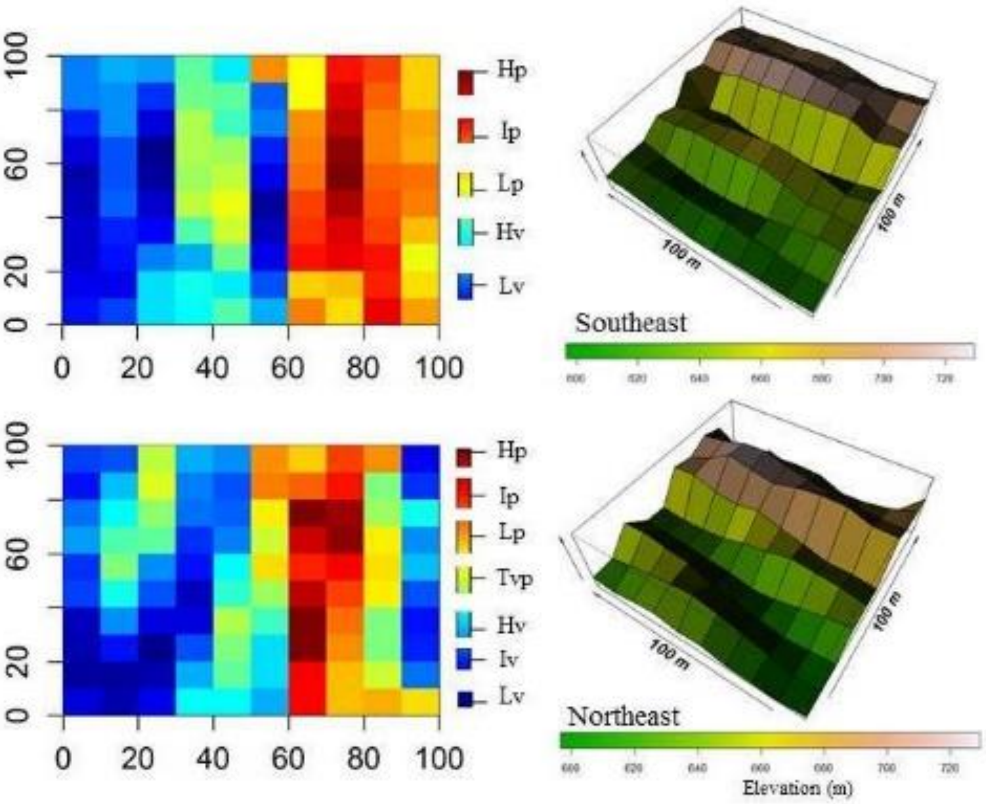


Fig. S.3. Habitats types (left) and topographic maps (right) of the two study areas within 2-ha permanent patches in Atlantic forest, Minas Gerais, Brazil. According to the MRT, the patches were divided into of the following habitats: i) High plateau (Hp); ii) intermediate plateau (Ip); iii) low plateau (Lp); iv) high valley (Hv); v) low valley (Lv); vi) i) intermediate low valley (Iv), and ii) a transition area between high valley and low plateau (Tpv). (Rodrigues, et al., 2020).

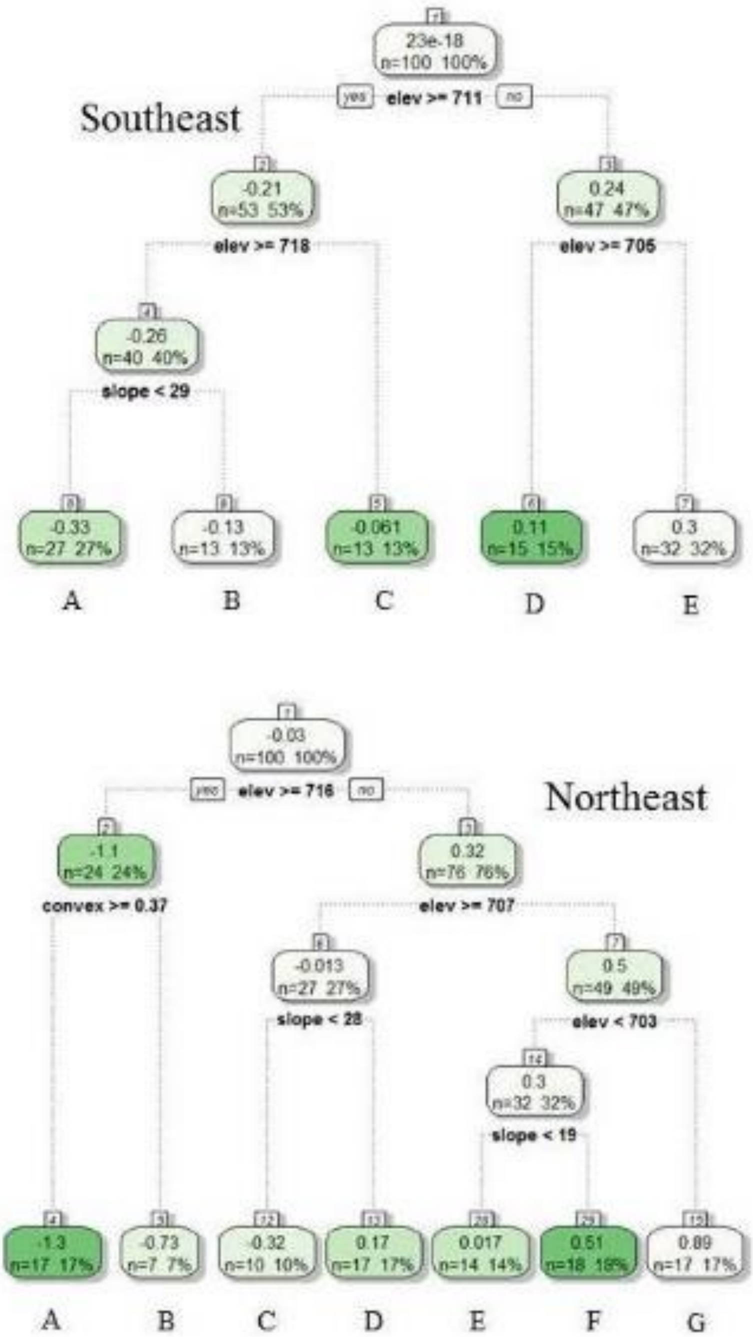


Fig. S.4. Habitats types of the two study areas within 2-ha permanent plots in Atlantic forest, Minas Gerais, Brazil. According to the multivariate regression tree, the patches were divided into of the following habitats: i) High plateau (Hp); ii) intermediate plateau (Ip); iii) low plateau (Lp); iv) high valley (Hv); v) low valley (Lv); vi) i) intermediate low valley (Iv), and ii) a transition area between high valley and low plateau (Tpv). (Rodrigues, eta al., 2020).

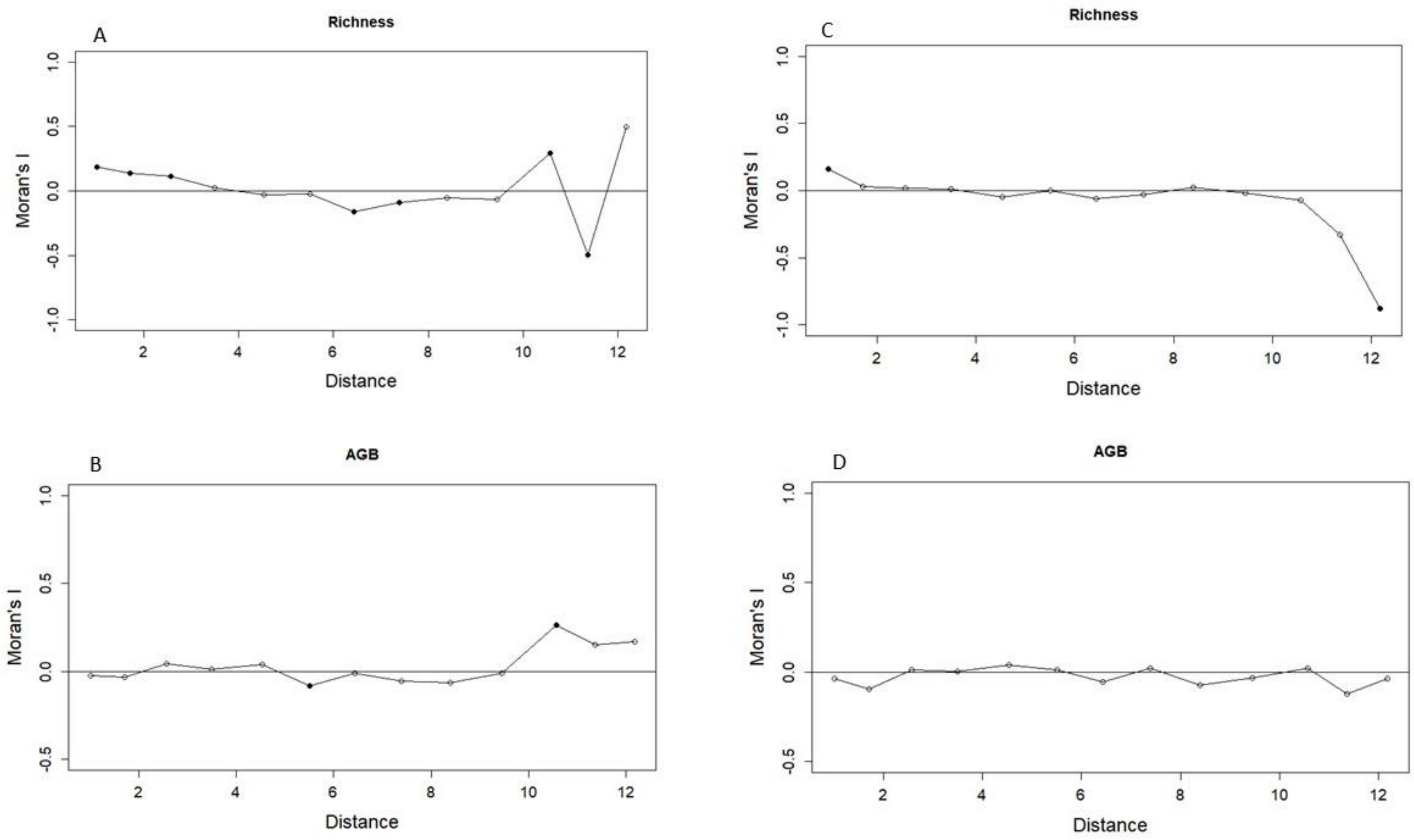


Fig. S.5. Moran's I spatial correlograms to estimate the spatial autocorrelation between the subplots of the northeastern (A and B) and southeastern (C and D) patches. The distances correspond to spatial distance in meters between subplots. The values oscillating along the zero values means absence of autocorrelation.

CHAPTER 3

Carbon and biodiversity cobenefits of second-growth tropical forest: the role of leaf phenology

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Rodrigues, A.C., Silla, F., Villa, P.M., Meira-Neto, J.A.A., Gomes, L.P., Neri, A.V. Carbon and biodiversity cobenefits of second-growth tropical forest: the role of leaf phenology (2022).

ABSTRACT

Second-growth tropical forests offer important carbon and biodiversity cobenefits, and comprise different functional types of tree species. For example, leaf deciduousness is an important functional trait that can contribute to seasonal and spatial changes in carbon balance. In this context, we investigated the distribution pattern of carbon stock, species richness, and functional dominance among trees with differing leaf phenology (evergreen, semideciduous and deciduous) as well as the carbon and biodiversity cobenefits of tree communities in contrasting topographical conditions in a second-growth tropical Atlantic forest. We studied 14 plots established in the forest with contrasting topographical conditions. We found that evergreen species showed higher richness, while the deciduous species had a greater contribution to aboveground carbon stock. Thus, leaf phenology can affect the relationships between species richness and aboveground carbon stock. For example, deciduous species are key to maintaining higher carbon stock with smaller numbers of species, while evergreen species are important to maintain a higher species richness. Thus, leaf phenology group's distribution could be responsible for important cobenefits (i.e. positive aboveground carbon stock and species richness relationship) in tropical forests. Therefore, this study showed a relevant result for conservation and management of tropical forest, which evidences the relative contribution of leaf phenology groups in the carbon and biodiversity cobenefits along topographic gradient and can allow us to select species for better management, conservation, and restoration of tropical forests.

Keywords: aboveground carbon stock, Atlantic forest, ecosystem services, functional composition, leaf deciduousness, species richness

INTRODUCTION

Second-growth forests (SGFs) are important reservoirs of biodiversity and provide multiple ecosystem services, such as global carbon uptake and stock (Chazdon et al., 2016; Rozendaal et al., 2019). Based on the carbon and biodiversity cobenefits approach, SGFs can promote a positive relationship between carbon stock recovery and tree species richness (i.e., cobenefits) concerning old-growth forest (Matos et al., 2020; Osuri et al., 2020; Villa et al., 2020). In this context, Brazilian Atlantic Forest is a hotspot of biodiversity and one of the most species-rich and threatened biomes in the world (Scarano and Ceotto, 2015). These forests are found mainly as SGFs and constitute priority areas where carbon and biodiversity cobenefits can occur due to high carbon storage capacity and high biodiversity (Matos et al., 2020; Osuri et al., 2020). The Atlantic Forest exhibits many patches of forest fragments with different tree functional and taxonomic composition (Magnago et al., 2014; Maia et al., 2020). Further, these forests differ considerably based on leaf phenology, such as deciduous, semideciduous and evergreen forests due to the climatic gradient along the Brazilian coast (Maia et al., 2020; Veloso, 1991). Moreover, different tree functional types based on leaf phenology can occur even within a single forest type (Maia et al., 2020; Singh and Kushwaha, 2016). These variations in leaf deciduousness amongst tree species play a significant role in forest ecosystem productivity and carbon stock capacity (Maia et al., 2020; Way and Montgomery, 2015). Thus, leaf deciduousness is an important functional trait in tropical forests that may contribute to the seasonal and spatial changes in the local and global carbon balance (Bohlman, 2010; Jolly and Running, 2004; Maia et al., 2020; Malhi et al., 2002).

The leaf functional traits based on leaf deciduousness are related to the plant's carbon and water economy under different water availability conditions (Aguirre-Gutiérrez et al., 2019). Furthermore, leaf deciduousness is determined by duration of the dry period, which selects species showing adaptations associated with avoidance and resistance to water stress (Álvarez-

Yépiz et al., 2017; Lusk et al., 2003; Pringle et al., 2011). Broad-leaved evergreen species have a resource conservation strategy to extend their photosynthetic activity beyond the rainy season with leaf traits characterized by low specific leaf area (SLA), dense mesophyll layer, and cells with thick cell walls, maximizing water efficiency use and avoiding wilt under drought conditions (Aguirre-Gutiérrez et al., 2019; González-M. et al., 2021; Poorter et al., 2009; Pringle et al., 2011). On the other hand, semideciduous and deciduous species present a resource acquisition strategy to maximize carbon gain in the short period of water availability, with leaf traits characterized by high specific leaf area (SLA), high water content and high N:C ratios (Lusk et al., 2003; Pringle et al. 2011; Álvarez-Yépiz et al. 2017). Additionally, evergreen and semideciduous species are mostly confined to moist microsites and tend to dominate in the more humid lowland sites (Méndez-Alonzo et al., 2013). In contrast, deciduous species have adaptations to tolerate low soil water availability during the dry season (Singh and Kushwaha, 2016) and are predominantly distributed in upland forests (Méndez-Alonzo et al., 2013). This reflects high sensitivity of trees to small changes in habitats and micro-site variations caused by topography (Singh and Kushwaha, 2016). Thus, factors such as terrain topography may be related to the species distribution and their degree of deciduousness because topographical soil water content gradients co-vary shaping the distribution of plant functional types (Alvarez-Yepiz et al., 2014; Kitajima and Poorter 2008). However, there are a lack of studies that address the functional differentiation between topographic gradients and the leaf phenology types species and carbon stock, especially in the Atlantic Forest.

Functional composition can affect ecosystem functions due to the relative importance of functional traits of tree communities in tropical forests (Lohbeck et al., 2015; Phillips et al., 2019). In this sense, there has been increasing evidence that functional dominance strongly affects AGB in tropical forests (Lohbeck et al., 2015; Prado-Junior et al., 2016; Rodrigues et al., 2022). The community weighted mean (CWM) is an independent functional diversity metric that has been used to test the effects of variability of functional traits within a community on aboveground biomass (AGB) (Ali et al., 2017; Lohbeck et al., 2015). CWM quantifies the value of the dominant functional trait weighted by the relative abundances of species in a community (Díaz et al., 2007) and it is important to test the "mass ratio hypothesis" postulating that ecosystem processes are primarily determined by the functional traits of the dominant species in a community (Grime, 1998). Further, the relationship between AGB and CWM of the functional traits of trees may be affected by environmental factors (Poorter et al., 2017; van der Sande et al., 2017; Villa et al., 2020), such as topography conditions (Rodrigues et al., 2022; van der Sande et al., 2017).

Increases in atmospheric CO_2, temperatures, frequency and duration of droughts are expected to affect ecosystem functioning through physiological plant trait responses and forest loss in the coming decades (Hubau et al., 2020; Li et al., 2018; Mitchard, 2018). Understanding how and why the carbon-biodiversity relationship differs between contrasting leaf phenology groups is critical to identifying key species to conserve carbon and biodiversity cobenefits and multiple ecosystem services under climate change (Poulsen et al., 2020; Watson et al., 2018). This cobenefits approach is crucial under the global challenge to restore degraded forests, conserve and enhance forest carbon stocks and biodiversity (Matos et al., 2020). Understanding the effect of local environmental conditions, such as topography and vegetation type, on carbon and biodiversity cobenefits would provide important insights since most information is derived from global-and regional-scale (Deere et al., 2018).

