UNIVERSIDADE FEDERAL DE LAVRAS

ALISSON BORGES MIRANDA SANTOS

USO DE DIFERENTES ABORDAGENS FILOGENÉTICAS NA COMPREENSÃO DA MONTAGEM DAS FLORESTAS TROPICAIS ATLÂNTICAS

LAVRAS – MG
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Orientador
Prof. Dr. Rubens Manoel dos Santos

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USE OF DIFFERENT PHILOGENETIC APPROACHES IN UNDERSTANDING THE ASSEMBLY OF ATLANTIC TROPICAL FORESTS

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Deus,

À Família,

Aos Amigos,

A todos os Brasileiros.

Dedico.

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*"Entenderemos a natureza de comunidades naturais
quando soubermos como recriar aquilo que,
inadvertidamente, muitas vezes, temos desmontado"*
(Begon, Townsend e Harper).

RESUMO GERAL

As florestas tropicais são comunidades naturais complexas devidos serem um conjunto de espécies que coexistem no espaço e no tempo, interagindo entre si (espécie-espécie) e com o ambiente (espécie-ambiente). Essas florestas são resultados de processos e mecanismos ecológicos atuais e do passado que influenciam na distribuição das espécies, a composição e funcionamento das comunidades. Diante dessa complexidade, a história evolutiva das espécies tem se mostrado uma abordagem frutífera para melhorar a compreensão dessas comunidades naturais. Assim, a presente tese teve como objetivo compreender a montagem das comunidades arbóreas em um gradiente de florestas tropicais através de abordagens de parentesco filogenético entre as espécies arbóreas. As abordagens utilizadas para compreender a montagem das florestas tropicais verificaram o *turnover* taxonômico e filogenético entre os sítios florestais, o papel da identidade taxonômica e do ambiente e a presença de assinatura filogenética na expressão absorção e estoque de carbono nas florestais tropicais. Para tal, foram utilizados dados de inventário de parcelas permanentes disponíveis no banco de dados ForestPlots.net system, sendo selecionado entre 14 a 30 sítios de florestas tropicais (totalizando entre 10,4 e 33,8 ha amostrais). As variáveis ambientais utilizadas foram os atributos químicos e texturais dos solos e os dados climáticos relacionados a precipitação e temperatura do ar. Nas florestas tropicais analisadas, a distância espacial via ambiente na dissimilaridade taxonômica e filogenética apresentou um fraco efeito indireto. Nessas florestas, o *turnover* entre as comunidades foram impulsionadas pelos efeitos diretos de mecanismos relacionados a processos neutros, de nicho e históricos. Quanto as expressões armazenamento e absorção de carbono nas florestas tropicais analisadas, essas foram influenciadas pela identidade taxonômica, com o ambiente apresentando um papel secundário e indireto nessas expressões. Além disso, as expressões armazenamento e absorção de carbono não apresentaram uma assinatura filogenética entre os gêneros aparentados (ausência de sinal filogenético), indicando que esses gêneros apresentam estratégias distintas no armazenamento e absorção carbono.

Palavras-chave: distância espacial, distância ambiental, turnover taxonômico e filogenético, sinal filogenético, condições ambientais, identidade taxonômica.

GENERAL ABSTRACT

Tropical forests are complex natural communities because they are a collection of species that coexist in space and time, interacting with each other (species-species) and with the environment (species-environment). These forests are the result of current and past ecological processes and mechanisms that influence the distribution of species and the composition and functioning of communities. Given this complexity, the evolutionary history of species has proven to be a fruitful approach to improve the understanding of these natural communities. Thus, this thesis aimed to understand the assembly of tree communities in a tropical forest gradient by means of phylogenetic relatedness approaches among tree species. The approaches used to understand tropical forest assembly verified taxonomic and phylogenetic turnover among forest sites, the role of taxonomic and environmental identity, and the presence of phylogenetic fingerprint in the expression of carbon uptake and storage in tropical forests. For this purpose, permanent plot inventory data available in the ForestPlots.net system were used, and between 14 and 30 tropical forest sites were selected (totaling between 10.4 and 33.8 ha of sampling). The environmental variables used were the chemical and textural attributes of the soils and the climatic data related to precipitation and air temperature. In the tropical forests analyzed, spatial distance via environment showed a weak indirect effect on taxonomic and phylogenetic dissimilarity. In these forests, turnover among communities was driven by the direct effects of mechanisms related to neutral, niche and historical processes. Carbon storage and uptake in the tropical forests analyzed were influenced by taxonomic identity, with environment playing a secondary and indirect role. Furthermore, carbon storage and uptake did not show a phylogenetic fingerprint among related genera (absence of phylogenetic signal), indicating that these genera have distinct strategies in carbon storage and uptake.

Keywords: spatial distance, environmental distance, taxonomic and phylogenetic turnover, phylogenetic signal, environmental conditions, taxonomic identity.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Um dos grandes desafios na ecologia é compreender processos e mecanismos que expliquem a distribuição, a composição e o funcionamento das comunidades naturais. Esse desafio é grande devido às comunidades naturais serem muito complexas, sendo um conjunto de espécies que interagem entre si e que são influenciadas por vários processos que agem em diferentes escalas espaciais e temporais.

Os processos relacionados à montagem de comunidades são os processos de nichos, neutros e históricos. Os processos baseados em nichos estão relacionados com a capacidade de resposta das plantas ao ambiente, denominados de filtros ambientais, como o clima e solo; ou as interações entre as espécies, como a competição. Os neutros estão relacionados aos papéis da dispersão, perturbação e eventos estocásticos na montagem das comunidades, enquanto os eventos históricos e biogeográficos referem-se à deriva genética e especiação. Esses processos são reconhecidos como estruturadores da comunidade, afetando diretamente a distribuição das plantas, a composição e o funcionamento das comunidades.

Nas últimas décadas, aumentou o interesse sobre a história evolutiva das espécies e como isso influência na montagem das comunidades naturais, principalmente porque o entendimento da história evolutiva das espécies facilita a compreensão do papel dos diferentes processos na montagem das comunidades. Para isso, foram desenvolvidas medidas filogenéticas que partem da premissa que os organismos descendem de ancestrais comuns e que as características são compartilhadas entre os organismos por meio da descendência. Assim, indivíduos mais próximos filogeneticamente tendem a ser mais semelhantes ecologicamente. O uso das diferentes medidas filogenéticas possibilita abordagens como: descrever os padrões de biodiversidade, explicar a coexistência em comunidades biológicas, entender a distribuição espacial das espécies e compreender se a similaridade fenotípica está associada ao parentesco evolutivo. Nessas abordagens, as comunidades são avaliadas quanto às relações evolutivas entre os táxons que as compõem, e a partir disso, é possível saber como as comunidades são estruturadas em função das modificações do ambiente que ocorrem em diferentes escalas espaciais e temporais.

Nessa tese, as relações de parentesco entre as espécies são utilizadas para esclarecer os processos estruturadores das comunidades em diferentes fisionomias de florestas tropicais. Assim, buscou-se entender o efeito direto e indireto de processos determinísticos (ambiente), neutros (distância espacial) e históricos na diversidade beta taxonômica e filogenética (Artigo

1) e a influência da identidade taxonômica e do ambiente na expressão ganho e estoque de carbono e verificação da presença de sinal filogenético nessa expressão em gêneros presentes ao longo do gradiente de deciduidade das florestas tropicais (Artigo 2).

2 REFERENCIAL TEÓRICO

2.1 PROCESSOS DE MONTAGEM DE COMUNIDADES

Uma comunidade ecológica é frequentemente definida como um conjunto de espécies que coexistem no tempo e no espaço, interagindo potencialmente umas com as outras, sendo resultado de processos ecológicos atuais e do passado, e de processos evolutivos (MCPEEK; MILLER, 1996). Na literatura, a montagem de comunidades tem sido discutida com base em processos relacionados ao nicho, processos neutros, e processos históricos e biogeográficos (CAVENDER-BARES et al., 2009; KRAFT et al. 2015). Os processos relacionados ao nicho são estruturados com bases nos mecanismos da filtragem ambiental e no princípio da exclusão competitiva (ou similaridade limitante), que ocorrem simultaneamente ao longo de vários eixos ambientais durante a montagem determinística, mesmo dentro de uma única comunidade, e influenciam a estrutura da comunidade (CORNWELL; ACKERLY, 2010; MASON et al., 2011; WEIHER; KEDDY, 1995).

A teoria da filtragem ambiental refere-se às interações espécie-ambiente, sendo que a persistência das espécies dentro de uma comunidade está relacionada à sua tolerância ao ambiente abiótico (WEIHER; KEDDY, 1995). Neste caso, o ambiente é visto como uma força seletiva, descartando espécies incapazes de tolerar condições em um determinado local (KRAFT et al., 2015). Nessa perspectiva, as espécies tendem a ser mais dispersas filogeneticamente em comunidades de baixa heterogeneidade ambiental e tornam-se mais agrupadas à medida que a heterogeneidade ambiental aumentava (STEVENS et al., 2012). Além disso, a influência desse processo na montagem de comunidades tende aumentar com a escala espacial, que possibilita abranger uma maior heterogeneidade ambiental (CARBONI et al., 2016; KEDDY; WEIHER, 1999).

Já a teoria da coexistência concentra-se na dinâmica de espécies que são capazes de tolerar as condições abióticas na comunidade, sendo uma etapa após a filtragem ambiental (KRAFT et al., 2015). A coexistência ocorre quando as diferenças de nicho estabilizam a competição pelos mesmos recursos limitantes (CAVENDER-BARES; KEEN; MILES, 2006). A importância da competição pode diminuir com o aumento da escala espacial devido à importância crescente da filtragem ambiental local (já que as diferenças ambientais geralmente se correlacionam com distâncias espaciais) ou limitação de dispersão (TATSUMI; CADOTTE; MORI, 2019). Em geral, espera-se que a similaridade limitante exclua as espécies semelhantes entre as espécies coexistentes, enquanto a filtragem ambiental deve

selecionar espécies muito semelhantes entre aquelas coexistentes que compartilham condições de habitat semelhantes (ANDERSEN et al., 2012).

Os processos neutros enfatizam a grande importância da deriva genética aleatória das espécies, em vez da influência do ambiente (KIMURA, 1991). Eles partem da premissa que todas as espécies são ecologicamente equivalentes quanto à aptidão no estabelecimento, dispersão e especiação. Neste caso, a distribuição das espécies são determinadas por processos estocásticos como limitação de dispersão e distúrbios naturais (HUBBELL, 2001).

Já os processos biogeográficos e históricos estão relacionados a processos que ocorrem em escalas temporais e espaciais mais longas e envolvem a especiação, extinção e dispersão, que influenciam na montagem, composição e diversidade das comunidades (CAVENDER-BARES et al. 2009; RICKLEFS, 1987). Com isso, o caráter ecológico das espécies nas comunidades vegetais atuais reflete a história biogeográfica das espécies e de seus ancestrais recentes (WEBB et al. 2002).

Esses processos não são excludentes na montagem das comunidades, com muitos estudos, por exemplo, mostrando que processos aleatórios neutros e baseados em nichos podem impulsionar em conjunto a montagem da comunidade em ecossistemas naturais (ASEFA et al., 2018; KEMBELL, 2009; KRAFT et al., 2007; SWENSON; ENQUIST, 2009).

2.2 DIVERSIDADE BETA: TAXONÔMICA E FILOGENÉTICA

Os padrões de diversidade nas comunidades naturais podem ser estudados a partir de diferentes níveis, como o taxonômico e o filogenético. A diversidade taxonômica é uma medida de diversidade de uma comunidade que pode ser expressa pelo número de espécies em função de uma unidade de área (densidade de espécies) ou de um determinado número de indivíduos (riqueza de espécies) (KREBS, 1989). Nestes casos, as espécies raras e abundantes nas comunidades possuem o mesmo peso. Visando melhorar as estimativas de diversidade taxonômica, índices de diversidade, como os de Shannon e Simpson, foram desenvolvidos combinando o número de espécies, a riqueza, a equabilidade e a maneira em que os indivíduos se distribuem pelas espécies (MAGURRAN, 2013; RICOTTA, 2003). Desta forma, altas riquezas e equabilidades passam a ser correlacionadas com elevadas diversidades (RICOTTA, 2003). No entanto, a principal limitação da diversidade taxonômica consiste em considerar as espécies como evolutivamente independentes e ecologicamente equivalentes (SWENSON et al., 2012), o que resulta numa capacidade limitada de inferir processos envolvidos na montagem de comunidades (McGILL et al., 2006).