We investigated the distribution pattern of carbon stock, species richness, and functional dominance among leaf phenology groups (i.e., evergreen, semideciduous and deciduous species) as well as the carbon and biodiversity cobenefits, of tree communities in contrasting topographical conditions in a second-growth tropical Atlantic Forest. Thus, we addressed the following research questions: 1) How does tree species richness and aboveground carbon stock change among leaf phenology groups in contrasting topographical conditions? 2) Does functional composition of leaf phenology groups, assessed using the CWM metric, explain differences in aboveground carbon stock at plot level? 3) What are the cobenefits between aboveground carbon stock and tree species richness and the relative contribution of leaf phenology groups? Futher, we hypothesized that topographic conditions shape differences in species richness and aboveground carbon stock between leaf phenology groups, as well as the carbon-biodiversity cobenefits within the tree communities. We predicted the highest values of these stand-forest attributes under higher topographical heterogeneity, which is an indicator of niche partitioning and resources availability (e.g., Brown et al., 2013; Liu et al., 2018). Furthermore, we expected that higher values of functional traits related to carbon stock will explain the dominance of leaf phenology groups, such as deciduous tree species. Finally, we emphasize that answering these questions related to carbon and biodiversity cobenefits can allow us to select species for better management, conservation, and restoration of tropical forests.

MATERIAL AND METHODS

Study area, land-use history and vegetation sampling

We studied a Semideciduous Seasonal Atlantic Forest fragment in Minas Gerais state, Southeastern Brazil (20°45′14″S, 42°45′53″W) of approximately 75 ha that was used for coffee cultivation until 1926 and since then is in natural regeneration. Brazilian Atlantic forest is a hotspot of biodiversity and one of the most species-rich and threatened biomes in the world (Scarano and Ceotto, 2015). These forests are found mainly as second-growth forests in small remnant fragments that represent less than 12% of the original forest (Scarano and Ceotto, 2015). Historical land use has generated fragments of remnant forest surrounded by matrices of agriculture, pastures, monocultures, or urban areas (Scarano and Ceotto, 2015).

According to the Köppen-Geiger classification, the study area climate is tropical altitude (Cw_b), with a dry season between May and September, and wet season occurring between December and March (Alvares et al., 2013). The mean annual temperature is 21°C and the mean annual precipitation is 1,270 mm, with the highest volumes of rain concentrated from October to March (140 mm to 200 mm per month) and often low values of accumulated precipitation from April to August (50 mm per month) (Avila-Diaz et al., 2020; UFV, 2020). The study area is located between 620 and 820 m elevation and the relief vary from strongly undulating to mountainous and has marked differences in the spatial distribution of topographical variables, mainly elevation and convexity (Rodrigues et al., 2020, 2019). The site is characterized by the presence of two dominant soil classes: a red-yellow alsicose latosol covers hilltops and mountainsides; while a cambic yellow-red podzolic dominates the upper fluvial terraces (Ferreira-Júnior et al., 2007).

We studied 14 plots of 20 m x 40 m established in the forest with contrasting topographical conditions, the Southeastern and Northeastern areas (Fig. 1). The Southeastern area was less topographically heterogeneous and the Northeastern area was more topographically heterogeneous (Fig. S.1, Appendix/from Electronic Supplement Material, ESM hereafter). In each plot, all trees with diameters at breast height (DBH) ≥ 5 cm were inventoried (height and diameter measurement) and botanically identified to the species level in both patches. All individuals were identified using specialized literature, through consultation to herbarium, or by taxonomists. The Angiosperm Phylogeny Group IV (APG IV, 2016) was used for taxon classification.

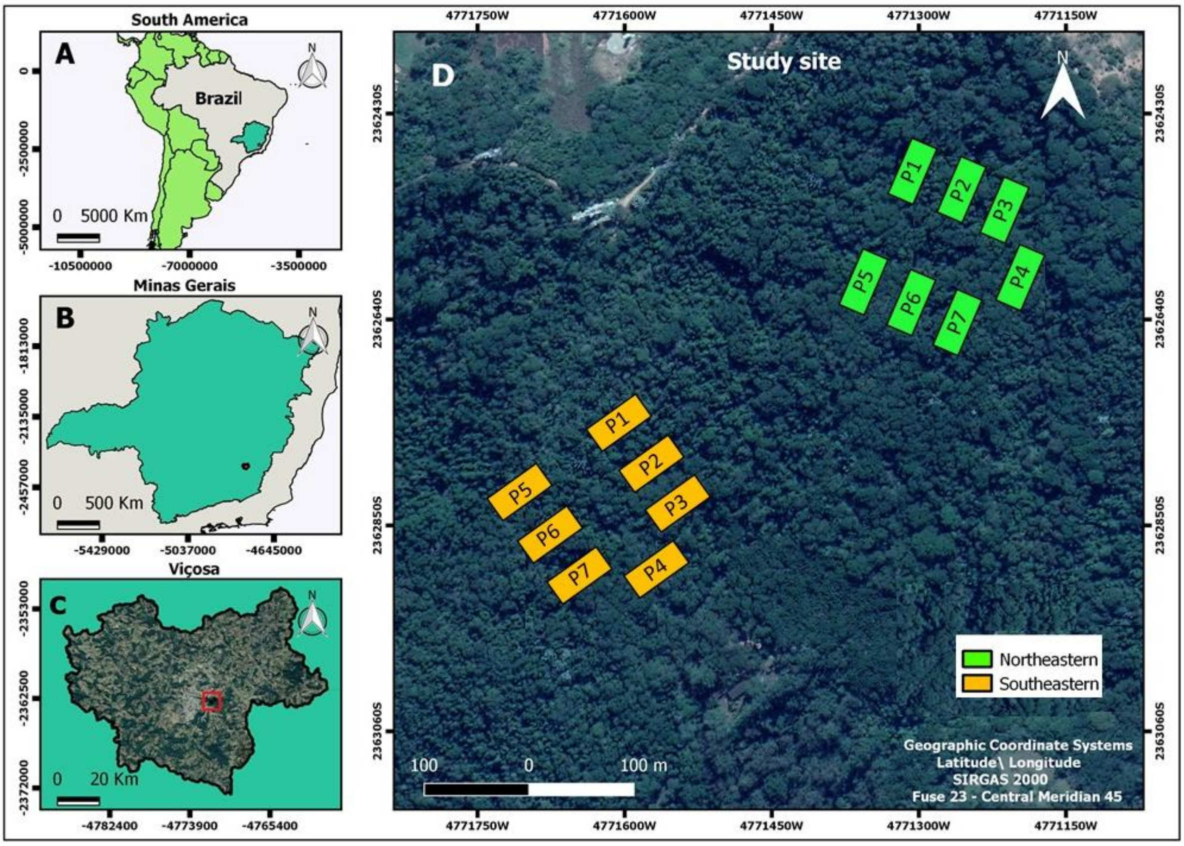


Fig. 1. Location of the study area in relation to South America (a), the Minas Gerais State, Brazil (b), and the forest fragment within the campus of the Federal University of Viçosa (UFV), Viçosa municipality, Minas Gerais state, southeastern Brazil (c). Location of the sample plots within the forest fragment (d).

Estimation of aboveground carbon (AGC)

The AGC stocks are widely estimated from the allometric equations for forest biomass. Generally, the carbon concentration of the different organs of a tree is assumed approximately 50% of the dry biomass (Chave et al., 2009). In this study, aboveground biomass (AGB) of trees for each stem sampled was calculated from a combination of variables using the general allometric equation (Eq.1) proposed by Chave et al. (2014) based on tree diameter at breast height (DBH, cm), height (H, meters) and species wood density (ρ, cm^{-3}). We used data from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009) to obtain each species' wood density (i.e., Jucker et al. 2018; Ali et al. 2019) and measure the tree diameter and height in the field.

$$AGB = 0.0673\ (\rho\ \times DBH^2 \times\ H)^{0.976} \qquad \text{Eq. 1}$$

The total AGB per patch was the sum of the AGBs of all trees having DBH ≥ 5 cm, which was then converted to megagrams per hectare (Mg ha^{-1}) (Ali et al. 2017). Species-level biomass was calculated as the sum of the biomass of all stems from a species. Estimation of aboveground biomass was performed using the 'BIOMASS' package in R (Réjou-Méchain et al., 2017).

Functional traits and leaf phenology groups classification

We selected the following mean functional traits related to carbon stock capacity in tropical forest: wood density (WD) and maximum tree height (H) (Matos et al., 2020; Poorter et al., 2019). Further, we classified tree species into three categories groups with respect to the leaf phenology (i.e. deciduous, semideciduous, and evergreen species) according to field observations and literature. These functional traits are related to the seasonal changes in the carbon balance in different spatial scales (Malhi et al., 2002).

Quantification of the community-weighted mean of stem traits

We calculated community-weighted mean (CWM) metrics based on wood density and height and we separated them by functional categories groups: i) evergreen, ii) semideciduous and iii) deciduous species as the mean value of the trait in the community, weighting by species' relative abundance (Garnier et al., 2004). We used the relative abundance of species rather than the basal area because it prevents circular redundancy derived from the use of DBH to calculate functional traits and aboveground biomass (Ali et al., 2017). We evaluated community-weighted mean using the following equation:

$$\mathrm{CWM}\chi = \sum_{i=1}^{S}(\mathrm{pi} * \mathrm{ti}) \qquad \text{Eq. 2}$$

where CWMχ is the CWM for trait χ in each plot, s is the number of species in each plot, *pi* is the relative abundance of the *i*th species in each plot and *ti* is the trait value for the *i*th species. The CWM indices were calculated using the 'vegan' package (Oksanen et al. 2018).

Data analysis

We estimated the species richness and carbon distribution divided into the following groups: evergreen, semideciduous and deciduous in each plot. We assessed differences in species richness in each area and functional group using sampled-based rarefaction and extrapolation curves, which were constructed with the first Hill numbers (Chao et al., 2014). Extrapolations were based on presence/absence data (Hill number of order q= 0 with 100 replicate bootstrapping runs to estimate 95% confidence intervals), up to twice the sample size (Colwell et al., 2012), using the 'iNEXT' package (Hsieh et al., 2016). Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al., 2012).

The taxonomic and structural attributes (richness and AGC) and topographic variables (elevation, slope and convexity) by leaf phenology group were summarized through principal components analysis (PCA) on the correlation matrix, using the 'FactoMineR' package

(Husson et al. 2018). We applied Hellinger transformation methods on abundance data to improve the performance of the Euclidean distance using the decostand function in the 'vegan' package (Oksanen et al., 2018). The Euclidean distance of the transformed data was then equivalent to the Hellinger distance, which improves the representation between different communities (Legendre and Borcard, 2018). Finally, we corroborated the correlation between all variables and the PCA1 and PCA2 axes because they explain the higher data variability (Fig. S2 from SM).

We constructed linear mixed-effect models (LMMs, with random and fixed effects) to test the cobenefits between AGC and leaf phenology group (evergreen, semideciduous and deciduous species) on species richness at community level (e.g. Matos et al. 2020; Coelho et al. 2022). Species richness was the response variable and predictors with fixed effects were AGC (continuous explanatory variable) and leaf phenology group as discrete variable (three levels, evergreen, semideciduous and deciduous species). In all models tested, the plots were used as a random effect (1 | plots). We tested the distributions of residuals to select the most suitable distribution and link function, i.e., Gaussian error distribution by the Q-Q graph (Fig. S3 from SM) and Shapiro–Wilk test (Crawley, 2012). All models were calculated in R using the packages 'lme4', 'nlme', and 'MASS' (Bates et al., 2019; Pinheiro and Bates 2017; Ripley, 2017).

Finally, we tested whether functional trait dominance of leaf phenology groups explain carbon storage comparing the mean AGC between Southeastern and the Northeastern patches and leaf phenology groups and CWM of trait values (WD and H) between categorical functional groups (evergreen, semideciduous and deciduous species) performing Wilcoxon-tests (non-normally distributed data). We estimated the relative proportion of each functional group in relation to the total number of species in the community per area based on the definitions adopted by Bastin et al. (2015) and Fauset et al. (2015). Data were tested for normal distribution with the Shapiro-Wilk test and a Q-Q plot (Crawley, 2012). All analyses were performed in R (R core team, 2019).

RESULTS

Gradient analysis

The first two axes of PCA explained 55.5 % of the variation in species richness and AGC between leaf phenology groups and topographical variables (Fig. 2). The first axis (PCA1) explained 31.3% of the variation and was correlated positively with propotion of specien in each group and richness (Fig S1 SM). The second axis (PCA2) explained 24.2% of the variation and was correlated positively with topographical variables and AGB. The richness presented a high correlation with PCA2 and AGC with PCA1, showing a marked difference between the leaf phenology groups responsible for high richness (evergreen species) and high carbon stock (deciduous species).

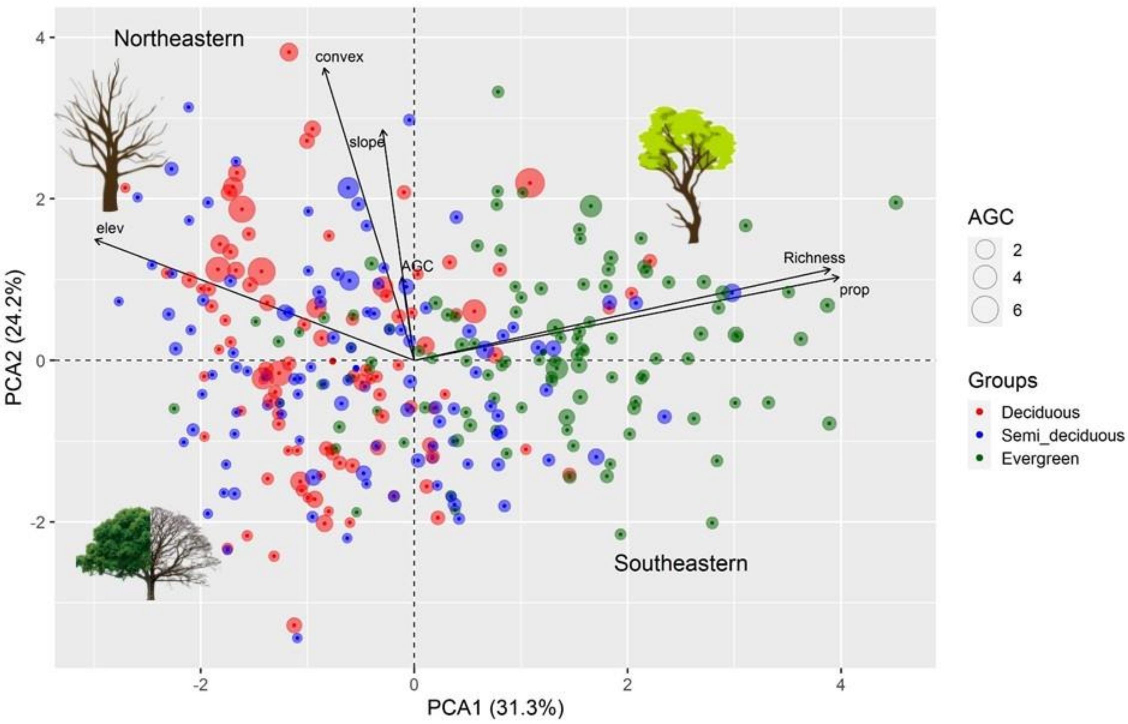


Fig 2. Principal Component Analysis (PCA) of the topographic variables (elevation, slope and convexity), aboveground carbon stock (AGC, Mg ha^{-1} by leaf functional group) distribution

and species richness of different leaf phenology groups – Evergreen, Semideciduous and Deciduous species.

Species richness and functional groups

Evergreen species richness was higher in relation to other leaf phenology groups in both areas, using the individual-based rarefaction approach. In the Northeastern area differences were observed between evergreen and deciduous species, while in the Southeastern area a lower proportion of deciduous species was found in relation to the other groups using the individual-based rarefaction approach (Fig. 3).

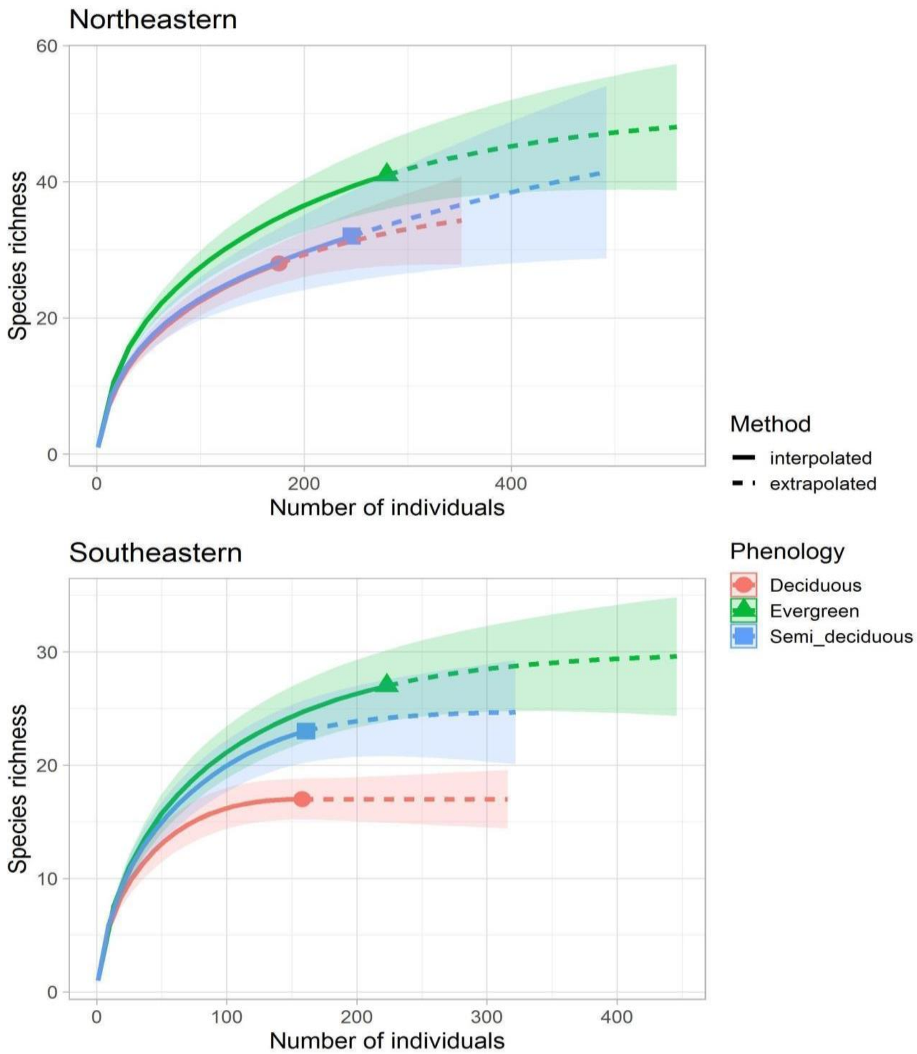


Fig 3. Rarefaction (solid lines) and extrapolation curves (dashed lines) of evergreen, semideciduous and deciduous tree species based on the first Hill numbers (q = 0, species richness) in the Northeastern and Southeastern areas.