A diversidade filogenética é uma medida da diversidade de uma comunidade que incorpora as diferenças entre espécies usando a distância filogenética (MAGURRAN, 2013), que consiste na soma do comprimento de todos os braços de uma determinada árvore filogenética (FAITH 1992a,b). A partir disso, a diversidade filogenética descreve a quantidade de história evolutiva compartilhada entre as espécies (HARDY et al., 2012), e representa a magnitude das diferenças fenotípicas entre elas (CAVENDER-BARES et al., 2009; WEBB et al., 2002). Essa medida de diversidade tem como premissa principal a que, a diversidade é maior em uma comunidade em que as espécies são filogeneticamente mais distintas, ou seja, maiores os comprimentos dos braços em uma determinada árvore filogenética (CIANCIARUSO; SILVA; BATALHA, 2009). Esta abordagem da diversidade possibilita entender os padrões de biodiversidade no tempo e espaço, sendo utilizada nos estudos de montagem de comunidades para medir a rotatividade espacial das linhagens impulsionada pela filtragem ambiental e/ou limitação de dispersão (SWENSON et al., 2007; TATSUMI; CADOTTE; MORI, 2019; WANG et al., 2015), o potencial evolutivo das espécies (WINTER et al., 2013), dentre outros. A abordagem filogenética da comunidade fornece uma maior compreensão de como a evolução das características afeta a montagem da comunidade, especialmente nos casos em que as características são obscuras e difíceis de serem obtidas (WEIHER et al., 2011).

Nestas abordagens, a diversidade é formada por três componentes: alfa, beta ou gama. A diversidade gama reflete a diversidade total de espécies observada em todos os habitats de uma região (ou seja, o *pool* de espécies) e pode ser dividida nos outros dois componentes da diversidade: a alfa e a beta. A diversidade alfa ou local consiste na diversidade em escala local, ou o número total de espécies em um habitat. Por fim, a diversidade beta é a mudança na composição de espécies ao longo de um gradiente ou entre locais (MAGURRAN, 2013; TUOMISTO, 2010a,b). A medida mais utilizada de diversidade beta é a taxonômica, que é a variação na composição das espécies entre os locais (GRAHAM; FINE, 2008). A diversidade beta também pode ser medida como a variação nas linhagens filogenéticas, sendo definida como uma medida de diversidade que mede como as relações filogenéticas mudam através de gradientes ambientais e/ou espaciais, fornecendo assim uma abordagem evolutiva para avaliar as variações nas comunidades vegetais (GRAHAM; FINE, 2008). A ideia essencial da diversidade beta é entender como a composição de espécies e a composição filogenética muda nos gradientes ambientais e espaciais (GRAHAM; FINE, 2008), sendo que a diversidade beta tende a aumentar com a dissimilaridade ambiental ou extensão espacial (SOININEN; HEINO; WANG, 2018).

A diversidade beta pode ser decomposta em dois componentes: diferença de riqueza ou aninhamento (nestedness) e substituição de espécies/linhagens (turnover) (BASELGA, 2010), sendo que esses componentes podem estar ligados a diferentes processos (SI et al., 2016). A diferença de riqueza (aninhamento) mede a perda de espécies ou linhagens ao longo de gradientes, ou entre locais, ou seja, diferentes comunidades apresentam variação entre as suas riquezas de espécies ou linhagens (ALMEIDA-NETO; FRENSEL; ULRICH, 2012; BASELGA, 2010), o que muitas vezes está relacionado à dinâmica ordenada de extinção-colonização (SI et al., 2016). O aninhamento ocorre quando a composição de espécies ou linhagens de comunidades pequenas (ou menos diversas) é um subconjunto de comunidades grandes (ou mais diversas) (ULRICH et al., 2009). O turnover mede a substituição de espécies ou linhagens ao longo de gradientes ambientais, ou entre locais (BASELGA, 2010), refletindo a seleção das espécies ou linhagens pelas diferentes condições ambientais, ou restrições históricas na dispersão que geram endemismos (SI et al., 2016), o que promove uma renovação espacial da composição (BASELGA, 2010). As abordagens da diversidade beta têm-se concentrado amplamente no turnover e na substituição de espécies ou linhagens entre as comunidades devidas esse componente predominar em vários ecossistemas e grupos taxonômicos (ANDERSON et al., 2011; KRAFT et al., 2011; SOININEN; HEINO; WANG, 2018). Em estudos de montagem de comunidades, ela tem sido utilizada para separar o papel de processos neutros, como a limitação de dispersão, de processos baseados em nichos, como a filtragem ambiental, nos padrões de diversidade regional (GRAHAM; FINE, 2008). Isso fornece a possibilidade de identificar a escala e as condições sob as quais processos neutros *versus* baseados em nicho predominam (CAVENDER-BARES et al., 2009).

Os estudos dos padrões de diversidade beta podem fornecer informações importantes para a indicação de áreas prioritárias de conservação (SOCOLAR et al., 2016). Um papel importante da substituição de espécies ou linhagens indica a necessidade de dedicar esforços de conservação em um grande número de locais diferentes, enquanto um papel importante do aninhamento sugere a necessidade de conservar os locais mais ricos (BASELGA, 2010).

2.3 SINAL FILOGENÉTICO

Uma observação importante na ecologia é que as espécies descendem de ancestrais comuns e esse parentesco resulta em semelhanças na maioria dos aspectos do fenótipo (BLOMBERG; GARLAND; IVES, 2003). Assim, espécies estreitamente relacionadas compartilham características por meio da descendência e conforme as linhagens divergem, os traços serão mais semelhantes dentro dos clados do que entre os clados (CRISP; COOK,

2012). Essa semelhança é determinada pelo sinal filogenético, que investiga o grau de parentesco filogenético entre as espécies, sendo utilizado para descrever uma tendência de organismos evolutivamente relacionados a se assemelharem filogeneticamente (BLOMBERG; GARLAND; IVES, 2003; CRISP; COOK, 2012).

O sinal filogenético pode ser detectado para uma determinada característica e a sua existência possibilita realizar inferências sobre esta característica para parentes próximos simplesmente pelo conhecimento de sua posição filogenética (BLOMBERG; GARLAND; IVES, 2003). A presença do sinal filogenético é observada quando os caracteres evoluem de forma semelhante ao movimento browniano. Isso significa que a quantidade de mudança na característica é geralmente pequena e aleatória, condicionado pela deriva genética ou seleção natural que flutuariam aleatoriamente ao longo do tempo (CRISP; COOK, 2012). Neste cenário, quanto menor a quantidade de tempo desde que duas espécies compartilharam um ancestral comum (ou seja, quanto mais intimamente relacionadas são as duas espécies), menor será a diferença fenotípica esperada entre elas (BLOMBERG; GARLAND, 2002). No entanto, táxons intimamente relacionados podem ser menos semelhantes que o esperado, apresentando uma ausência do sinal filogenético (BLOMBERG; GARLAND; IVES, 2003). Isso ocorre quando a evolução convergente nas características condicionadas por pressões ambientais semelhantes levam as espécies distantemente relacionadas a serem mais semelhantes umas com as outras do que o esperado (WAKE, 1991), ou quando temos o deslocamento de caractere, o que faz com que organismos intimamente relacionados se assemelhem menos do que o esperado (LOSOS, 2000).

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SEGUNDA PARTE - ARTIGOS

ARTIGO 1 - Disentangling spatial, environmental and historical effects on tropical forest tree species turnover

(artigo apresentado na íntegra, conforme foi aceito, nas normas do *Journal of Plant Ecology*)

Running title: Disentangling community assembly processes

Disentangling spatial, environmental and historical effects on tropical forest tree species turnover

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Abstract

Aims

We aimed at disentangling the effects of spatial distance, current, and past environmental dissimilarity, and their combinations on tree community taxonomic and phylogenetic turnover by addressing the following questions: a) Is tree community taxonomic and phylogenetic turnover related to the indirect effects of spatial distance via environmental dissimilarity? b) Does tree community taxonomic and phylogenetic turnover respond to paleoclimate (Last Glacial Maximum and Mid-Holocene)?

Methods

The study was carried out in 14 Atlantic rainforest sites in Brazil (20.4 ha sampled) containing 615 tree species from 83 plant families. We obtained plot-level geographic coordinates and soil variables and site-level bioclimatic variables in the current, Mid-Holocene, and Last Glacial Maximum. We used structural equation models (SEM) with a distance-based approach to (i) test the direct effects of spatial distance and environmental dissimilarity, and (ii) test the indirect effects of spatial distance via environmental dissimilarity on taxonomic (Bray-Curtis distance) and phylogenetic turnover (Comdist and Comdistnt distances).

Important Findings

Our results suggest a weak indirect effect of spatial distance via environmental dissimilarity on taxonomic and phylogenetic turnover. Tree community turnover was driven by the direct effects of neutral, niche-based and historical processes. Thus, we inferred that the paleoclimate (historical processes) promoted the selection of the clades that gave rise to the current flora, while spatial distances (neutral processes) limited the dispersal range of species from the regional pool and environmental conditions (niche-based processes) locally selected the taxa that are able to persist.

Key-words: assembly processes, phylogenetic communities, environmental filtering, neutral communities, phylogenetic turnover, ecological niche, paleoclimate effects

Introduction

Understanding the processes and mechanisms that drive species distribution is a central issue in ecology (Hardy *et al*. 2012; Zhang *et al.* 2013). Species distribution and community assembly reflect stochastic, deterministic and historical processes (Cavender-Bares *et al*. 2016; Chase 2014). These processes co-occur and may interact throughout history, hampering a detailed understanding of their individual effects on community assembly and species distribution. This knowledge is crucial to understand and predict species distribution and community assembly patterns in face of global change.

The effects of each process can be inferred from mechanisms such as spatial distance (dispersal), environmental distance (environment) and past events (paleoclimates). The effects of spatial distance are attributed to neutral processes, such as dispersal limitation (Diniz-Filho *et al*. 2012; Zhang *et al*. 2013), which can be interpreted as the failure of individuals to reach environmentally suitable areas (Eiserhardt *et al*. 2013). Thus, the capacity of propagules to arrive at a given site should influence the floristic and phylogenetic similarity between communities. When dispersal only occurs over short distances, this low capacity to exchange propagules between spatially distant communities should promote an increase in taxonomic and phylogenetic turnover with an increase in spatial distance (Cadotte 2006; Myers and Harms 2009; Soininen *et al*. 2018).

The influence of environmental conditions on species distribution and community assembly is attributed to niche-based (deterministic) processes related to the environmental filtering of species (Cadotte and Tucker 2017; Diniz-Filho *et al*. 2012; Zhang *et al*. 2013). Environmental filtering refers to species–environment interactions, whereby species

persistence within a community is related to their tolerance to the abiotic environment (Weiher and Keddy 1995). The main environmental filters that shape plant communities are related to climate (which in general operates at larger spatial scales and determines the distribution of biomes; Harrison *et al*. 2010; Svenning *et al*. 2015) and soil (which in general predominates at smaller spatial scales and influence the local distribution of species; John *et al.* 2007).

However, space and environment can act together because environmental conditions are often spatially structured. This hampers our ability to disentangle the direct effects of spatial distance and environmental dissimilarity on species turnover and community assembly (Diniz-Filho *et al*. 2012; Lobo *et al*. 2001). In this case, the environmental gradient emerges as spatial distance increases and environmental conditions change. Along a spatially structured environmental gradient, species turnover occurs through the gradual replacement of species by others more adapted to the newly emerging environmental conditions (Chase 2014; Keddy and Weiher 1999; Soininen *et al.* 2018).