Differences in AGC

In the Southeastern area we found significant differences in aboveground carbon stock (AGC) between deciduous, evergreen, and semideciduous species with greatest aboveground carbon stock values observed in deciduous species in both areas. However, in the Northeastern area we detected differences between evergreen and deciduous species only (Fig. 4). The CWM values of wood density (WD) and maximum height (H) of the deciduous species showed significant differences only in the Southeastern area (Fig 6).

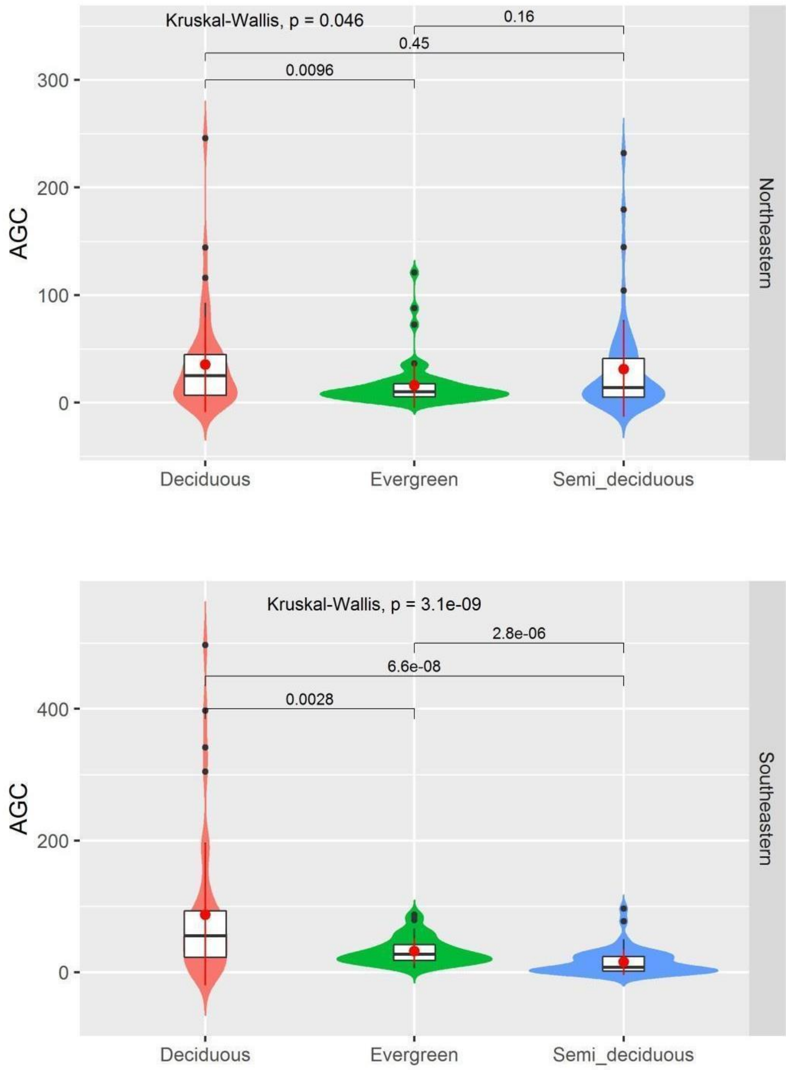


Fig 4. Proportional aboveground carbon stock distribution and species richness of leaf phenology groups in the Northeastern and Southeastern areas. Differences between leaf phenology groups was observed (Dunn's test, $P < 0.05$).

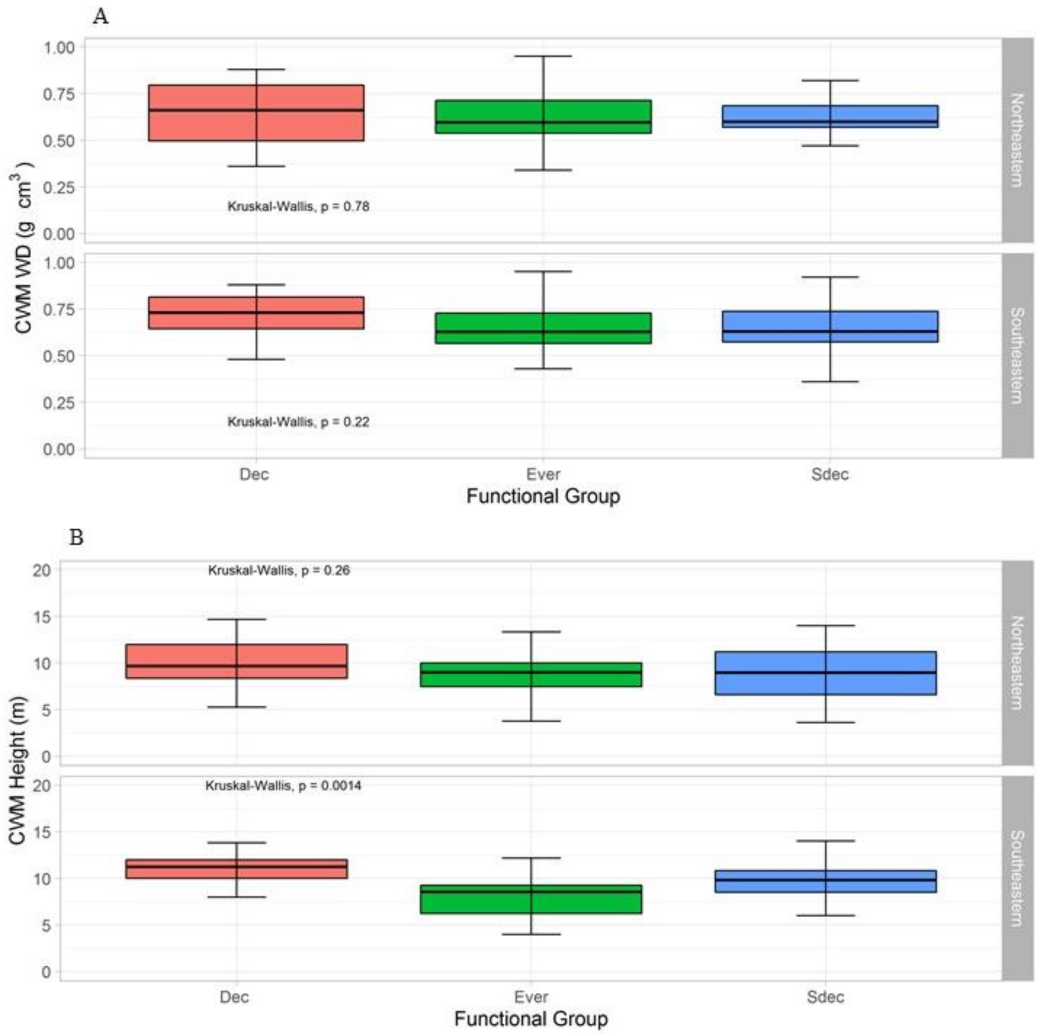


Fig 6. The relative importance of community-weighted mean (CWM) of the functional traits wood density – WD (A) and maximum height (B) of evergreen, semideciduous and deciduous species per area.

Species richness and AGC distribution

We observed that the proportional relation of species maintained the same pattern between leaf phenology groups, that is, we found that in both areas evergreen species contributed the most to species richness, accounting for 40.8% and 40.6% of the total richness in the Northeastern and Southeastern area, respectively, followed by semideciduous species (31,7% and 34,4%) and deciduous species (27,6% and 25%) (Fig. 5 A, B).

In contrast, AGC has an opposite proportional relationship, with the largest proportion of carbon stored in deciduous species, followed by evergreen and semideciduous species. Thus, the proportion of carbon stock among leaf phenology groups is variable among the topographic areas studied. When we analyze AGC distribution between the same leaf phenology group, but in different areas, the deciduous species stored the most carbon in both, accounting for 49,6% and 62,7% of the total of AGC in the Northeastern and Southeastern area, respectively. Followed by semideciduous species in the Northeastern area (account 31.5%) and evergreen species in the Southeastern area (account 25,1%) (Fig. 5 C, D).

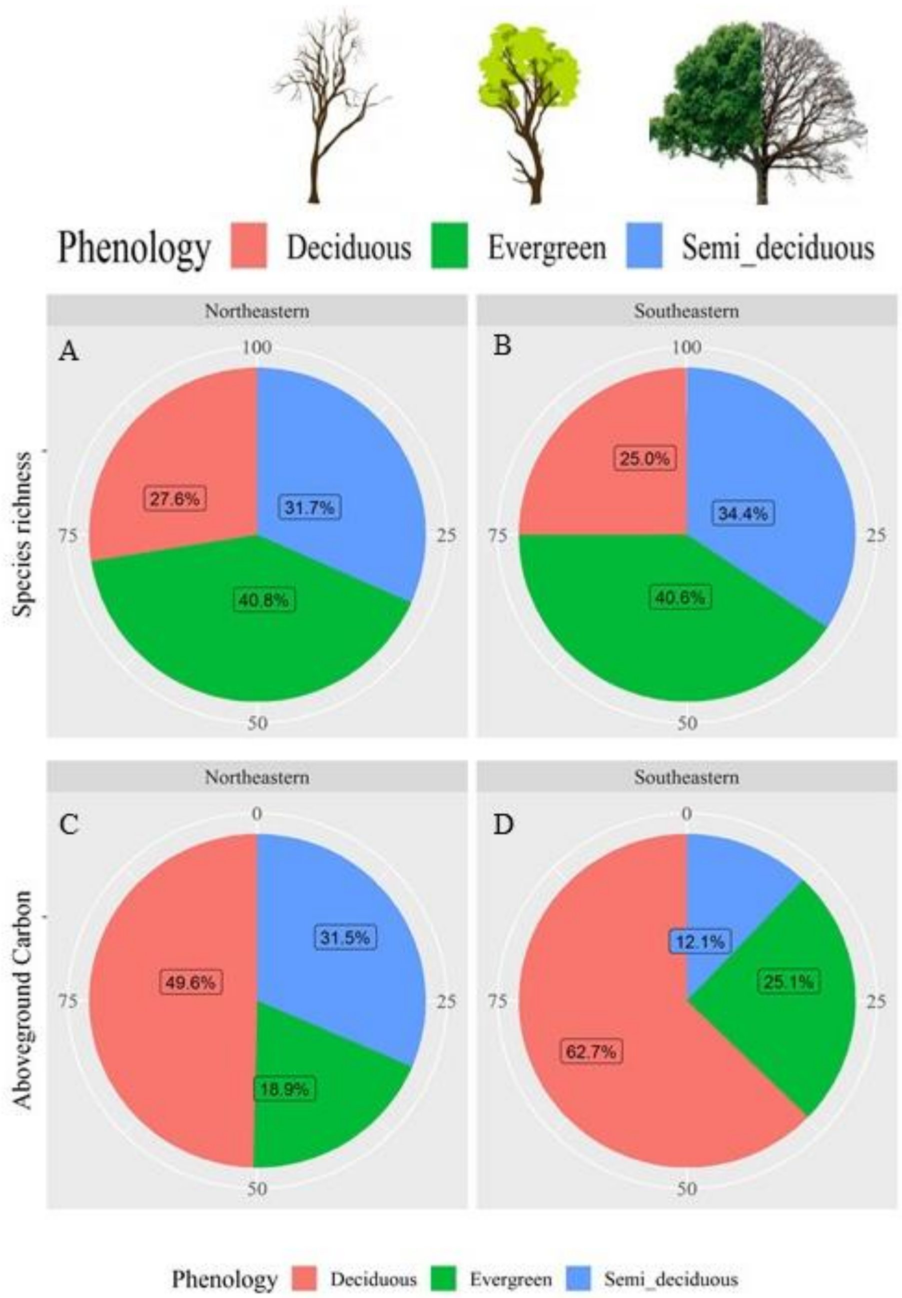


Fig 5. Relative proportion of aboveground carbon stock (AGC) and species richness in each functional group based on the total number of tree species in the community per area.

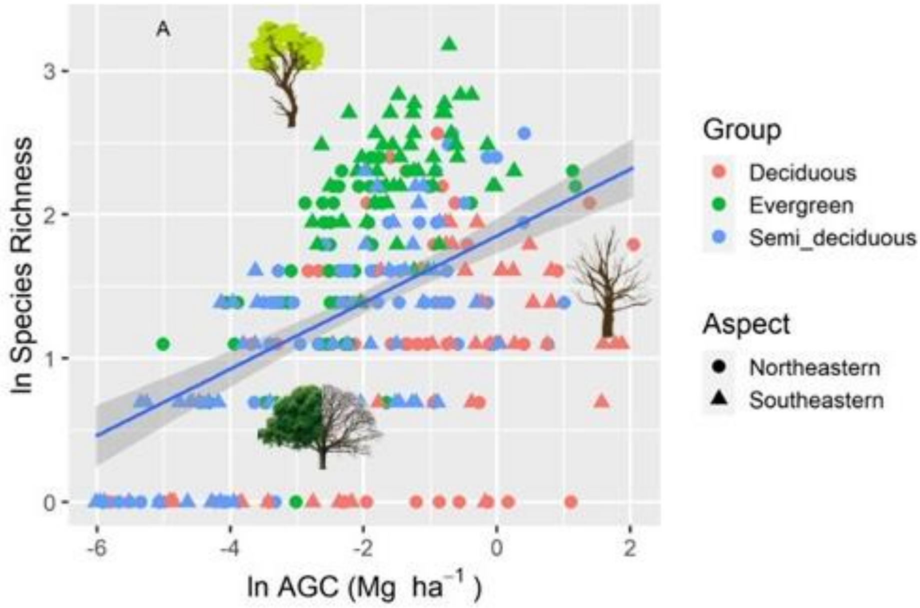
Carbon stock-tree species richness cobenefits

Our tested models showed a significant positive relationship between aboveground carbon stock and species richness (Est. = 0.18, t = 5.7, $p < 0.001$, $R^2 = 0.55$) (Table 1, Fig. 7). Thus, the variation in aboveground carbon stock had the strongest positive effect on species richness of evergreen (Est. = 1.39, t = 11.00, p <0.001), and semideciduous trees (Est. = 0.65, t = 5.45, p <0.001). Furthermore, when analyzing the interaction between predictors, it is observed that evergreen (Est. = 1.18, t = 3.21, p <0.001) and semideciduous trees (Est. = 0.11, z = 2.42, p <0.016) are responsible for a strong and positive relationship between AGC and species richness. However, no effects of deciduous trees were observed (Table 1).

Table 1 Main candidate of different linear mixed-effects models predicting the species richness with Gaussian error distribution (linear mixed effects model - lme). Predictors are AGC and evergreen, semideciduous and deciduous groups. The averaged parameter estimates (standardized regression coefficients) of model predictors are indicated.

Response variable: Richness

Randon effects (variance)	Predictors	Estimate	t	df	P
0.53	(Intercept)	1.26	18.3	16.99	0.001
	~AGC	0.18	5.7	292.75	0.001
	~Evergreen	1.39	11.00	272.26	0.001
	~Semidecidous	0.65	5.45	267.74	0.001
	~AGC:Evergreen	0.18	3.21	270.71	0.001
	~AGC:Semidecidous	0.11	2.42	206.60	0.016



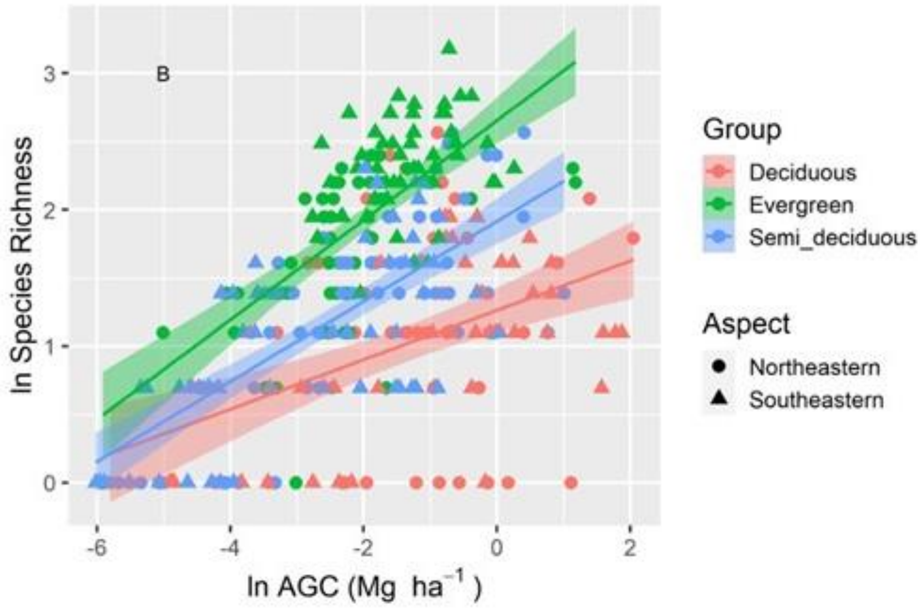


Fig 7. Cobenefits between aboveground carbon stock and species richness in second-growth Atlantic Forest. Solid lines represent fitted (predicted) values of the models, and the shaded polygons the 95 % associated with the modeled predictions. Leaf phenology groups distribution are indicated.