Although taxonomic turnover and phylogenetic turnover are commonly associated with assembly processes from recent time scales (Cavender-Bares et al. 2016), they reflect evolutionary dynamics at multiple temporal scales (Bose et al. 2019). Past diversification and adaptations determine the phylogenetic diversity of extant taxa, reflecting the influence of adaptations inherited over time and recent processes, such as current environmental constraints (Bose et al. 2019 and your references; Gerhold et al. 2018). Historical events associated past climatic conditions (e.g. during the Last Glacial Maximum [LGM] and Mid-Holocene [HOL]) have played an important role in community assembly. Through environmental filtering, selection of taxa and their role in lineage diversification and extinction, these events have contributed to shaping present-day species distribution and community diversity (Gerhold *et al*. 2018; Hewitt 2000; Svenning *et al*. 2015). As ecological

and historical processes both affect community assembly (Neves *et al*. 2015; Zobel 2016), disentangling their roles on taxonomic and phylogenetic turnover is a fundamental step toward understanding community assembly rules (Asefa *et al*. 2019; Massante and Gerhold 2020; Yang *et al*. 2015). Using both taxonomic and phylogenetic turnover provides a complementary picture of community change, since species turnover influences phylogenetic turnover (Hardy *et al.* 2012). Also, investigating these two facets of community change improves our understanding of the diversity of natural communities, providing an essential basis to define priority areas for conservation.

Here, we aim at disentangling the effects of spatial distance, historical effects and environmental dissimilarity on tree community taxonomic and phylogenetic turnover. For this, we used data from 14 sites of Brazilian Atlantic rainforest and metrics of phylogenetic beta diversity sensitive to basal and terminal branching in the phylogeny (Mazel *et al*. 2016). Specifically, we address the following questions: (i) Is tree community taxonomic and phylogenetic turnover related to the indirect effectsof spatial distance via environmental dissimilarity? As environmental variation is often spatially structured (Diniz-Filho *et al*. 2012; Lobo *et al*. 2001), we expect taxonomic and phylogenetic turnover to be driven by the effects of environmental conditions (i.e. nichebased processes); (ii) Does tree community taxonomic and phylogenetic turnover respond to paleoclimate (Last Glacial Maximum and Mid-Holocene)? As the climate conditions in which species evolved have a lasting influence on the assembly of plant communities (Cavender-Bares *et al.* 2016), we expect paleoclimate to have a direct effect on taxonomic and phylogenetic turnover, especially on deeper nodes of the phylogeny (basal clades).

Material and Methods

Study areas and database

The study was carried out in 14 forest sites inserted in the Atlantic forest domain *sensu lato* in the state of Minas Gerais, Brazil. These are secondary forest fragments at advanced successional stages, that hold no record of major disturbances in recent decades (approximately 50 years) due to their partial or full environmental protection. The greatest distances between sites are approximately 115 km (latitude) and 110 km (longitude). The climate of the region is classified as Koppen Cwa (mesothermal climate, with dry winters and hot summers), with a minimum average temperature of 14 °C, an average of 21 °C and a maximum average of 27 °C (Martins *et al.*2018; Reboita *et al.* 2015).

The 14 sites constitute a database of long-term vegetation monitoring, hosted in the ForestPlots.net system (https://www.forestplots.net) and available upon request (see area codes in Supplementary Table S1). The oldest site was sampled for the first time in 1987 and the most recent site was sampled for the first time in 2011. All sites have been inventoried a different number of times, but here we only selected the most recent inventory of each (all of which took place between 2016 and 2019). In each site, between 25 and 126 permanent plots were sampled (a total of 588 plots and a mean 42 plots per site), with plot size varying between 200 and 400 m^2 (mean 382.1 m^2 per plot and a total sampled area of 20.4 ha). In each plot, we measured and identified all trees with diameter at breast height of 1.30 m equal to or higher than 5 cm. We included trees with multiple stems when their equivalent diameters (square root of the sum of squares of the individual stem diameters) met the inclusion criterion (Scolforo and Mello 1997). Plant identification followed APG IV (Angiosperm Phylogeny Group 2016; Chase et al. 2016) and was performed by experts in the field or through herbarium visits. A total of 615 tree species and 83 plant families were sampled.

Taxonomic and phylogenetic turnover

To synthesize taxonomic turnover, we obtained Bray–Curtis distances between plots using an abundance matrix through the *vegan* package (Oksanen *et al*. 2018). To calculate the metrics of phylogenetic turnover, we obtained an ultrametric tree containing all species of our species pool. We used as a reference the mega-tree available in the package *V.PhyloMaker* (GBOTB.extended, Jin and Qian 2019), which contains 74 533 species and all families of extant vascular plants. When a species or genus from our dataset was not included in the mega-tree we adopted the approach recommended by Qian and Jin (2016), whereby the tips of these species and genera were bound to the half-point of the genus or family branch, which is the branch between the genus or family root node and the basal node. To summarize differences in phylogenetic composition between plots, we calculated the metrics intercommunity mean pairwise distance (Comdist) and intercommunity mean nearest taxon distance (Comdistnt) using the package *picante* (Kembel *et al*.2010). While Comdist captures distances related to the deeper nodes of a phylogeny, Comdistnt captures the distances related to recent divergences.

Climate data

With the sites' coordinates (latitude and longitude), we obtained the 19 bioclimatic variables (bio1– 19) from the WorldClim Global Climate Data repository (Hijmans *et al*. 2005), whereby plots of the same fragment were assigned to the same cell and therefore had the same climate value. The 19 bioclimatic variables were: annual mean temperature (bio1), mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), annual temperature range (bio7), mean temperature of the wettest quarter (bio8), mean temperature of the driest quarter (bio9), mean temperature of the warmest quarter (bio10),

mean temperature of the coldest quarter (bio11), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (bio15—coefficient of variation of annual monthly precipitation), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18) and precipitation of the coldest quarter (bio19).

We extracted these variables with 30 arc-seconds resolution (1-km spatial resolution) for the current climate and HOL and with 2.5 arc-minutes resolution for the LGM. Bioclimatic data for the LGM and the HOL were obtained using the General Circulation Model (GCM). Only one GCM was used for each scenario due to the collinearity between GCMs. Thus, we randomly selected for the HOL the climate model 'MRI-CGCM3' from the Meteorological Research Institute, and for the LGM the 'MPIESM-P' from the Max Planck Institute. The variables extracted from WorldClim (bio1–19) were the same ones extracted from the two GCMs to describe the climate of the LGM and the HOL (e.g. bio1, annual mean temperature, represents the same variable in the three climate databases). Climate data were obtained using the raster and sp packages (Hijmans 2017; Pebesma and Bivand 2005).

Soil data

The explanatory variables of soil chemistry and texture were obtained from 1-L samples of superficial soil (0–20 cm of depth) collected in each plot of each site. The collected soil was stored in labeled plastic bags and sent to an authorized laboratory of soil analysis, which followed the protocol by the *Empresa Brasileira de Pesquisa Agropecuária* (Embrapa 1997). The chemical variables obtained were pH, phosphorus (mg/cm^3) (P), potassium (mg/cm^3) (K), calcium ($cmol/dm^3$) (Ca), magnesium ($cmol/dm^3$) (Mg), aluminum ($cmol/dm^3$) (Al), organic matter of soil (dag/kg), potential acidity (H + Al), sum of bases (SB), effective CEC (cation exchange capacity), CEC at pH 7.0, aluminum saturation (m%)

and base saturation (V%); the textural variables were sand percentage (dag/kg), silt percentage (dag/kg) and clay percentage (dag/kg).

Data analysis

As a first explanatory step, we evaluated the multivariate relationships between spatial variation (latitude and longitude) and climate data through principal component analysis (PCA): one PCA for each set of climatic data (current, HOL and LGM). We further evaluate the multivariate relationship between spatial variation (latitude and longitude) and soil data also using a PCA. For this, used the packages*factoextra*, *FactoMineR* and *ggplot2* (Kassambara and Mundt 2020; Lê *et al.* 2008; Wickham 2016) in the software R version 3.6.1 (R Core Team 2019). Posteriorly, we graphically analyzed the relationship between spatial distance and taxonomic and phylogenetic turnover to verify how the metrics behaved with the increase in spatial distance.

Then, we gathered our explanatory variables in groups that synthesized the explanation of the variables. The groups were as follows: spatial distance (based on latitude and longitude), soil fertility (soil chemical variables), soil texture (sand, silt and clay), present-day temperature (bio1–11), present-day precipitation (bio12–19), HOL temperature (bio1–11 from the HOL), HOL precipitation (bio12–19 from the HOL), LGM temperature (bio1–11 from the LGM) and LGM precipitation (bio12–19 from the LGM). In these groups, we used plot-level geographic coordinates (latitude and longitude) and soil data and site-level bioclimatic variables in the current, HOL and LGM. That means that, although climate values were the same for plots within the same site, each plot had a distinct geographic coordinate and set of values for soil variables. Later, we calculated Euclidean distances between plots for each group and standardized their values. Euclidean distances were obtained using all variables associated with each group, and no method was used to reduce them (as PCA), e.g.,

in the soil fertility group, we calculated Euclidian distances between plots using all soil chemical variables (phosphorus, organic matter, SB, among others). Moreover, the contribution of explanatory variables in each group was not quantified; e.g. the contribution of the phosphorus variable to the soil fertility group was not measured. We used structural equation models (SEMs), through a distance-based approach, to test the direct and indirect effects of spatial distance and environmental variables on taxonomic turnover (Bray–Curtis distance) and phylogenetic turnover (Comdist and Comdistnt distances). The SEM approach is able to integrate multiple processes into a single model. Here, we use SEM to test the effects of neutral (spatial distance), niche-based (soil and current climate) and historical (paleoclimate) processes on taxonomic and phylogenetic turnover. As a direct effect, we consider the directional relationship between two variables, e.g. the effect of an independent variable (spatial distance, soil and climate) on a dependent variable (Bray–Curtis distance); as an indirect effect, we consider the effect of an independent variable (spatial distance) on a dependent variable (Bray– Curtis distance) through one or more intervening or mediating variables (soil and climate). Thus, the models were built as follows: X being the spatial distance (explanatory variable); M being soil fertility, soil texture, temperature and precipitation distances (mediating variables) and Y being Bray–Curtis, Comdist and Comdistnt distances (response variables). We tested the direct effects of X and M on Y and also the indirects effect of X on Y via M. We constructed the models of each response variable for each scenario (current, HOL and LGM). This approach enabled us to (i) test if spatial distance leadsdirectly to taxonomic and phylogenetic turnover, (ii) test if taxonomic and phylogenetic turnover occurs through the effects of spatial distance on environmental variables (i.e. if spatially structured environmental change leads to spatially structured patterns of taxonomic and phylogenetic change) and (iii) verify the direct effects of environmental variables on taxonomic and phylogenetic composition. The relationships

between the response variables with the climate of each temporal scenario were assessed by the comparison of their effects sizes (coeffcients). We checked for model goodness of ft through: Comparative Fit Index (CFI >0.90), Tucker–Lewis Index (TLI >0.90), Goodness of Fit Index (GFI >0.90), Root Mean Square Error of Approximation (RMSEA <0.05) and Standardized Root Mean Square Residual (SRMR <0.05). We did not consider the chi-square statistic due to the high number of observations (>100 000). Regressions were checked for residuals normality. We used maximum log-likelihood to estimate the statistical significance of direct and indirect effects. All SEM analyses were run through the *lavaan* package (Rosseel 2012) in R version 3.6.1 (R Core Team 2019)

Results

The two main dimensions (axis) of the PCA with the climate (current, HOL and Last Glacial Medium) explained, respectively, 83.5%, 83.4% and 83.5% of the variation, with axis 1 explaining more than 65% in the three PCAs (Supplementary Figs S1–S3 and Tables S2–S4). In general, the PCA presented two groups on axis 1, a group with longitude and precipitation variables and the second group with latitude and temperature variables (Fig. 1a–c). Soil PCA, the two main axes explained 59% of the variation (axis 1 with 41.3% and axis 2 with 17.7%) (Fig. 1d, Supplementary Fig. S4 and Table S5). Two groups were formed, one with latitude and edaphic variables related to high soil fertility, such as base saturation (V), SB and cation exchange capacity and the other group, with longitude and variables related to low fertility and acidic soils, such as aluminum saturation (m), potential acidity (H + AL) and aluminum (AL) (Fig. 1d). The relationship between spatial distance and taxonomic and phylogenetic turnover showed a positive correlation, indicating that taxonomic and phylogenetic turnover increases with spatial distance (Fig. 2). The SEM results revealed that all relationships were significant ($P < 0.001$). Spatial distance had a positive effect on all

environmental dissimilarity variables, meaning that increasing spatial distance predicts increasing environmental dissimilarity between plots. Soil fertility, however, did not follow this pattern and displayed contrasting values in spatially close plots (Tables 1 and 2; Figs 3–5).