DISCUSSION

Our study tested the hypothesis that contrasting topographicaly-dependent conditions induce changes in species richness and aboveground carbon stock in relation to the distribution of leaf phenology groups of tree communities in a secondary tropical forest. We observe that evergreen functional group shows higher species richness, meanwhile the deciduous functional group has a greater contribution to aboveground carbon stock. Furthermore, the functional composition (estimated based on CWM metric) shows that the deciduous functional group has the highest values of height and wood density (hard functional traits), which probably determines a high aboveground carbon stock in this group. This study, showed a relevant result for conservation and management of tropical forest, which evidences the relative contribution of leaf phenology groups (i.e., evergreen, deciduous and semideciduos tree species) in the carbon and biodiversity cobenefits along topographic gradient. In this way, we tested the prediction that the functional groups composition based on leaf phenology can affect the relationships between species richness and aboveground carbon stock. For example, the results highlight that deciduous functional species are key to maintaining higher carbon stock with smaller numbers of species; meanwhile evergreen function group species are important to maintain a higher species richness at local scale; however, this group showed lower carbon stock. This coexistence might arise due to the different phenological strategies, yielding comparable net carbon gain in the long term despite contrasting phenology (Vico et al., 2017). Thus, we presumed that the phenological functional groups distribution and variability can be responsible for the cobenefits (positive aboveground carbon stock and species richness relationship) in tropical forests

The results show a positive relationship between AGC and species richness along the topographic gradient, highlighting the potential of this tropical secondary forest to conserve and maintain diversity of tree species and ecosystem functioning, simultaneously. Specifically, the models tested in this study show that evergreen species, followed by semi-deciduous contribute most to increasing species richness while deciduous species maintaining an increase in aboveground carbon stock. Previous studies have demonstrated this positive relationship in secondary tropical forests (Coelho et al., 2022; Liang et al., 2016; Matos et al., 2020; Osuri et al., 2020), using different dimensions of diversity, i.e., taxonomical, phylogenetic and functional (Matos et al., 2020). Currently, this cobenefits relationship has been using functional groups (i.e., successional categories, dispersal syndromes and fruit types), highlighting the high contribution of tree species with animal-dispersed seed in the increase of carbon (Coelho et al., 2022). However, studies demonstrating the relative contribution of leaf functional groups (or leaf deciduousness) over cobenefits are currently still unexplored.

In tropical forests, leaf deciduousness is an adaptation that results from the integrated effect of environmental conditions, such as drought, temperature and soil moisture and tree traits (Singh and Kushwaha, 2016). Phenological strategy is favored depending on the long-term balance of carbon costs and gains it imposes because of the rotation of wet and dry seasons and the unpredictability of rainfall events (Menezes-Silva et al., 2019). Thus, reductions in the length of the wet season or precipitation, as predicted under climate change scenarios, should promote a shift towards more drought-deciduous communities (Menezes-Silva et al., 2019; Vico et al., 2017), probably affecting the balance of diversity and carbon stock.

Our trait-based approach directly related to the acquisition or conservation of the resources (i.e., AGC) strategies (i.e., phenological functional groups), and functional composition (CWM of wood density and height) has significant potential for management and conservation in the current and future climate change scenarios (O'Sullivan et al., 2020). Thus, the response of tropical forest diversity and carbon stock can be a critical component of global climate adaptation and mitigation. It will assist selecting key tree species based on phenological groups to increase and maintain aboveground carbon stock. However, climate change can induce an important shift in the taxonomic and functional composition of tree communities (e.g., Didion-Gency et al., 2021; González-M. et al., 2021; Menezes-Silva et al., 2019), and consequently on forest ecosystem carbon stock (Maia et al., 2020; Menezes-Silva et al., 2019; Page et al., 2022). In this context, the understanding of current and future patterns of leaf functional groups can be an important support in the decision of adaptation strategies.

Evergreen species are probably more vulnerable and deciduous ones more resistant according to their physiological functional traits and the increase in frequency, intensity, and duration of extreme weather events can trigger massive tree mortality and affect species recruitment (Menezes-Silva et al., 2019). The denser-wood deciduous species may present resource-conservative strategies to increase and maintain the aboveground carbon stock distributed in a smaller number of species with hard functional traits, such as height and wood density (Cielo-Filho, 2021; Poorter and Markesteijn, 2008; Prado-Junior et al., 2016). Denser-wood deciduous species may show higher tree survival due to the higher carbon allocation per unit of wood produced, which can result in thicker wood and, consequently greater resistance to drought-induced cavitation of vessels (Chave et al., 2009). However, the efficient water use of evergreen tree species may contribute to their higher relative abundance, which can be a functional advantage against deciduous tree species in water-limited environments (Álvarez-Yépiz et al., 2017). Thus, we highlight the importance of evaluating the individual responses of tree species and phenological functional groups to different climate change scenarios, which will prevent the loss of cobenefits and maintain a positive relationship between species richness and carbon stock. Assuming a negative scenario of the evergreen species vulnerability (or loss of species) to increased drought and temperature on a global scale, it is necessary to consider the potential of deciduous and semi-deciduous tree species to maintain species richness, resilience, and resistance of the tropical forest.

CONCLUSIONS

This research reveals that beyond the species richness on cobenefits the leaf phenological functional groups classification can be the main predictors that explains the aboveground carbon stock and species richness relationships. In addition, this study evidenced the contribution of evergreen functional group to richness and reveal that deciduous species highly contribute to carbon stock, highlighting an important carbon and biodiversity cobenefits of these functional groups. Moreover, this research showed that changes in phenological groups from denser-wood large deciduous species to softer-wood smaller evergreen promotes differences in functional composition and carbon stock along the topographical gradient. Thus, our results also suggest that changes in the functional composition will be mediated by the traits associated with each phenological strategy. The greatest contribution of our study was highlighting the importance of the different leaf functional group to carbon stock and biodiversity cobenefits. Evidencing that the deciduous species even if with low species number contribute significantly to above ground carbon stock. Finally, we highlight the importance of evaluating the individual responses of tree species and leaf functional groups in climate change scenarios, for decision making to maintain the species richness, resilience, and resistance of tropical forest species.

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Supplementary material

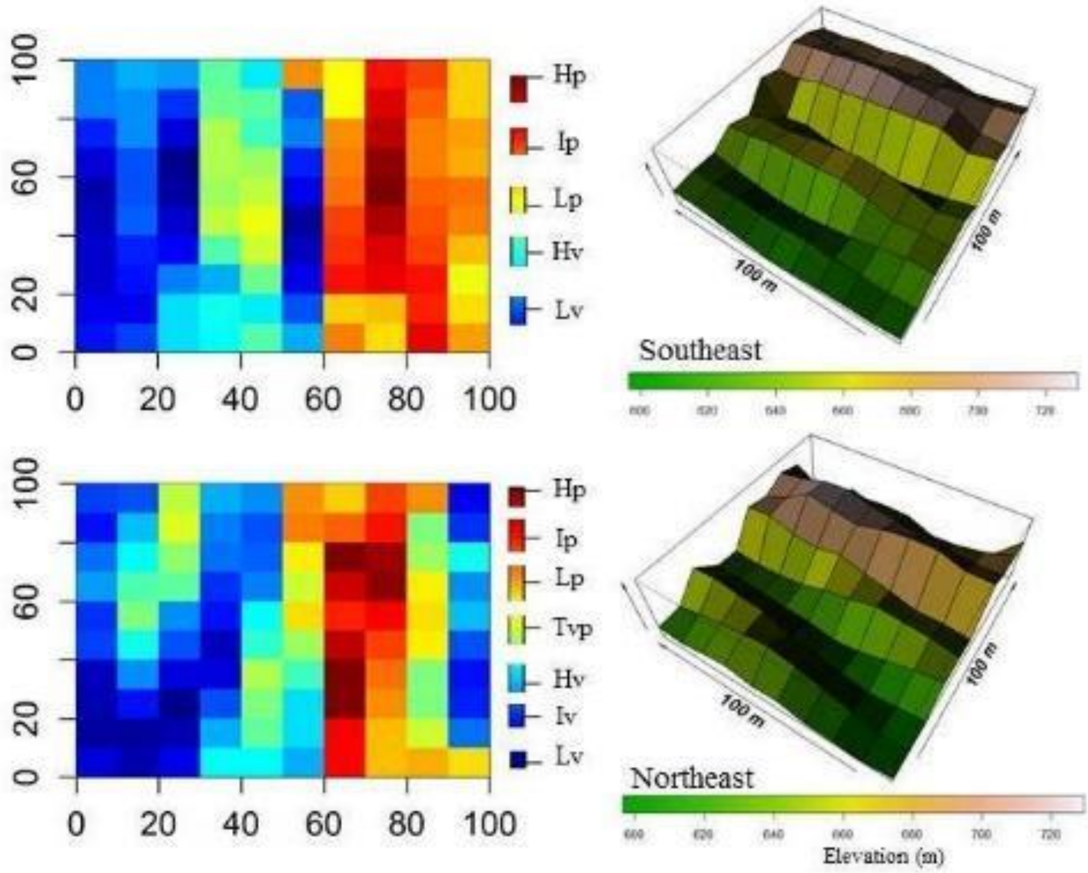

Fig. S.1. Habitats types (left) and topographic maps (right) of the two study areas within 2-ha permanent patches in Atlantic Forest, Minas Gerais, Brazil. According to the MRT, the patches were divided into of the following habitats: i) High plateau (Hp); ii) intermediate plateau (Ip); iii) low plateau (Lp); iv) high valley (Hv); v) low valley (Lv); vi) i) intermediate low valley (Iv), and ii) a transition area between high valley and low plateau (Tpv). (Rodrigues, et al., 2020).

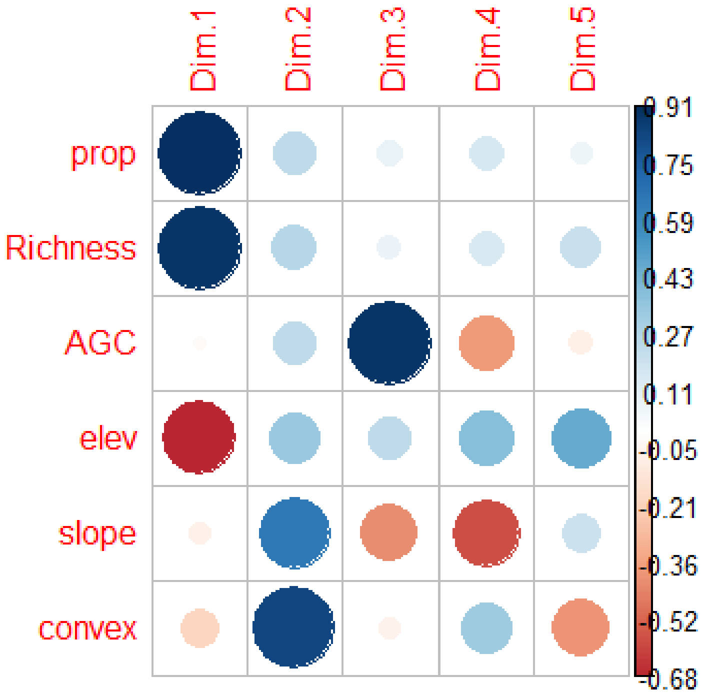

Fig. S.2. Significance levels are based on Spearman correlation coefficients between species richness, AGC and three topographical variables (elevation, slope and convexity) and principal components of PCA-from 14 plots of different areas by leaf phenology group.

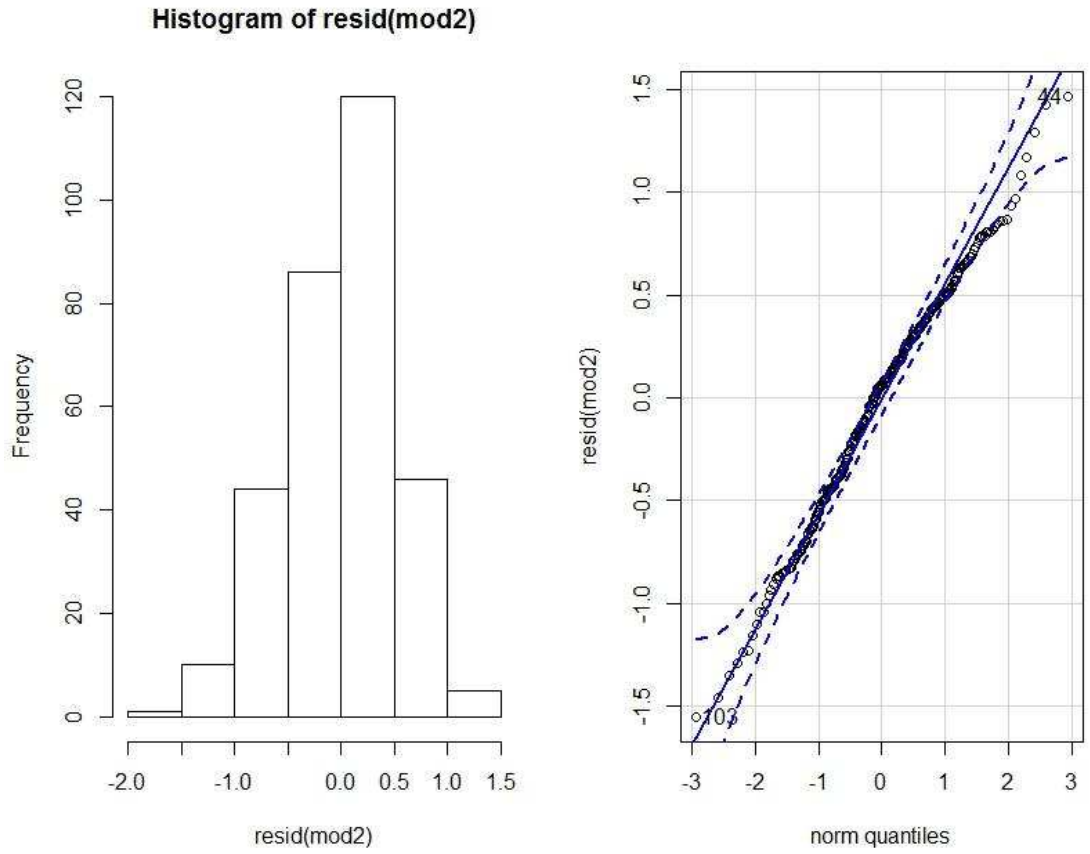

Fig. S3. Example to test the most suitable distribution and link function using histogram and Q-Q considering the bests models with AIC < 2.0 (i.e., model1 = Species richness ~AGC).

CHAPTER 4

Exploring the effects of abiotic drivers on the classification of leaf phenology groups in a tropical forest using machine learning

Abstract

The vegetation distribution is largely determined by the environmental drivers and stand age. Predicting future vegetation changes in response to abiotic drivers is crucial to identify and understand the patterns, processes in tropical forests. Different ecological and environmental researchers for model forest types and ecosystem services classification and distribution have used machine learning. Thus, in this study we employed different machine learning algorithms to predict the association of the abiotic factors and stand age for the classification of tree leaf phenology groups (evergreen, deciduous, and semideciduous) in an Atlantic tropical forest, southeast Brazil. Especially, we used machine learning models with the climate data (climatological water deficit, CWD), soil data (sum of basic exchangeable cations (SB) and exchangeable acidity potential (H + Al)) and topographic data (elevation, slope and convexity) during tropical late-secondary forest succession to predict the classification of functional leaf phenology groups. Among the performance machine learning-based classification algorithms analyzed, random forest classifier was the best algorithm model. Using random forest, it was observed that the most influential predictor in the classification of functional groups was topography and soil properties. Specifically, elevation shows a high explanatory contribution in the three functional groups followed by soil properties such as SB and HAL. Our results showed that topography, mainly elevation, is an important driver for leaf phenology group classification at the local scale in tropical forests. The prediction of functional groups classification can be the basis for the identification of key species to be used during ecological restoration projects under different topography and soil-depedent conditions on a local and fine scale.

Keywords: Tree classification, Random Forest, classification and regression tree, Support Vector Machines

1. Introduction

The vegetation distribution is largely determined by the environmental drivers such as soil, topography and climatic conditions (Poorter et al. 2017; Rozendaal et al. 2019). Additionally, forest stand age is an important driver related with forest succession (Mora et al. 2018; Ali et al. 2019). Thus, understanding the roles of these drivers in community assembly, ecosystem functioning and biodiversity patterns is a central focus in tropical forest ecology (Ali et al. 2018; Poorter et al. 2017; Rozendaal et al. 2019). Tropical forests harbor more than half of the global biodiversity and have influence on the mitigation of climate change while providing important ecosystem services and cobenefits (Matos, et al., 2020; Lewis et al. 2015). In this sense, predicting future vegetation changes in response to environmental drivers is crucial to identify and understand the patterns, processes and the main mechanisms underlying community assembly in structurally complex natural tropical forests (Beigaitė et al., 2021).

Several studies have shown that abiotic-related factors, such as climate, topography and soil properties can determine plant growth (Moeslund et al. 2013), species distribution (Toledo et al. 2012), changes in tree community composition (Rodrigues et al. 2019) and resource availability (e.g., soil nutrientes) at fine-scale (Rodrigues et al. 2021). Soil properties and topography (i.e., elevation, convexity, slope) can determine different habitats and promotes the differential use of resources by tree species at fine-scale (McEwan and Muller 2006; Brown et al. 2013, Chiang et al. 2016; Ali et al. 2018b) and therefore shape tree community assembly in tropical forest (Brown et al. 2013; Liu et al. 2014; Jucker et al. 2018). Especificaly, elevation is the main topographical factor that affects tree species communities and functional traits variability (Ali et al. 2019; Jucker et al. 2018; Rodrigues et al. 2021). Conversely, it is well understood that climatic factors (e.g., mean annual temperature and precipitation) influence species diversity and structure of the forests over a large scale (Jucker et al. 2018; Ali et al. 2019). In this context, it is understandable that topographic, climatic and edaphic factors determine the differentiation of trees in tropical forests (i.e., Wang et al. 2016; Guo et al. 2017), due to the heterogeneity of the available resources (Liu et al. 2014; Guo et al. 2017; Ali et al. 2018a, b, 2019; Rodrigues et al. 2019).

The Atlantic Forest in Brazil exhibiting different functional leaf phenology such as deciduous, semideciduous and evergreen trees (Singh and Kushwaha, 2016; Maia et al., 2020). The accurate characterisation of tree phenological groups distribution in these forest areas is important for forest management and forest research. The climatic water balance (CWD) strongly influences local moisture conditions (Holden et al 2019), affects the spatial distribution of plant functional types (Stephenson 1998), and is an important driver of ecosystem functioning (Hoylman et al 2019a). The climate and other environmental drivers can have significant effects on the structure of tropical forests (Poorter et al., 2017). For example, local variations in elevation and slope angle influence solar radiation, evapotranspiration and air temperature and interact with the available soil moisture derived from precipitation to determine latent and sensible heat partitioning (Hoylman, et al., 2021). Therefore, the spatial mosaic of drought stress on plants across complex terrain has been recognized in many studies as an effective control on vegetation distributions (Hoylman et al., 2018; Hoylman, et al., 2021). Therefore, tree communities are responding by adjusting the functional groups composition through functional traits based on the plant's life history, such as leaf phenology (Aguirre-Gutierrez et al., 2019). Tree communities that previously had more evergreen species, actually tend to have more deciduous species due climate change (Aguirre-Gutierrez et al., 2019). Thus, determining the factor driving the distribution of leaf functional groups in tree communities can be relevant for tropical forest management and conservation, mainly at a fine and local scale.

Machine learning techniques have become increasingly popular and have been used in different ecological and environmental researchers at multiple spatial scales (Scowen et al., 2021; Reichstein et al., 2019; Onishi et al. 2021; Beigaitė et al. 2022; Cetin et al. 2021). These algorithms have also been used to model forest types and ecosystem services classification and distribution (Chatterjee et al., 2016; Scowen et al., 2021; Beigaitė et al. 2022). Among machine learning approaches, support vector machines (SVMs), random forest (RF) (Onishi and Ise 2021) and classification and regression tree (CART) algorithm (Beigaitė et al., 2022) are important supervised learning that have been used for the classification of natural vegetation (i.e., Scowen et al., 2021; Beigaitė et al. 2022). SVMs is a non-parametric supervised machine learning algorithm that performs the classification process based on the statistical learning concept with adaptive computational learning (Ray and Mishra, 2016). RF, an especially popular example of a CART, is a non-parametric machine learning algorithm based on the bagging principle of decision tree classifiers (Breiman, 2001). The RF algorithm provides reliable classifications with the estimations acquired from an ensemble of CARTs (Le Louarn et al., 2017). CARTs are used in supervised classification to predict membership and to assess variable importance or for the selection of relevant predictor variables (Rositano et al., 2018; Silveira et al., 2019). As machine learning often allows the combination of continuous with categorical predictor variables (Cutler et al., 2007), its use allows the prediction of natural events with high degree of accuracy, generating robust predictions (Diedrichs et al., 2018b; Hosseini et al., 2019; Beigaitė et al. 2022).

Thus, in this study we employed machine learning algorithms (Breiman et al., 1984) to predict the association of the abiotic factors and stand age for the classification of tree leaf phenology groups (evergreen, deciduous, and semideciduous) in Atlantic tropical forest, southeast Brazil. Especially, we used machine learning models with the climate data (climatological water deficit, CWD), soil data (sum of basic exchangeable cations (SB) and exchangeable acidity potential (H + Al)) topographic data (elevation, slope and convexity) during tropical late-secondary forest succession to predict the classification of functional leaf phenology groups. This approach is very relevant because it allows us to understand the leaf functional groups classification based on abiotic factor influence on a local scale, allowing us to identify key species for forest management, restoration and conservation.

2. Methods

2.1. Study site and vegetation sampling

We studied a Semideciduous Seasonal Atlantic Forest fragment in Minas Gerais state, Southeastern Brazil (20°45′14″S, 42°45′53″W) of approximately 75 ha that was used for the coffee cultivation until 1926 and since then it is in natural regeneration. According to the Köppen-Geiger classification, the study area climate is tropical altitude (Cw_b), with a dry season between May and September, and wet season occurring between December and March (Alvares et al., 2013). The mean annual temperature is 21°C and the mean annual precipitation is 1,270 mm, with the highest volumes of rain concentrated from October to March (140 mm to 200 mm per month) and often low values of accumulated precipitation from April to August (50 mm per month) (Avila-Diaz et al., 2020; UFV, 2020). The study area is located between 620 and 820 m elevation and the relief vary from strongly undulating to mountainous and has marked differences in the spatial distribution of topographical variables, mainly elevation and convexity (Rodrigues et al., 2020, 2019). The site is characterized by the presence of two dominant soil classes: a red-yellow alsicose latosol covers hilltops and mountainsides; while a cambic yellow-red podzolic dominates the upper fluvial terraces (Ferreira-Júnior et al., 2007).

Our research group has been monitoring Atlantic forest fragments through the methodology of permanent plots for three and a half decades (1984-2019). Thus, we have a valuable and extensive set of data on the dynamics of this forest ecosystem that can provide us with evidence of the effects of climate change and other environmental factors on the structure of these forests. We have patches established in 1984 and 1993, with measurements in 1984, 1993, 1998, 2003, 2004, 2011, and 2017. The forest sampling areas are in contrasting topographic conditions and have 100 plots of 10 x 10 m each, totalizing 200 plots (2 ha) sampled. Within each plot, all trees having a diameter at breast height (DBH) 10 cm were identified to the species level and tagged for the measurement of tree height. All individuals were identified using specialized literature, through consultation with the Herbarium of Universidade Federal de Viçosa, or by taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for táxon classification. We classified tree species into three categories of functional groups with respect to the leaf phenology (deciduous, semideciduous, and evergreen species). The species were classified according to field observations and using literature.

2.2. Topographic variables

We measured three topographic variables (i.e., slope, elevation, and convexity) within each plot. Topographic variables were measured using a total station, which measures vertical and horizontal angles and linear distances and is positioned at an obstacle-free location and aimed at a prism. The prism sits on a metal stick and is placed over the point to be measured. The total station then emits a laser beam that reflects in the prism and returns to the equipment. Using the response time of the laser beam to the equipment and the angle of rotation of the station's bezel, the internal computer calculates the angles and distances and stores the data in its internal memory (Kahmen and Faig 1988). The data was then transferred to a computer and analyzed with AutoCAD software (Autodesk Inc., San Rafael, CA, USA). Elevation was calculated using the mean elevation at each of the four corners of the plot. The slope (measured in degrees) was the mean angular deviation of the horizontal of each of the four triangular planes formed by the connection of three of its edges (Guo et al. 2017). Convexity was determined by subtracting the elevation at the center of the quadrat from the mean elevation of the eight surrounding plots. On edge plots, convexity was calculated as the altitude of the plot of interest minus the mean altitude of the surrounding plots (Lan et al. 2011).

2.3. Soil properties

Within each plot, a composite sample of the surface soil (0–10 cm depth) was collected. Soil properties of the samples were measured in the Soil Analysis Laboratory of the Federal University of Viçosa, following standard protocols (EMBRAPA 1997). The following soil properties were assessed: soil organic carbon (C); total N; available P, K, Ca, Mg, Fe, Zn; effective cation exchange capacity (CEC); exchangeable acidity potential (H + Al); sum of basic exchangeable cations (SB); base saturation (V); aluminum saturation (m); pH and organic matter (OM).

2.4. Climate data

We used daily, monthly and annual precipitation and evapotranspiration datasets (recorded from 1980 to 2017) to estimate water balance. The potential evapotranspiration (PET) and actual evapotranspiration (AET) output from these water balance models was used to calculate the climatic water deficit (CWD = PET − AET; mm). We then calculated the total annual CWD for each year, which represents the unmet atmospheric demand for moisture, an ecologically relevant metric of accumulated drought stress. The dataset was collected in the database of the Instituto Nacional de Meteorologia (INMET). The weather station where data were collected is based in Viçosa, Minas Gerais State, at the Campus of Federal University of Viçosa. Breaking point detection techniques were used to evaluate the temporal evolution of water deficit, as well as to investigate the incidence of discontinuity in the time series. Breaking point detection techniques were based on three different tests: Pettit test (Pettitt 1979), Buishand test (Buishand 1982) and Standard Normal Homogeneity test (SNHT). These tests detect the shift in the average associated with the moment when a rupture in the climate series.

2.5. Data analysis

All analyzes were performed in the R program 4.2.1 (R Development Core Team, 2022), using different packages. For example, for the trend and detection of breaking points (i.e., trend package), principal component analysis (i.e., FactoMineR package) and learning machine modeling (i.e., caret, RandomForest, rpart packages). To draw the graphs illustration in this study, we used the 'ggplot2' package (Hadley 2015).

2.5.1. Evaluation of trend and detection of breaking points

Different breaking point detection methods were used to evaluate the temporal CWD variation based on the incidence of discontinuity in the time series. Thus, the following breaking point detection methods were used: Mann-Kendall (M-K), Pettitt test, Buishad U test, Standard Normal Homogeinity test, Lanzante's test procedures (Yu and Ruggieri, 2019; Pohlert, 2020). These tests were used to identify trends and deviations in the temporal series of CWD data on seasonal scales, which show a significant breaking point in the time series of 30 years of data in the Viçosa region (Fig. S1 SM). For example, all these tests (at 95% significance level) allows if the null hypothesis (H0) lies in the lack of no trend in climate extremes over time and that the alternative hypothesis (H1) lies in the evidence of a monotonic trend in them (increasing or decreasing). These analyses were calculated in the "trend" package (Pohlert, 2020). This test was calculated using seasonal scales, which part of the premise is that significant changes based on the period of higher water deficit may indicate changes in climate. These methods are widely used in climate studies to determine trends in time series data, indicating that when there is a larger deviation from zero greater is the trend (Yu and Ruggieri, 2019).

2.5.2. Principal Analysis component

We used a principal component analysis (PCA) on the correlation matrix to describe the topographical and soil gradients between leaf phenology groups, reducing the number of redundant variables on the PCA axes. This analysis was preceded by variable standardization to equalize their contributions on the PCA ordination axes (i.e., Schmitz et al. 2020), using the 'FactoMineR' package (Husson et al. 2018). Thus, we constructed two PCA analyses, a first PCA to represent the fertility and texture gradient due to the high correlation of the variables with the PCA axes. Subsequently, we analyzed the Spearman correlation between properties related to fertility and texture with the PCA axes to evaluate the contribution of variables (Fig. S2 from Supplementary Material, SM).

2.5.3. Machine learning algorithms

We used three main machine learning algorithms for classification, in order to compare the effectiveness and performance in predicting the distribution of the leaf functional groups of the tree community (evergreen, deciduous, and semideciduous) using multiple predictive variables (CWD, elevation, slope, convexity, SB, HAL, and stand age). Thus, we tested the Random Forest (RF), Support Vector Machine (SVM) and classification and regression tree (CART) algorithms to predict the importance relative of CWD, soil properties, topography and stand age for the leaf phenology classification (i.e., Onishi et al. 2021; Beigaitė et al. 2022; Cetin et al. 2021). We tested the Random Forest (RF) using the randomForest (Liaw and Wiener, 2002) and caret (Kuhn et al., 2016) packages, which had the same predictions and results in this study. Meanwhile, the support vector Machines (SVM) classifier using the caret package. Finally, we used the rpart (Therneau and Atkinson, 2021) and the caret (Kuhn et al., 2008) packages for fitting the decision trees (i.e., Beigaitė et al. 2022).

2.5.3.1. *Algorithms description*

The Random Forest model is a supervised machine learning algorithm based on decision trees using 'bootstrap' aggregation (Bagging), which is robust to data reduction, generating an internal unbiased estimate of the generalization error as the forest building progresses, and having higher accuracy than individual decision trees and low sensitive to parameter adjustment than other machine learning models (Breiman 2001, Khaledian and Miller, 2020). In Random Forest, each tree is built using a deterministic algorithm by selecting a random set of covariates and a random sample from the training dataset (Khaledian and Miller, 2020).

The Support Vector Machine (SVM) is a technique used for classification tasks, which operates by identifying the optimal decision boundary that separates data points from different groups (or classes), and then predicts the class of new observations based on this separation boundary (Khaledian and Miller, 2020; Diniz et al. 2021). The different groups classification might be separable by a linear straight line or by a non-linear boundary line. Thus, SVM can handle both linear and non-linear class boundaries and can be used for both two-class and multi-class classification problems. However, the separation boundary is generally nonlinear, and the SVM algorithm performs a non-linear classification using the kernel strick (Khaledian and Miller, 2020), mainly to predict association of abiotic factors and phenological functional groups (i.e., Beigaitė et al. 2022). Therefore, in this study the *radial kernel* transformation was used (i.e. Diniz et al. 2021).

The classification and regression tree (CART) algorithm is a non-parametric supervised learning algorithm, which is used for both classification and regression tasks. It has a hierarchical, tree structure, which consists of a root node, branches, internal nodes and leaf nodes (Breiman 1984). This algorithm to reach reasonably high accuracy and extract the abiotic thresholds responsible for the separation of different leaf functional groups, which employ ensembles of decision trees (Breiman 1984; Beigaitė et al. 2022). However, as we focused on the extraction of the threshold values, we used a single tree model, which is more transparent for interpretation and has a lower risk of overfitting the data (Beigaitė et al. 2022). Then, a decision tree model was built iteratively by first splitting the training data set based on the abiotic variable that is the most informative regarding leaf functional groups classes. Therefore, the most informative variable is often selected until the observations at the final nodes of the tree are classified. This algorithm typically utilizes Gini impurity to identify the ideal attribute to split on (James et al., 2013). To avoid possible overfitting, we regulate the complexity parameter, which indirectly controls the number of splits by imposing a relative cost for each split (Maindonald and Braun, 2013).

2.5.3.2. Data processing for modeling

In supervised machine learning the dataset is split into two subsets. One subset, the training data, is used to 'train' the algorithm how to carry out the task e.g., how to classify (i.e., Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022). This training data contains the target output and the user indicates what this is. The second subset, the test data, is reserved to 'test' the performance of the algorithm in carrying out its task. In this phase, the target is not supplied to the algorithm so that the output produced by the algorithm can be compared to target output data (Breiman, 2001). Thus, in this study each time the algorithm was run using the createDataPartition function of the caret package, it will be trained on 70% of the data and tested on 30%, and each run of the algorithm will change which 30% of the data the algorithm is tested on (i.e., Breiman 2001, Diniz et al. 2021).

2.5.3.3. Accuracy assessment methods

We have used the Kappa index and three main accuracy methods (i.e., k-fold Cross Validation, Repeated k-fold Cross Validation and Bootstrap) of the machine learning algorithm, before estimating the relative importance of all predictors. The best classification found, chosen based on the accuracy rate (<70%) and Kappa index (~50 and 60%). The k-fold cross validation method involves the training set being split into k smaller sets (i.e., Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022); for example, in this study we have used k = 10. This will split the dataset into 10 parts (10 folds) and the algorithm will be run 10 times (i.e., i.e., Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022). This process is completed until accuracy is determined for each instance in the dataset, and an overall accuracy estimate is provided. The Repeated k-fold Cross Validation is the process of splitting the data into k-folds that can be repeated several times, and the final model accuracy is taken as the mean from the number of repeats (i.e., Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022). Thus, we used 10 resamples iterations based on the repeatedcv argument of the "Caret" package. Finally, the bootstrap resampling involves taking random samples from the dataset (with re-selection) against which to evaluate the model, and typically a large number of resampling iterations are performed (thousands or tens of thousands). Thus, the results provide an indication of the variance of the model's performance (i.e., Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022). In the three methods randomly determined the calculation of the hyperparameters using "random" argument (Bergstra and Bengio, 2012).

2.5.3.4. Variables importance

Variable importance refers to how much a given model "uses" that variable to make accurate predictions (i.e. Breiman 2001, Diniz et al. 2021; Beigaitė et al. 2022). The more a model relies on a variable to make predictions, the more important it is for the model. It can apply to many different models, each using different methods described in the previous section. However, in this study, we consider the relative importance of predicted variables with RF that showed higher accuracy (Table 1; Breiman 2001, Diniz et al. 2021).

3. Results

The prediction of distribution of the leaf functional groups classification based on multiple abiotic predictors showed higher accuracy and suitable Kappa using the Random Forest (RF) compared to the classification and regression tree (CART) and Support Vector

Machines (SVN) algorithms (Table 1). The highest accuracy (A = 0,753, K = 0,629) based on RF was achieved specifically using the k-fold Cross Validation method, compared to the Bootstrap and Repeated k-fold Cross Validation methods (Table 1). Using the CART algorithm, it was possible to observe a moderate prediction based on the Repeated k-fold Cross Validation method; however, being of lower precision compared to RF (Table 1). Conversely, the lowest efficiency of leaf functional groups classification using all the predictors was the SVN algorithm using all methods (repeated cross-validation; cross-validation and bootstrap) with Kappa between 0.40 and 0.47 and accuracy from 0.60% to 0.64 % (Table 1).

Table 1. Performance of the learning algorithms in the caret package to classification of leaf phenology groups. RF = Random Forest; SVM = Support Vector Machines and; CART = Classification and Regression Tree Algorithm. Methods 1, 2 and 3 are repeated cross-validation; cross-validation and bootstrap respectively, for k-fold cross validation that the three models were tested.

	RF	**SVM**	**CART**
Method 1			
Kappa	0.622	0.473	0.674
Accuracy (%)	0.749	0.649	0.510
Method 2			
Kappa	0.629	0.460	0.470
Accuracy (%)	0.753	0.640	0.648
Method 3			
Kappa	0.569	0.410	0.455
Accuracy (%)	0.713	0.607	0.637

After selecting the best method (k-fold Cross Validation method) with high accuracy using RF, it was observed that the most influential predictor in the classification of functional groups was topography and soil properties. Specifically, elevation shows a high explanatory contribution in the three functional groups between 92 and 100 (table 2), followed by soil properties such as SB and HAL (Figure 1). These three predictors had a greater influence on deciduous, while the elevation was more important in predicting the evergreen functional group (Table 2). Coincidentally, analyzing the results generated by the CART algorithm based on the method of moderate accuracy (Repeated k-fold Cross Validation methods) indicates the similar relative importance of these predictors (Elevation, SB, and HAL). This result using the CART algorithm corroborates the prediction using RF and maintains the same relative importance order of the three main predictors (Figure 2).