For taxonomic turnover, in the model using the current climate, the greatest direct effect on Bray–Curtis distance were produced by soil fertility (0.224, $P < 0.05$) and spatial distance (0.202, $P < 0.05$) (Fig. 3a). All indirect effects of spatial distance on Bray– Curtis distance via the environmental variables were smaller than the direct effects of environmental variables alone (Fig. 3a and Table 2). In the models using paleoclimate data from the HOL and LGM, the greatest direct effects on Bray–Curtis distance were produced by spatial distance (0.30 and 0.26, $P < 0.05$ and $P < 0.05$, respectively), followed by soil fertility (0.23 and 0.23, $P < 0.05$ and $P < 0.05$) (Fig. 3b and c). The model with the HOL climate also revealed a direct effect of HOL the precipitation (0.18, $P < 0.05$) (Fig. 3b). The model with the LGM climate revealed a direct effects of LGM precipitation (0.18, $P < 0.05$) and soil texture effect (0.15, $P < 0.05$) and indirect effects of spatial distance via LGM precipitation (0.14, $P < 0.05$) on Bray–Curtis distance (Fig. 3c and Table 2). All other (direct and indirect) effects were smaller than those cited above (Fig. 3 and Table 2).

For the turnover of terminal clades, the greatest effect on Comdistnt distance in models using the current climate were the direct effects of soil fertility (0.17, $P < 0.05$) and spatial distance (0.16, $P < 0.05$) (Fig. 4a). Considering the model using HOL climate data, the greatest effects were produced by a spatial distance (0.24, $P < 0.05$) and soil fertility (0.18, $P < 0.05$), with only a small contribution of all other (direct and indirect) effects (Fig. 4b and Table 2). The model using the LGM climate highlighted the effects (Fig. 4c). This model also highlighted an indirect effect of spatial distance via LGM precipitation (0.14, $P < 0.05$) (Table 2).

For the turnover of basal clades, in the models using the current climate, the greatest effects on Comdist distance were the direct effect of spatial distance (0.16, $P < 0.05$) and the indirect effect of spatial distance via precipitation (0.10, $P < 0.05$) (Fig. 5a and Table 2). The models that used climate data from the HOL revealed a direct effect of HOL temperature and an indirect effect of spatial distance via HOL temperature (0.21 and 0.17, $P < 0.05$ and $P < 0.05$, respectively) (Fig. 5b and Table 2). For the climate data of from LGM, the direct effects were generally weak. The greatest direct effects were produced by LGM precipitation (0.12, $P < 0.05$), spatial distance (0.10, $P < 0.05$) and LGM temperature (0.09, $P < 0.05$), while, the greatest indirect effect was produced by spatial distance via LGM precipitation (0.09, $P < 0.05$) (Fig. 5c and Table 2). All other (direct and indirect) effects had a low contribution to Comdist distance variation. Although the associations were statistically significant, the explanatory power was small, with R-square below 10% (Fig. 5 and Table 2).

Discussion

Although the environmental variables are mostly spatially structured, the indirect effects of spatial distance via environmental variables on taxonomic and phylogenetic turnover are weak. However, the strong direct effects produced by environmental variables suggest that spatially structured environmental change can contribute to turnover. In general, our analyses suggest that neutral and niche-based processes have played important roles in determining taxonomic and terminal clade turnover at the spatial scale examined herein. Despite the weak explanatory power of the models, the paleoclimates had a strong effect on basal clade turnover, highlighting the role of historical processes on present-day tree communities.

The role of different ecological processes as driversof phylogenetic and taxonomic turnover has been documented in other studies (Asefa *et al.* 2019; Neves *et al.* 2015; Zobel

2016). These findings highlight that neutral and niche-based processes can concurrently influence the regional species pool (Neves *et al.*2015; Zobel 2016). In our study, we believe that this influence is hierarchical, according to the traditional view of the species pool selection (Cadotte and Tucker 2017; Zobel 2016). In this perspective, neutral and niche-based ecological processes (e.g. dispersal, abiotic environment) impose filters to the colonization and establishment of species, which shape patterns of ecological diversity at different spatial scales and across different ecosystems (Emerson and Gillespie 2008; Hardy *et al.* 2012; Zhang *et al.* 2013). Thus, any species from the regional species pool undergoes these ecological processes to establish and persist in a given community (Zobel 2016).

The strong direct effect of spatial distance is evidence of the role played by dispersal limitation in community assembly (Fine and Kembel 2011; Zhang *et al.* 2013), the first filter in the hierarchy (Zobel 2016). Dispersal limitation can be conceptualized as the failure of individuals and/or species to colonize suitable habitats (Eiserhardt *et al.* 2013), which decreases the possibility of propagule Exchange among local communities. Thus, local communities that are closer in space tend to be floristically and phylogenetically more similar than spatially distant communities due to decreasing dispersal capacity across long distances (Cadotte 2006; Smith and Lundholm 2010; Soininen *et al.* 2018). In our findings, tree community taxonomic and phylogenetic turnover increased with spatial distance (i.e. distant sites were taxonomically and phylogenetically dissimilar) (Soininen *et al.* 2018), highlighting the role of dispersal limitation in community assembly.

We expected environmental variation to be spatially structured and, therefore, to promote the spatial turnover of species and clades, but our results revealed a weak indirect effect of spatial distance via environmental dissimilarity on taxonomic and phylogenetic turnover. However, the direct effects of the environmental variables on community assembly suggest the spatial structure of environmental conditions as a driver of spatial structure in

species distribution. Consequently, taxonomic and phylogenetic turnover should be related to environmental changes (Smith and Lundholm 2010) even across short spatial distances (Rezende *et al.* 2015; Yang *et al.* 2015). Thus, from the perspective of hierarchical filtering, even if a propagule from a taxon the regional species pool surpasses the dispersal filter and reaches a given community, local environmental conditions would still select (filter) the arriving individuals, largely influencing overall plant survival, establishment and growth (Cadotte and Tucker 2017; Emery *et al.* 2012; Zobel 2016). Among the environmental variables, soil fertility had the greatest direct effect on taxonomic and terminal clade turnover. Soil fertility is known to influence the spatial distribution of many neotropical tree species at small spatial scales and is, therefore, considered, a strong filter for species selection, highlighting the role played by niche processes (John *et al.* 2007).