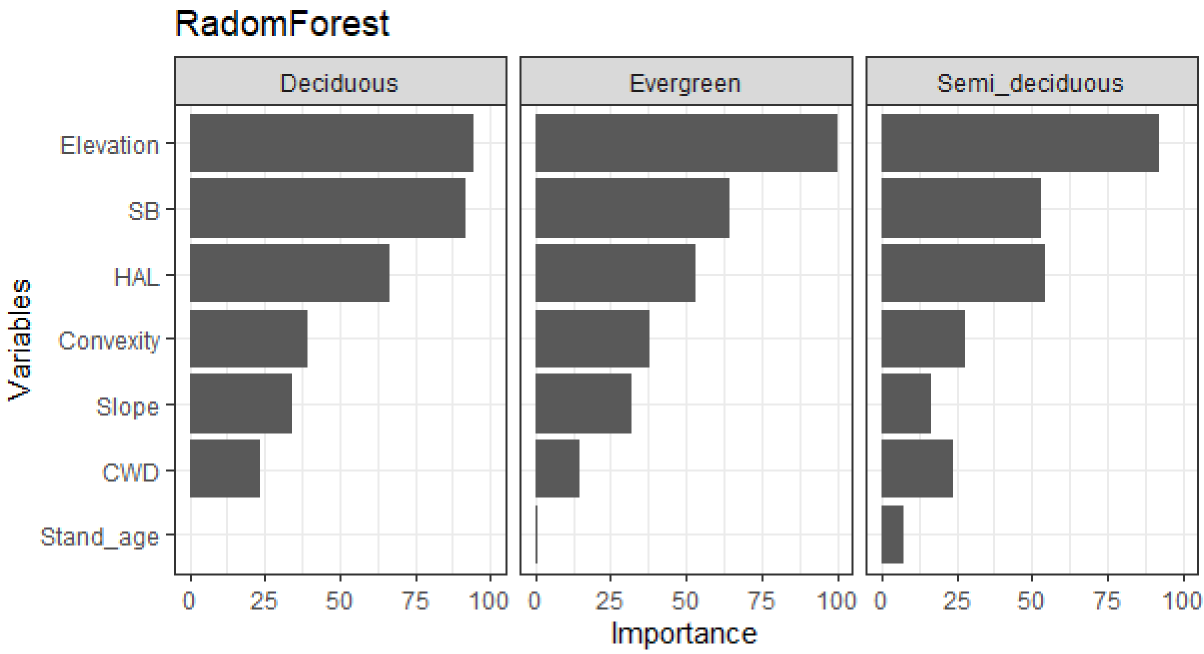

Figure 1. Relative importance of explanatory variables predicting leaf functional groups classification using Radom Forest Algorithm based on k-fold Cross Validation method. The predictors are ranked in order of importance starting with elevation, SB (sum of basic exchangeable cations), HAL (changeable acidity potential), Convexity, Slope, CWD (Climatological Water Deficit) and Stand age (i.e., successional stage of the late-secondary forest).

The CART algorithm for the classification of leaf functional groups using abiotic predictors and stand age produced moderately accurate results, but similar classification of the RF algorithm, which shows the best accuracy method. The decision trees start the splitting based on the elevation variable (< 703 m). If this variable is <703 m along the topographical gradient, the new split is assigned mainly to the evergreen functional group based on HAL (≥ 8.5). Thus, classification from the elevation separation depends simultaneously on the SB and HAL (Figure 2). Analyzing the CWD in the predicted decision tree, the deciduous functional group is separated from the evergreen functional group (Figure 2).

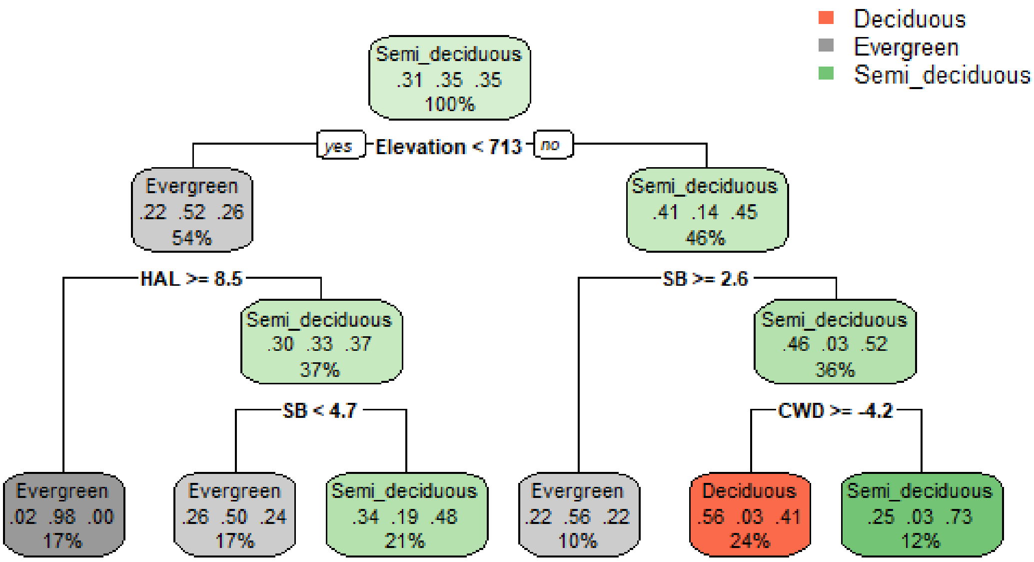

Figure 2. Decision tree using the multiple abiotic predictors. elevation, SB (sum of basic exchangeable cations), HAL (changeable acidity potential), CWD (Climatological Water Deficit) are indicated in the best CART selected.

Table 2. Relative importance of explanatory variables predicting leaf functional groups classifications in each learning algorithm in the caret package. RF = Random Forest; CART = Classification and Regression Tree Algorithm. Methods 1, 2 and 3 are repeated cross-validation; cross-validation and bootstrap respectively, for k-fold cross validation that the three models were tested. SB: sum of basic exchangeable cations; HAL: changeable acidity potential; CWD: climatological water deficit.

Random Forest			
Predictor	Importance		
Method 1	Deciduous	Evergreen	Semi deciduous
Elevation	94.25	100.00	92.56
SB	91.91	64.51	52.94
HAL	66.69	53.27	54.39
Convexity	39.49	38.14	27.77
Slope	33.93	31.79	16.83
CWD	23.44	14.47	23.80
Stand age	0.00	0.81	7.56
Method 2	Deciduous	Evergreen	Semi deciduous
Elevation	98.34	91.29	100.00
SB	80.00	55.42	36.46
HAL	44.66	43.45	39.19
Convexity	25.23	23.33	18.66
Slope	17.56	15.25	12.00
CWD	14.57	5.27	16.61
Stand age	1.84	0.00	6.95
Method 3	Deciduous	Evergreen	Semi deciduous
Elevation	100.00	97.32	90.80
SB	89.09	60.18	54.74
HAL	57.80	48.46	46.79
Convexity	39.78	39.61	23.35
Slope	32.84	26.97	16.64
CWD	22.88	11.82	20.45
Stand age	0.10	0.00	5.51

4. Discussion

We found that elevation followed soil properties SB and HAL were the main factors explaining leaf phenology group classification in the studied area. Despite the climatic water deficit breaking point based on climatic water deficit indicating variation in the climate during the period analyzed, CWD was not the main predictor for leaf phenology group classification. For example, Hoylman et al., (2021), found that the climatic water balance imparts a strong control over the spatial distribution of plant functional types at large spatial scales. Still, this research explains that CWD provides an integrated metric on the effects of regional-scale climate patterns on water and energy available to plants, but these resources are mediated by local topography in fine scale. These findings along with our results would explain the greater importance of topographic and soil predictors in relation to CWD in our study area. However, a larger time series of climatic data and a larger spatial or latitudinal scale would probably be needed to detect a greater influence of CWD as a predictive variable for classification. For example, the thresholds of climate extremes (e.g. extreme cold or drought) have been found to be essential for the dominance of certain vegetation types such as evergreen needleleaf forest and deciduous needleleaf forest classification at global scale using machine learning (Beigaitė et al. 2022).

Although we demonstrate detection of breaking points in CWD due to climatic changes in this region (i.e. Avila-Diaz et al., 2020), we presume that the low CWD prediction in the classification of leaf phenology groups is our short time series. We analyzed the relationship between climate and vegetation for just over thirty years, and our previous results show that there are no significant changes in the tree community composition (Rodrigues et al. 2022). Although our algorithms detect a low prediction of CWD to classify phenology groups, specifically CART detects separation of deciduous trees; we suggest long time samples of vegetation using permanent plots in future studies at local scale, which can better explain the effect of climate in the species composition of tree leaf function groups. Alternatively, the palynology and future scenario modeling approach may be more accurate in detecting changes in floristic composition due to climate change over a long time.

Conversely, variables that do not change temporally in 30 years of study could have a spatial influence on the classification of functional groups as detected by RF and CART algorithms. The decision trees for separating different leaf phenology groups start the splitting based on the elevation variable and then simultaneously on the SB and HAL, followed by CWM. These results are consistent with our ecological understanding on the environmental filtering processes that promote vegetation classification. The observed leaf phenology group classification due to topography is probably linked to the underlying spatial variation of light, soil nutrients and climatic water availability, which are strongly influenced by topographic factors (John et al. 2007; Moeslund et al. 2013; Ali et al. 2019). Topography heterogeneity in tropical forests is an important driver that plays a key role in the distribution patterns of tree species and ecosystem functioning (Moeslund et al., 2013; Holl and Zahawi, 2014; Rodrigues et al., 2020; 2021). Topographic variability causes small-scale heterogeneity in resources availability (Kubota et al., 2004; Townsend et al., 2008) and strongly affects forest community composition (Holl and Zahawi, 2014; Guo et al., 2016). Several studies have shown that topographical conditions shape functional traits composition and aboveground carbon stock of second-growth forest at local scale (Powers et al., 2009; Zhang et al., 2014; Rodrigues et al., 2020; Villa et al., 2018a, 2020). Thus, we presume that the habitat heterogeneity (by topography and soil properties) can determine changes in tree community composition and leaf phenology group, and consequently the distribution of ecosystem services. For example, we have previously shown that evergreen species are associated with low elevations and high topographic heterogeneity, while deciduous species dominate higher elevation habitats and low heterogeneity (i.e., low fertility, convexity, and slope) in this study area (Rodrigues et al. 2022).

Topography heterogeneity may affect resources such as light, water and constraints local soil nutrient and contribute to variance in microclimates and the climatic water balance (Hoylman et al 2019b; Moeslund et al., 2013), within which trees grow, that in turn strongly affect forest species structure, composition and function (Jucker et al., 2018). Furthermore, topographic variability causes fine-scale heterogeneity of nutrient availability, meaning that species can then differentially explore patchily distributed resources, which can lead to higher species richness and species turnover (Questad and Foster, 2008).

Our main predictors for the classification of leaf phenology groups were elevation, followed by SB, which is a proxy for soil fertility already described in studies in tropical forests (Poorter et al. 2017; Ali et al. 2019). According to the PCA methods (Rodrigues et al. 2021, 2022), there was a strong correlation of evergreen species with area with higher topographic heterogeneity, and deciduous species with area of less topographic heterogeneity. In addition, the area studied with greater topographic heterogeneity show a uniform spatial distribution of the SB, in relation to the area with less heterogeneity. Furthermore, the highest SB values are allocated to the lowest elevations, showing a relationship between topography and soil fertility distribution (Rodrigues et al., 2022). In relation to CWD split, its can be derived from the ecophysiological climate response of the tree leaf phenology groups (e.g. Geange et al., 2021). For example, a higher mortality of trees from less tolerant groups to the greater climatic water deficit and this may be influencing this split.

The success of the RF algorithm against the other can be explained by the fact that the RF is suitable for handling unbalanced samples and adds additional randomness to the classification model during the as well as searching for only the best features among a random subset of features in the splitting process of each node (Indira et al., 2020). Most of the tree species classification studies in the literature have used data from LiDAR or other remote sensing tools (Cetin et al., 2022; Hovi et al., 2016; Shi et al., 2018). In this study, we used a set of field data at a local scale to test the effects of environmental drivers on the classification of tree functional groups. In our study, as well as in those using data at regional scales, machine learning proved to be a robust tool to predict these patterns. Thus, the obtained accuracies of the machine learning-based classifications in our study are comparable with similar studies in regional scales.

5. Conclusions

The results of this study provide preliminary findings for evergreen, semideciduous and deciduous tree species classification in a tropical forest based on abiotic drivers, mainly topography and soil properties, which operates at local and fine scale under the environmental filtering hypothesis. We found that elevation, among the three topographic variables, was the best predictor for the tree leaf phenology classification, followed by SB and HAL soil properties using RF algorithm. Among the performance machine learning-based classification algorithms analyzed, random forest classifier was the best algorithm model. The prediction of functional groups classification can be the basis for the identification of key species to be used during ecological restoration projects under different topography and soil-depedent conditions on a local and fine scale.

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Supplementary material

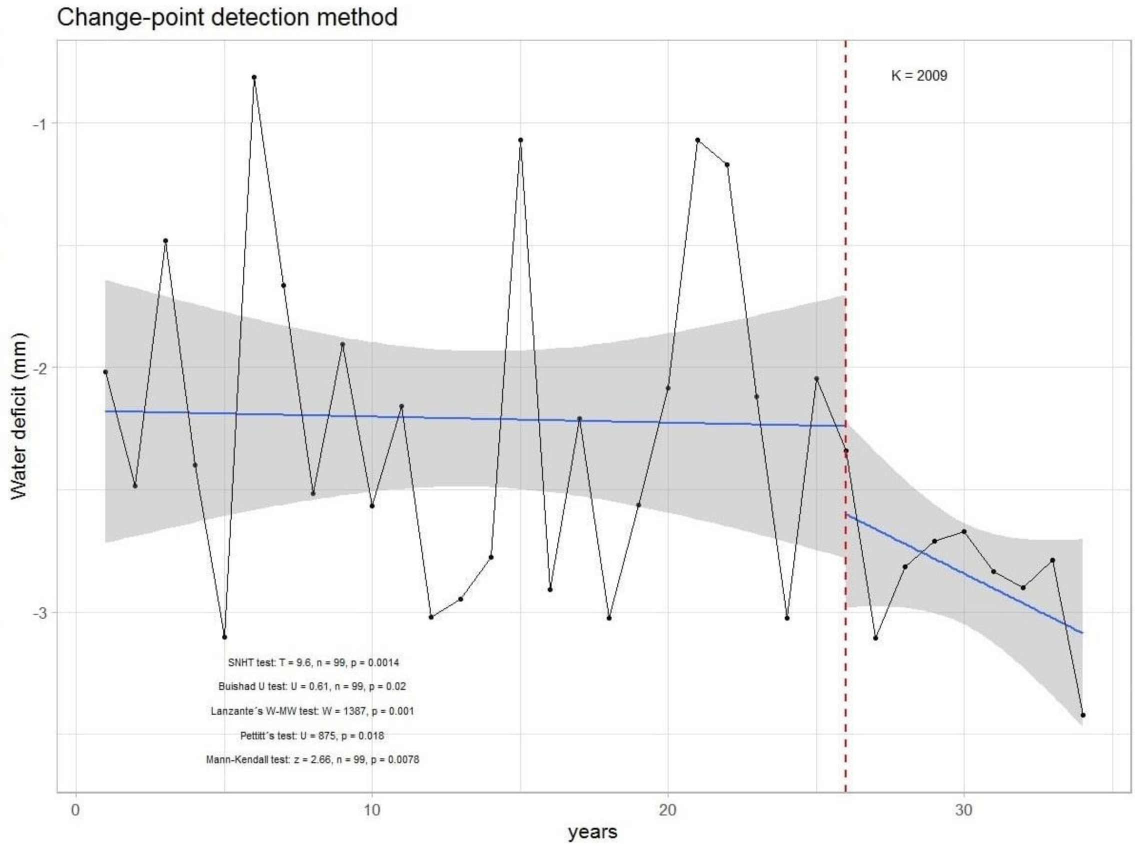

Figure S1. Temporal distribution of the water deficit that presented an abrupt change point during 1980–2017. Dashed red line indicates a non-homogeneous series and the respective year of rupture.

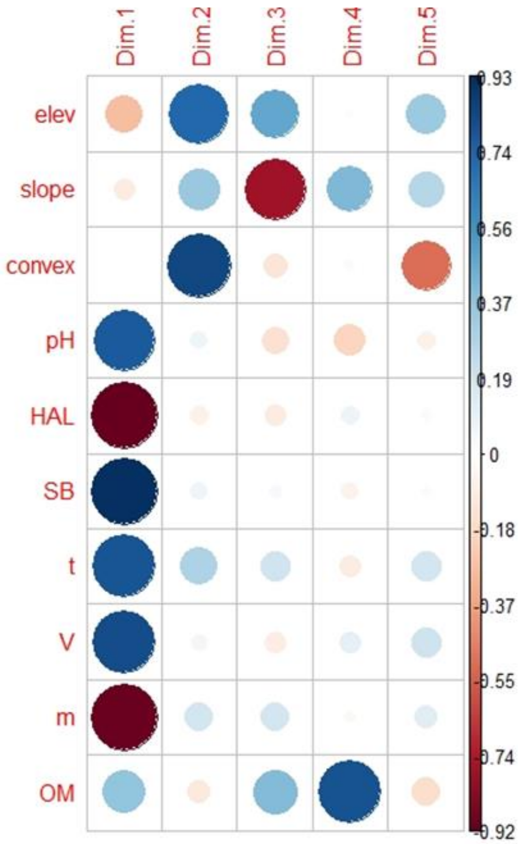

Figure S2. Significance levels are based on Spearman correlation coefficients between soil parameters and principal components of PCA fertility from 200 plots within 2-ha plots in Atlantic Forest, Minas Gerais, Brazil. For analysis, available: elevation (elev), convexity (convex), slope, exchangeable acidity potential (H + Al), aluminum saturation index (m), pH (H_2O), organic matter (OM); effective cation exchange capacity (t = CEC), sum of basic exchangeable cations (SB), bases saturation index (V).

CHAPTER 5

Distribuição espacial de fatores ambientais e atributos florestais usando rotinas práticas no R

Spatial distribution of environmental factors and forest attributes using practical routines in R

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RESUMO

Compreender os mecanismos subjacentes à contribuição relativa de diferentes fatores ambientais na montagem das comunidades vegetais é fundamental para se estabelecer estratégias de conservação e manejo. Para esse fim, a aplicação de análises estatísticas tem sido uma importante ferramenta para elucidar os padrões de distribuição dos fatores bióticos e abióticos que podem determinar a estrutura e diversidade das comunidades florestais. Com isso, o objetivo desse capítulo é demostrar uma metodologia de análise e construção de gráficos de distribuição de fatores ambientais e atributos florestais usando os pacotes estatísticos 'fields', 'raster' e 'ggplot2' no software R. Serão construídos passo a passo três tipos de gráficos, gráfico do tipo *grid*, gráfico tridimensional com contornos de nível e gráficos com distribuição das variáveis em *raster*. Apresentaremos ao longo desse capítulo toda a metodologia para a construção dos gráficos. Desde a obtenção das variáveis em campo, passando pela sistematização da planilha de dados, descrição de todos os comandos utilizados nos *scripts* e carregamento dos dados no R até o produto final das análises. Na maioria dos estudos que utilizaram essa ferramenta, essas análises foram utilizadas para determinar a formação de hábitats relacionados à variação dos atributos florestais. Essa metodologia é interessante para estudos onde se espera demonstrar associações de espécies e atributos da vegetação com habitats ou gradientes de variáveis ambientais. Sendo também útil em análises de processo de distribuição de nichos e regras de montagem de comunidades.

Palavras-chave: Fatores bióticos e abióticos, elevação, classificação de habitats, estrutura florestal, gradiente ambiental, *Kriging*.

ABSTRACT

Understanding the mechanisms underlying the relative contribution of different environmental factors in the assembly communities is fundamental for establishing conservation and management strategies. To this end, the application of statistical analysis has been an important tool to elucidate the distribution patterns of biotic and abiotic factors that can determine the structure and diversity of forest communities. Thus, the purpose of this chapter is to demonstrate a methodology for analyzing and constructing a distribution graph of environmental factors and forest attributes using the 'fields', 'raster' and 'ggplot2' statistical packages in the R software. Three types of graphs will be constructed, grid graph, three-dimensional contoured graph, and raster variable distribution graphs. We will present throughout this chapter all the methodology for the construction of graphs. From obtaining the variables in the field, through the systematization of the dataset, description of all commands used in the scripts and loading of data in R to the final product of the analysis. In most studies using this tool, these analyses were used to determine the formation of habitats related to the variation of forest attributes. This methodology is interesting for studies where it is desired to demonstrate species associations and vegetation attributes with habitats or gradients of environmental variables. Also useful in niche formation process analysis and assembly community rules.

Keywords: Biotic and abiotic factors, elevation, habitat classification, forest structure, environmental gradient, Kriging.

INTRODUÇÃO

Conhecer a contribuição relativa dos diferentes fatores que podem determinar a estrutura e diversidade das comunidades florestais tem sido um tema relevante na ecologia contemporânea (Rozendaal et al. 2019). Recentemente o impacto desses fatores ambientais, como solo, topografia e clima tem ganhado importância para conhecer melhor as florestas tropicais (Yuan et al. 2016; Rozendaal et al. 2019). Por exemplo, os estoques de biomassa acima do solo variam amplamente entre as florestas devido aos efeitos diferenciais dos fatores abióticos (como topografia, fertilidade do solo e clima) e bióticos (como a biodiversidade e os atributos estruturais da floresta).

Contudo, para compreender os mecanismos subjacentes à contribuição relativa de diferentes fatores ambientais na montagem das comunidades vegetais, é fundamental a aplicação de análises estatísticas com métodos que nos permitam elucidar os padrões de distribuição dos fatores bióticos e abióticos em nossas áreas amostrais. Sendo esse conhecimento, imprescindível para se estabelecer estratégias de conservação e manejo, bem como prever as respostas das comunidades vegetais à variabilidade de fatores ambientais e a mudanças climáticas.

O objetivo desse capítulo é demostrar uma metodologia de análise e construção de gráficos de distribuição de fatores ambientais e atributos florestais usando o software R. Construímos três tipos de gráficos, 1) tipo *grid*, 2) o tridimensional com contornos de nível e 3) com distribuição das variáveis em *raster*. Iniciaremos pela demonstração de como obter as variáveis em campo, passando pela sistematização da planilha de dados, descrição de todos os comandos utilizados nos *scripts* e carregamento dos dados no R até o produto final das análises.

METODOLOGIA

Obtenção das variáveis para análises

Para o desenvolvimento dos gráficos será utilizado como modelo uma área amostral que possui diferentes condições topográficas e está situada em um fragmento em estágio avançado de regeneração secundária de Floresta Atlântica. A amostra constituída de uma parcela de 1 ha, subdividida em 100 parcelas de 10 x 10 m (parcelas contiguas), abrangendo um gradiente topográfico desde o vale até o platô. Para esse capítulo serão utilizados, uma variável topográfica (elevação), um parâmetro químico do solo (pH) e um atributo estrutural das árvores (altura média), de cada parcela para a construção dos gráficos. Para amostragem de solo e atributos estruturais da vegetação, sugerimos a utilização de padrões usuais de amostragem. Para o levantamento das variáveis topográficas nas áreas de interesse, sugere-se a utilização de estação total para áreas menores que 5 ha e de *softwares GIS (Geographic Information System)* para áreas maiores.

No presente estudo, foi utilizado uma estação total para a obtenção das variáveis topográficas. Visto que a área de interesse possuía 1 ha e perderíamos a acurácia dos dados utilizando softwares GIS. Para cada parcela amostrada foram medidas e calculadas três variáveis topográficas (elevação, declividade e convexidade). A elevação foi calculada usando o valor médio de elevação de cada um dos quatro cantos da parcela. A declividade (°) foi medida como o desvio angular médio da horizontal de cada um dos quatro planos triangulares, formado pela conexão de três de seus cantos. A convexidade foi determinada subtraindo a elevação do centro da parcela da elevação média das oito parcelas circundantes, seguindo os métodos propostos por Wang et al., (2016).

Organização da planilha para análise no R

Após a obtenção das variáveis em campo, ou a partir de bancos de dados, é necessário organizá-las de forma sistemática em uma planilha eletrônica Excel. No material suplementar é mostrado como as variáveis devem ser sistematizadas na planilha (link).

Pacotes estatísticos e scripts

Para a construção dos gráficos, serão utilizados três pacotes: *'fields'* que é utilizado para ajustes de curvas, superfícies e funções com ênfase em dados espaciais, geoestatística e estatística espacial (Nychka, et. al., 2019). O pacote *'raster'*, que faz manipulações, análises e modelagem de dados espaciais em *grids* (Hijmans, et. al., 2019) e *'ggplot2'*, um pacote do R para criar gráficos baseados em mapeamento de atributos estéticos de formas geométricas (Wickham, et. al., 2019).

Descrição do comando ou script

A seguir descreveremos todos os comandos utilizados no script, desde o carregamento dos dados no R até o produto final das análises.

O primeiro passo é indicar endereço do arquivo ou a pasta de trabalho onde se encontra os dados/planilhas a serem analisadas. Nessa pasta também serão salvos todos os gráficos gerados nas análises.

```
> setwd ("~/endereço do arquivo/")
```

O comando a seguir é utilizado para discriminar a planilha em formato txt que será objeto de análise.

```
> dados <- read.table ("planilha x.txt", h=T)
```

A função *attach()* é utilizada como uma maneira de extrair partes do nosso conjunto dados de uma *dataframe* ou de tornar todas as variáveis de um conjunto de dados acessíveis. Vejamos como funciona essa função:

Se digitamos apenas *dados* na linha de comando a seguinte mensagem irá aparecer:

> dados

Error: object "dados" not found

Utilizando a função *attach*, e digitando *dados* novamente, os dados do conjunto de dados ficarão agora disponíveis. Atenção: O nome *dados* é um nome fictício, você pode chamar seu conjunto de dados de *data*, por exemplo.

> attach (data)

> data # agora todo o conjunto de dados está disponível

Se quisermos, por exemplo, que apenas os dados referentes a *elevação* fiquem disponíveis devemos digitar o seguinte comando:

> attach (elevação)

> elevação # agora os dados elevação estão disponíveis

Atenção: A função *attach* pode trazer problemas. Se a utilizarmos em dois *dataframes*, e essas possuírem variáveis com o mesmo nome, corre-se o risco de usarmos por engano a variável errada. Sempre que utilizarmos a função *attach* é preciso "desatachar" o objeto imediatamente após o seu uso. Para isso utilizamos a função *detach().*

> detach (dados)

dados # não está mais disponível

> detach (elevação)

elevação # não está mais disponível

```
> attach (dados)
                    #Após utilizá-los#
> detach (dados)
```

Sempre que quisermos consultar nosso conjunto de dados, as funções a seguir nos permitem visualizá-los, assim como as dimensões da matriz (função *dim*) e o nome e resumo das variáveis que estamos utilizando nas análises (funções *names* e *summary*).

```
> dados
> dim (dados)
> names (dados)
> summary (dados)
```

Antes de começar a análise propriamente dita dos dados, é necessário a instalação dos pacotes, podendo estes serem instalados com a seguinte função:

```
> install.packages ("nome do pacote")
>install.packages(fields)
>install.packages(raster)
>install.packages(ggplot2)
```

Após instalar o pacote, é necessário "carregar" o pacote sempre que você abrir o R e for utilizá-lo. A função *library* é utilizada para “carregar” pacotes.

```
> library (fields)
> library (raster)
> library (ggplot2)
```

Resultados e comandos do estudo de caso

Construção gráfico grid com a função image.plot

Feito os passos anteriores é possível agora começar a construção dos gráficos de interesse. A primeira tarefa é escolher em qual formato o gráfico será salvo (*jpeg, png*, *tiff,* entre outros), nesse estudo de caso o formato escolhido foi *tiff.* A função *file* permite nomear o arquivo (gráfico) que será salvo na pasta de trabalho previamente escolhida no diretório ou *setwd.*

Os argumentos *res, width, height e compression* correspondem à resolução, largura, altura e compressão do gráfico, respectivamente, e podem ser ajustadas conforme nosso interesse. A função *par* permite estabelecer o número de colunas e linhas para disposição de gráficos como uma única imagem composta. No nosso caso, foram escolhidas uma linha e uma coluna para a construção de um único gráfico de forma individual. Esta função *par* é muito útil quando se quer apresentar mais de um gráfico na mesma figura (ex., apresentar dois gráficos na mesma linha e em duas colunas), como faremos mais adiante nesse capítulo.

A função *image.plot* é utilizada para adicionar legenda no gráfico *grid*. Os argumentos *xlab e ylab* são utilizados para dar nomes aos eixos x e y respectivamente. Para colocar título no gráfico use o argumento *main.* Os argumentos *font.lab, font.main, cex.axis* e *cex.main* permitem estabelecer a fonte/tamanho dos eixos e legendas. O argumento *byrow* é utilizado para determinar se a matriz da legenda será preenchida por colunas (*byrow=F*) ou por linhas (*byrow=T*). Use a função *dev.off* para exportar a figura para a pasta de trabalho previamente selecionada em *setwd*.

```
> tiff (file = "nome_do_arquivo_a_ser_salvo.tiff", res = 300, width = 4400, height = 3100, compression = "lzw")

> par (mfrow=c (1,1))

> image.plot (0:10*10,0:10*10, matrix (as.numeric(elevação) ,10,10,byrow=T), xlab="", ylab="",font.lab=2,cex.axis=1.25,main="Elevação",font.main=4,cex.main=2)

> dev.off( )
```

Utilizamos o conjunto de dados do plot de 1 ha de Floresta Atlântica para a construção do gráfico *grid* (Figura 1A)¸ utilizando dados referentes à elevação. O argumento *matrix(as.numeric()* nos permite escolher dentro da matriz o conjunto de dados que desejamos plotar no gráfico.

Construção do gráfico tridimensional com contornos de nível utilizando a função drape.plot

Para a construção do gráfico 3D (figura 1B) segue-se os mesmos argumentos utilizados para o gráfico *grid.* Porém, nesse caso iremos utilizar a função *drape.plot* ao invés de *image.plot.* A Função *drape.plot* é utilizada para produzir gráficos do tipo *wireframe*, com as facetas sendo preenchidas por cores diferentes. Os argumentos *theta* e *phi* são utilizados para determinar a rotação dos ângulos/eixos x-y e z, respectivamente. No presente estudo de caso, utilizamos nos eixos x e y as dimensões da área de estudo e no eixo z a elevação da área de estudo. O argumento *zlab* é utilizado para nomear o eixo z. Os argumentos *shade* e *col* permitem fazer sombreamento e degrade de cores no gráfico.

```
> tiff (file = "nome_do_arquivo_a_ser_salvo.tiff", res = 300, width = 4400, height = 3100, compression = "lzw")

> par (mfrow=c (1,1))

> drape.plot (1:10,1:10,matrix (as.numeric(elev), 10, 10, byrow=T), theta =1023, phi = 50, expand = 0.64,shade = 1.7,col= terrain.colors (128),xlab="x=100 m", ylab= "y=100 m", zlab= "z=elevação", font.lab=2, cex.lab=1.3, main= "Mapa de Topografia", cex.main=1.6, font=2)

> dev.off()
```

Construção do gráfico grid com a função image.plot e do gráfico tridimensional com contornos de nível utilizando a função drape.plot na mesma figura usando a função par.

Para a construção de dois gráficos na mesma imagem (figura 1) será utilizado a função *par* especificando o número de colunas e linhas que desejamos na figura.

Por exemplo:

```
> par (mfrow=c (1,1)) # Figura com uma linha e uma coluna.

> par (mfrow=c (1,2)) # Figura com uma linha e duas colunas.

> par (mfrow=c (2,2)) # Figura com duas linhas e duas colunas.
```

No presente estudo, construiremos dois gráficos, o que corresponde ao argumento *par (mfrow=c (1,2))* para obtermos uma figura composta por uma linha e duas colunas (Figura 1). Note que, ao construirmos os dois gráficos é possível que tenhamos que ajustar as dimensões dos mesmos para que se adequem à imagem gerada, para isso podemos ajustar valores dos argumentos *width* e *height.*

```
> tiff (file = "nome_do_arquivo_a_ser_salvo.tiff", res = 300, width = 4400, height = 2400, compression = "lzw")

> par (mfrow=c (1,2))

> image.plot (0:10*10,0:10*10, matrix (as.numeric(elevação) ,10,10,byrow=T), xlab="", ylab="",font.lab=2,cex.axis=1.25,main="Elevação",font.main=4,cex.main=2)
```

```
> drape.plot (1:10,1:10,matrix (as.numeric(elev), 10, 10, byrow=T), theta =1023, phi = 50, expand = 0.64,shade = 1.7,col= terrain.colors (128),xlab="x=100 m", ylab= "y=100 m", zlab= "z=elevação", font.lab=2, cex.lab=1.3, main= "Mapa de Topografia", cex.main=1.6, font=2)

> dev.off( )
```

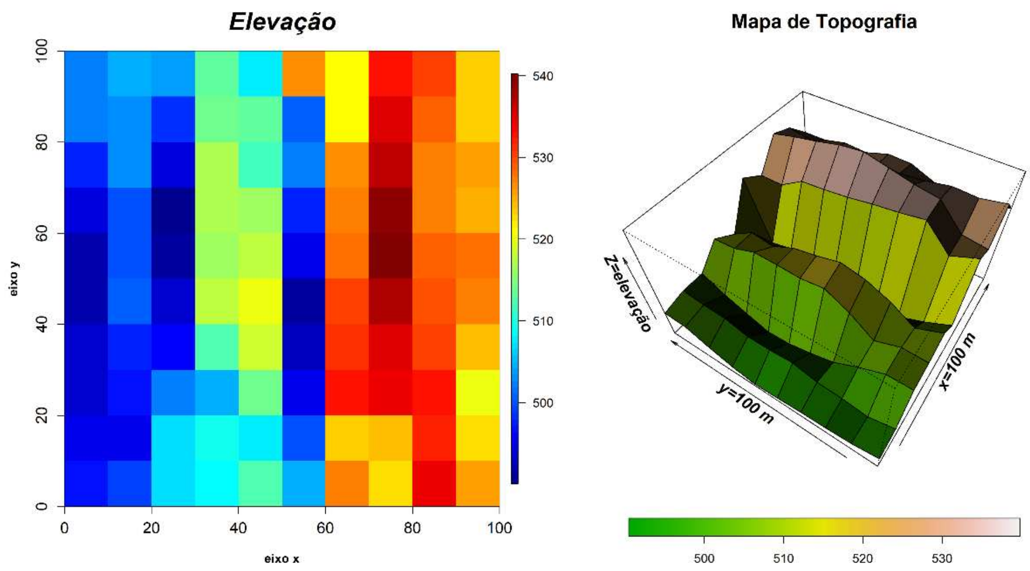

Figura 1. Gráfico grid e gráfico tridimensional com contornos de nível utilizando a mesma figura.

Construção gráfico grid com a função image.plot utilizando outras variáveis

É possível construir gráficos *grid* utilizando diferentes variáveis ambientais (topografia, solo e etc.) e atributos florestais (altura, densidade de madeira, diâmetro das árvores, área basal e etc.). Basta apenas selecionar as variáveis de interesse na barra de comandos. Por exemplo, se quiséssemos plotar a altura média das árvores em cada parcela ao invés de elevação, teríamos que usar os seguintes comandos:

```
> tiff (file = "altura média.tiff", res = 300, width = 4400, height = 3100, compression = "lzw")

> par (mfrow=c (1,1))
```

```
> image.plot (0:10*10,0:10*10, matrix (as.numeric(altura) ,10,10,byrow=T), xlab="",
ylab="",font.lab=2,cex.axis=1.25,main="altura",font.main=4,cex.main=2)

> dev.off( )
```

2.3.7. Construção de gráficos raster com a função geom_raster

Suponhamos que possuímos um *dataframe* de dados que possui três colunas: x, y e z. Onde x e y são as respectivas coordenadas (no presente estudo o número de parcelas nas coordenadas x e y, respectivamente) e z um valor contínuo (elevação, pH, altura, etc.). Esse valor de z poderá ser plotado como uma imagem no gráfico em relação às coordenadas x e y. Essa imagem pode ser definida como um preenchimento em gradiente e pode ser plotada usando a função *geom_raster ()* usando o pacote estatístico ggplot2. Vejamos alguns exemplos a seguir utilizando essa função:

Primeiramente segue-se os mesmos passos iniciais descritos anteriormente.

```
> setwd ("~/endereço do arquivo/")
> dados <- read.table ("planilha x.txt", h=T)
> attach (dados)
                    # Após utilizá-los #
> detach (dados)
```

Para a construção dos gráficos ‘raster’ será necessário a instalação do pacote ‘ggplot2’. Cabe ressaltar que para algumas análises será necessário também a instalação do pacote ‘raster’, pois, algumas funções ou argumentos podem estar conectados a este. Por isso, é recomendado a instalação de ambos os pacotes antes de se iniciar as análises.

```
> install.packages ("ggplot2/raster")
> library (raster)
> library (ggplot2)
```

A principal função do pacote ‘ggplot2’ é a função *ggplot ()* que permite construir gráficos peça por peça (passo a passo). Cada comando gráfico deve iniciar sempre com função *ggplot ()*. A função *aes ()* é usada para especificar eixos x e y (variáveis). Vejamos um exemplo:

Com os comandos básicos abaixo é possível criar um gráfico com os eixos x e y.

```
> ggplot (data, aes (x = x, y = y))
```

Se quisermos acrescentar um terceiro eixo (eixo z) no gráfico (Figura 2), sendo z um valor contínuo ou discreto, esse valor de z poderá ser plotado como uma imagem no gráfico em relação às coordenadas x e y utilizando os seguintes comandos:

```
> ggplot (data, aes (x = x, y = y, z = elevação, fill=elevação)) + geom_raster (interpolate = T)
```

Onde, o argumento *fill* corresponde à variável de interesse que queremos plotar no preenchimento do gráfico com interpolação (*interpolate* = *T*). Para obtermos um gráfico sem interpolação usamos *interpolate* = *F*. Para o estudo de caso do presente capítulo utilizamos os dados de elevação.

Para fins de demonstração, iremos construir quatro gráficos do tipo ‘raster’. Utilizaremos como variáveis altura média das árvores em cada parcela, elevação e pH. Para diferenciar os gráficos, iremos utilizar os objetos *mod1, mod2, mod3 e mod4,* como sendo gráficos 1(Figura 2A), 2 (Figura 2B), 3 (Figura 3A) e 4 (Figura 3B), respectivamente. Nos comandos, o argumento *scale_fill_gradientn ()* permite escolher o gradiente de cores que desejamos para cada gráfico. Nos exemplos abaixo escolhemos diferentes gradientes de cores para exemplificar. O argumento *theme*, permite escolher a formatação do gráfico, nesse caso escolhemos o formato *gray*. Dentro da função *theme_gray ()* pode-se ajustar automaticamente o tamanho das letras das legendas, eixos e linhas usando *base_size*. Um tamanho razoável para artigos científicos é entre 14 e 16. O argumento *labs*, é utilizado para dar título ao eixo x e y respectivamente. Utilizamos *aes (fill = elevação)*, para construir a legenda de barra de cores e *scale_x_discrete (limits = c)* para estabelecermos a escala dos eixos x e y. No presente estudo estabelecemos uma escala de 0 a10, correspondente às 100 parcelas (10 x 10 m) da nossa área amostral (100 x 100 m).

```
> mod1 <- ggplot (data, aes (x = x, y = y, z = elevação, fill =elevação)) +  geom_raster (interpolate = T) +  scale_fill_gradientn(colours = rainbow(10)) +  theme_gray (base_size = 14) +   labs(title="", x ="Número de parcelas", y = "Número de parcelas") + aes (fill = elevação) +  scale_x_discrete(limits = c(0,1,2,3,4,5,6,7,8,9,10)) +  scale_y_discrete(limits = c(0,1,2,3,4,5,6,7,8,9,10))
> mod1

> mod2 <- ggplot (data, aes (x = x, y = y, z = pH, fill =pH)) +  geom_raster (interpolate = T) +  scale_fill_gradientn(colours = rainbow(10)) +  theme_gray (base_size =
```

```
14) +   labs(title="", x ="Número de parcelas", y = "Número de parcelas") + aes (fill = pH) +
scale_x_discrete(limits = c(0,1,2,3,4,5,6,7,8,9,10)) +  scale_y_discrete(limits =
c(0,1,2,3,4,5,6,7,8,9,10))
        > mod2
```

Podemos construir também gráficos utilizando a função *geom_contour*, essa função é muito útil, uma vez que o ggplot2 não pode desenhar superfícies 3D verdadeiras, mas usando a função *geom_contour* podemos visualizar superfícies 3D em 2D. Para isso, os dados devem conter apenas uma linha para cada combinação exclusiva das variáveis mapeadas para o eixo x e y.

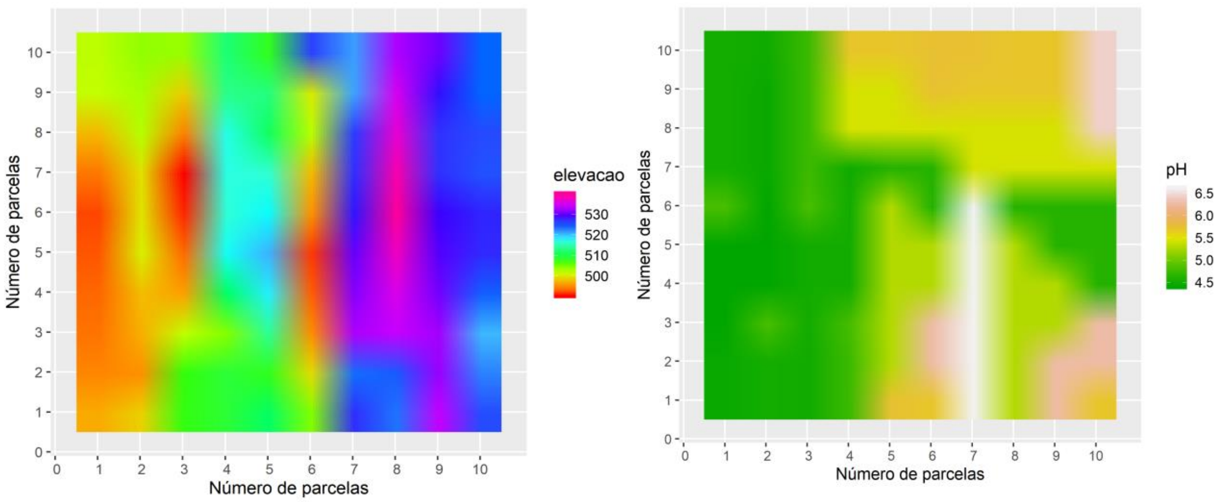

Figura 2. Gráficos raster com a função geom_raster para elevação (A) e pH (B), utilizando diferentes escalas de cores.

O contorno tende a funcionar melhor quando x e y formam um grid uniformemente espaçado. Se seus dados não estiverem uniformemente espaçados, convém interpolar para formar um grid antes de visualizá-los (Wickham, et. al., 2019). Nos exemplos abaixo, construímos gráficos sem interpolação da elevação (Figura 3A) e com interpolação da altura (figura 3B) utilizando diferentes escalas de cores, que podem ser ajustadas nos argumentos, conforme já descrito nesse capítulo.

```
        > mod3 <- ggplot(data, aes(x=x, y=y, z=elevacao)) + theme_gray(base_size = 14) +
  geom_raster(aes(fill=elevacao), interpolate=F) +   geom_contour (col='white', size=0.5) +
labs(title="Sem interpolação", x ="Número de parcelas", y = "Número de parcelas") +
  scale_x_discrete(limits=c(0,1,2,3,4,5,6,7,8,9,10))+scale_y_discrete(limits=
c(0,1,2,3,4,5,6,7,8,9,10))
```

```
> mod3
> mod4 <- ggplot(data, aes(x = x, y = y, z = altura))+theme_gray(base_size = 14)+
  geom_raster(aes(fill = altura),  interpolate = T)+  scale_fill_gradient(low = "white", high = "blue")+  geom_contour(colour = "black", binwidth = 1) +  labs(fill = "Altura", title = "Com interpolação", x = 'Número de parcelas', y = 'Número de parcelas') +  scale_x_ discrete (limits = c(0,1,2,3,4,5,6,7,8,9,10)) + scale_y_discrete(limits = c(0,1,2,3,4,5,6,7,8,9,10))> mod4
```

Finalmente, as funções a seguir podem ser utilizadas para salvar os gráficos separadamente (função *ggsave*) ou de forma conjunta (função *grid.arrange*). Para essa última é necessário a instalação do pacote ‘gridExtra’.

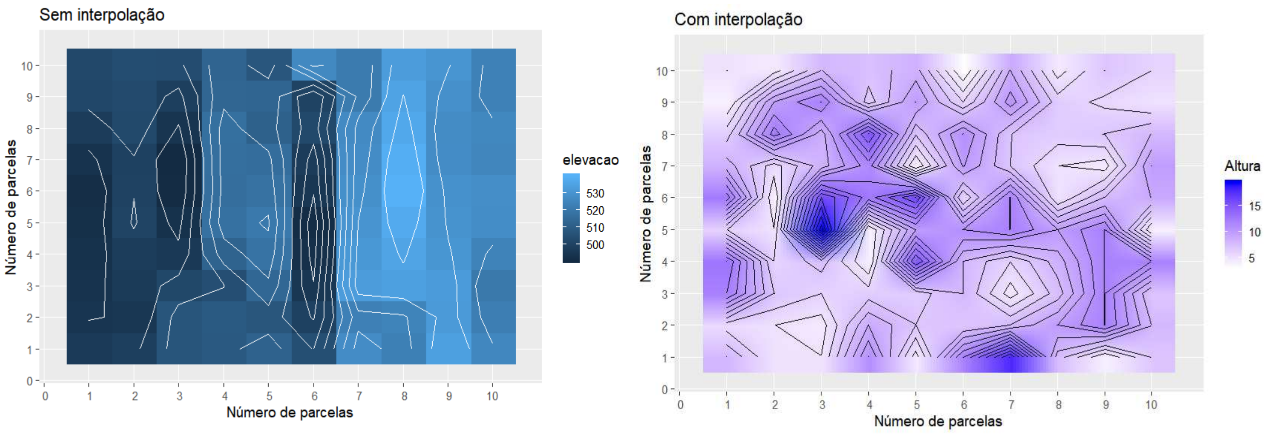

Figura 3. Gráficos raster com a função geom_raster e geom_contour, sem interpolação da elevação (A) e com interpolação da altura (B) utilizando diferentes escalas de cores.

```
> ggsave("nome_do_arquivo.png", width = 7, height = 6, dpi = 300)

> install.packages ("gridExtra")
> library(gridExtra)
>png("nome_do_arquivo.png", height=10, width=14, units="in", res=300)
grid.arrange(mod1, mod2, mod3,  mod4, ncol = 2, nrow=2)

>dev.off()
```

APLICAÇÃO DOS MÉTODOS EM ANÁLISES DE VEGETAÇÃO

Existem na literatura alguns trabalhos que utilizam essa metodologia de construção de gráficos descrita nesse capítulo (por exemplo: Liu, et al., 2014; Wang, et. al., 2016; 2016; Rodrigues, et. al., 2019 a, b). Na maioria desses estudos, essas análises foram utilizadas para determinar a formação de hábitats relacionados à distribuição espacial dos atributos florestais. Entre os habitats determinados, por exemplo, pela topografia, é provável que exista uma distribuição heterogênea de recursos, como água e nutrientes do solo, correlacionado com a existência de um gradiente edáfico. Essa heterogeneidade de distribuição dos fatores ambientais, na maioria desses estudos, foi relacionada diretamente com distribuição dos atributos da vegetação. Assim, esses gráficos constituem uma ferramenta interessante para demostrar de forma criativa ao leitor a relação entre distribuição de variáveis ambientais e atributos da vegetação.

Analisando a figura 1A e 2A, observamos que há um gradiente de elevação, desde o baixio até o platô. A distribuição dessa variável está relacionada com a distribuição do pH, na mesma área de estudo (figura 2B), o qual pode correlacionar-se, por exemplo, com a altura das plantas (figura 3B). Liu, et. al., 2014 demostrou em um estudo realizado no sul da China, que a composição de espécies, área foliar, altura máxima das árvores, a densidade de madeira e a massa das sementes relacionava-se com o gradiente de distribuição de variáveis ambientais tais com elevação, convexidade e declividade. Em um outro estudo, Wang et. al., 2016, encontrou uma relação entre variáveis topográficas e distribuição de espécies abundantes, raras, juvenis e adultos. Todos esses estudos usaram da ferramenta de construção de gráficos descrita nesse capítulo para mostrar de forma clara e objetiva esses achados.

Assim, essa metodologia de construção de gráficos pode ser bastante interessante para estudos onde se deseja demonstrar associações de espécies e atributos da vegetação com habitats ou gradientes de variáveis ambientais. Sendo também útil em análises de processo de formação de nicho e regras de montagem de comunidades.

Acessibilidade aos dados e comandos no R (script)

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Material suplementar

Tabela 1. Organização das variáveis na planilha Excel para análise no software R.

x	y	Topografia (ex: Elevação)	Atributo do solo (ex: pH, MO)	Atributo da floresta (ex: Altura, DAP, WD)
1	1	496	4,46	6
1	2	494	4,46	19.5
1	3	493	4,46	8
1	4	493	4,40	12.5
1	5	492	4,40	12
1	6	491	4,40	16
1	7	493	5.74	13
1	8	497	5.74	12.5
1	9	501	4.63	7.5
1	10	502	4.63	8.5
...	...	...	...	...
...	...	...	...	...
...	...	...	...	...
10	1	498	4.63	10
10	2	495	4.63	6.5
10	3	497	4.63	4.5
10	4	497	4.63	4
10	5	500	5.30	5
10	6	499	5.30	4.5
10	7	499	5.30	6
10	8	502	5.30	5.5
10	9	503	4.63	5
10	10	504	5.44	5

As colunas x e y correspondem ao número de parcelas nos eixos x e y do gráfico, respectivamente (Tabela 1). Cabe ressaltar que essa disposição dependerá do arranjo das parcelas no campo, mas sempre é recomendado que sejam parcelas contiguas. Assim, no presente estudo as subparcelas estão dispostas em um grande bloco, de forma que existem, dez parcelas no eixo x e dez no eixo y. As demais colunas correspondem aos valores das variáveis e atributos florestais em cada parcela. Após a sistematização dos dados na planilha é necessário salvá-la em formato txt.

CONCLUSÃO GERAL

O presente estudo realizado em um fragmento de Mata Atlântica no sudeste do Brasil mostrou que as variáveis topográficas, altitude e convexidade afetaram a fertilidade do solo nessa floresta. Por outro lado, apesar da diferença na riqueza e abundância de espécies arbóreas, os atributos florestais não tiveram efeito significativo na fertilidade do solo em escala local. Com base em nossos resultados as hipóteses propostas quanto a essa relação podem ser parcialmente aceitas, uma vez que algumas variáveis topográficas têm um efeito importante nos atributos do solo. Além disso, este estudo fornece informações valiosas de que uma avaliação da variabilidade espacial do solo em florestas com alta variabilidade topográfica deve ser uma premissa para otimizar os recursos durante as atividades de manejo. Portanto, nosso estudo demonstra que a variabilidade topográfica e a fertilidade do solo estão relacionadas e podem ser extremamente importantes para o desenvolvimento de planos de manejo para restauração e conservação florestal em escala local.

Encontramos também que as condições topográficas e o tempo de sucessão alteram a composição da comunidade arbórea, riqueza, abundância e proporção de espécies dominântes em carbono. Além disso, mostramos que os valores de CWM dos traços funcionais de WD e Dmax das espécies dominates em carbono determinam o estoque de AGC, corroborando a hipótese da razão de massa. Portanto, nosso estudo revela que tanto a composição funcional dos traços quanto a identidade taxonômica entre as espécies de dominantes em carbono moldam o estoque de AGC em nossas florestas estudadas. Observamos uma estabilização das espécies e famílias dominantes em carbono ao longo da sucessão secundária, sendo *Anadenanthera peregrina* a principal espécie dominate em carbono. Além disso, enfatizamos a relevância da abordagem baseada em traços para entender o funcionamento da floresta, o armazenamento de carbono e assim promover a recuperação da Mata Atlântica.

Esta pesquisa revela também que além da riqueza e abundância os grupos funcionais de fenologia foliar pode ser o principal preditor que explica as relações de estoque de carbono e riqueza de espécies. Além disso, este estudo evidenciou a contribuição das espécies sempre verdes na riqueza e revelou que as espécies decíduas contribuem altamente para o estoque de carbono, destacando um importante cobenefício de carbono e biodiversidade desses grupos funcionais. Além disso, econtramos que as mudanças nos grupos fenológicos de espécies decíduas de porte grande e com madeira densa para sempre verdes com porte menor e com madeira menos densa promovem diferenças na composição funcional e estoque de carbono ao longo do gradiente topográfico. Assim, nossos resultados também sugerem que mudanças na composição funcional serão mediadas pelas características associadas a cada estratégia fenológica. Assim, a maior contribuição desse estudo foi destacar a importância dos diferentes grupos funcionais de fenologia foliar para os cobenefícios entre estoque de carbono e biodiversidade. Evidenciando que as espécies decíduas mesmo com baixo número de espécies contribuem significativamente para o estoque de carbono. Por fim, destacamos a importância de avaliar as respostas individuais de espécies arbóreas e grupos funcionais foliares em cenários de mudanças climáticas, para a tomada de decisão na manutenção da riqueza, resiliência e resistência de espécies florestais tropicais.

Por fim, esse estudo fornece contribuições para a classificação de espécies de árvores sempre verdes, semidecíduas e decíduas em uma floresta tropical com base em fatores abióticos, principalmente topografia e propriedades do solo, que operam em escala local e fina sob a hipótese de filtragem ambiental. Verificamos que a elevação, dentre as três variáveis topográficas, foi o melhor preditor para a classificação da fenologia foliar das árvores, seguida das propriedades do solo SB e HAL usando *marchine learning algoritmos*. Entre os algoritmos de classificação baseados em aprendizado de máquina analisados, *ramdom forest* foi o melhor modelo de algoritmo. A previsão da classificação desses grupos funcionais pode ser a base para a identificação de espécies-chave a serem utilizadas em projetos de restauração ecológica sob diferentes condições topográficas e de solo em escala local.