Although we use plot-level soil data and sitelevel climate data from three different periods, our models had low explanatory power, especially for basal clade turnover, suggesting that there must be other, more important, drivers of taxonomic and phylogenetic turnover. Among the variables analyzed, paleoclimate variables (temperature and precipitation of the HOL and LGM) were the most important mediators of basal clade turnover. But while the paleoclimate also had significant direct effects for terminal clade and taxanomic turnover, they were weaker than those of other environmental variables. These effects provide evidence of the role of paleoclimates as environmental filters, acting as mediating the selection and distribution of clades in the past. Moreover, because the climate of origin of clade greatly influences present-day plant diversity (Boucher-Lalonde *et al.* 2015), terminal clades reflect cumulative diversification responses mediated by paleoclimates (Cavender-Bares *et al.*2016; Svenning *et al.* 2015). The effects of the paleoclimate can also explain why the direct effects of spatial distance were greater than the effects of the current

climate on tree community turnover. In this case, the spatial structure of paleoclimates would be reflected in the current effects of spatial distance on turnover.

In sum, our study shows that neutral, nichebased and historical processes act simultaneously on community assembly. Historical processes associated with the paleoclimate mediate of the selection and distribution of basal clades (and consequently the terminal clades) in present-day tree communities, while neutral and niche-based processes operate hierarchically in determining the distribution of species across space. Thus, dispersal capacity defines the spatial range that taxa from the regional species pool are able to colonize, while site environmental conditions (mainly related to soil fertility) locally select the species that are able to persist. Our findings highlight the singularity of tropical that tropical Atlantic forest remnant in terms of environmental heterogeneity, taxonomic and phylogenetic composition. Our results are relevant for planning conservation strategies that take into account taxonomic and phylogenetic diversity. A suggested approach to conserve this diversity is to protect as many communities spread across the landscape, encompassing a broader range of environmental conditions and taxonomic and phylogenetic compositions. Therefore, in addition to the existing conservation units, it is necessary to include more fragments across space to maximize the conservation of taxonomic and evolutionary diversity of tropical Atlantic forest remnants.

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Table Legend

Table 1: Effect of spatial distance on environmental variables.

Environmental variables	Effect size	P
Soil Texture	0.258	<0.05
Temperature	0.694	<0.05
Precipitation	0.572	<0.05
Soil Fertility	-0.030	<0.05
Holocene Temperature	0.801	<0.05
Holocene Precipitation	0.382	<0.05
Last Glacial Maximum Temperature	0.737	<0.05
Last Glacial Maximum Precipitation	0.749	<0.05

Table 2: Indirect effects of spatial distance via environmental variables on taxonomic turnover (Bray-Curtis distance); terminal clade turnover (Comdistnt distance) and basal clade (Comdist distance) in models with current climate data; Mid-Holocene (HOL) climate data and Last Glacial Maximum (LGM) climate data.

Metrics	Indirect Effects (IE)	IE size	P
Bray-Curtis	spatial distance via soil texture	0.037	<0.05
	spatial distance via temperature	0.111	<0.05
	spatial distance via precipitation	0.093	<0.05

	spatial distance via soil fertility	-0.007	<0.05
Comdistnt	spatial distance via soil texture	0.029	<0.05
	spatial distance via temperature	0.085	<0.05
	spatial distance via precipitation	0.058	<0.05
	spatial distance via soil fertility	-0.005	<0.05
Comdist	spatial distance via soil texture	-0.010	<0.05
	spatial distance via temperature	0.046	<0.05
	spatial distance via precipitation	0.058	<0.05
	spatial distance via soil fertility	-0.001	<0.05
Bray-Curtis	spatial distance via soil texture	0.021	<0.05
	spatial distance via HOL temperature	0.056	<0.05
	spatial distance via HOL precipitation	0.068	<0.05
	spatial distance via soil fertility	-0.007	<0.05
Comdistnt	spatial distance via soil texture	0.022	<0.05

	spatial distance via HOL temperature	0.038	<0.05
	spatial distance via HOL precipitation	0.029	<0.05
	spatial distance via soil fertility	-0.005	<0.05
Comdist	spatial distance via soil texture	-0.012	<0.05
	spatial distance via HOL temperature	0.167	<0.05
	spatial distance via HOL precipitation	0.016	<0.05
	spatial distance via soil fertility	-0.001	<0.05
Bray-Curtis	spatial distance via soil texture	0.038	<0.05
	spatial distance via LGM temperature	0.012	<0.05
	spatial distance via LGM precipitation	0.136	<0.05
	spatial distance via soil fertility	-0.007	<0.05
Comdistnt	spatial distance via soil texture	0.028	<0.05
	spatial distance via LGM temperature	-0.140	<0.05
	spatial distance via LGM precipitation	0.138	<0.05
	spatial distance via soil fertility	-0.005	<0.05

Comdist	spatial distance via soil texture	-0.006	<0.05
	spatial distance via LGM temperature	0.063	<0.05
	spatial distance via LGM precipitation	0.092	<0.05
	spatial distance via soil fertility	-0.001	<0.05

Figure Legends

Figure 1 - Principal component analysis (PCA) with spatial variation (latitude and longitude) and (a) current climatic data, (b) Mid-Holocene (HOL) climatic data, (c) Last Glacial Maximum (LGM) climatic data and (d) soil data. Legend: Contrib.: Contribution; Dim: Dimension (axis).

Figure 2: Relationship between spatial distance and turnover: (a) taxonomic – Bray-Curtis distance, (b) terminal clade – Comdistnt distance and (c) basal clade - Comdist distance.

Figure 3: Direct effects of spatial distances and environmental variables on taxonomic turnover (Bray-Curtis distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.

Figure 4: Direct effects of spatial distances and environmental variables on terminal clade turnover (Comdistnt distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Note: Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater

the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.

Figure 5: Direct effects of spatial distances and environmental variables on basal clade turnover (Comdist distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Note: Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of environmental variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.

Figure 1 - Principal component analysis (PCA) with spatial variation (latitude and longitude) and (a) current climatic data, (b) Mid-Holocene (HOL) climatic data, (c) Last Glacial Maximum (LGM) climatic data and (d) soil data. Legend: Contrib.: Contribution; Dim: Dimension (axis).
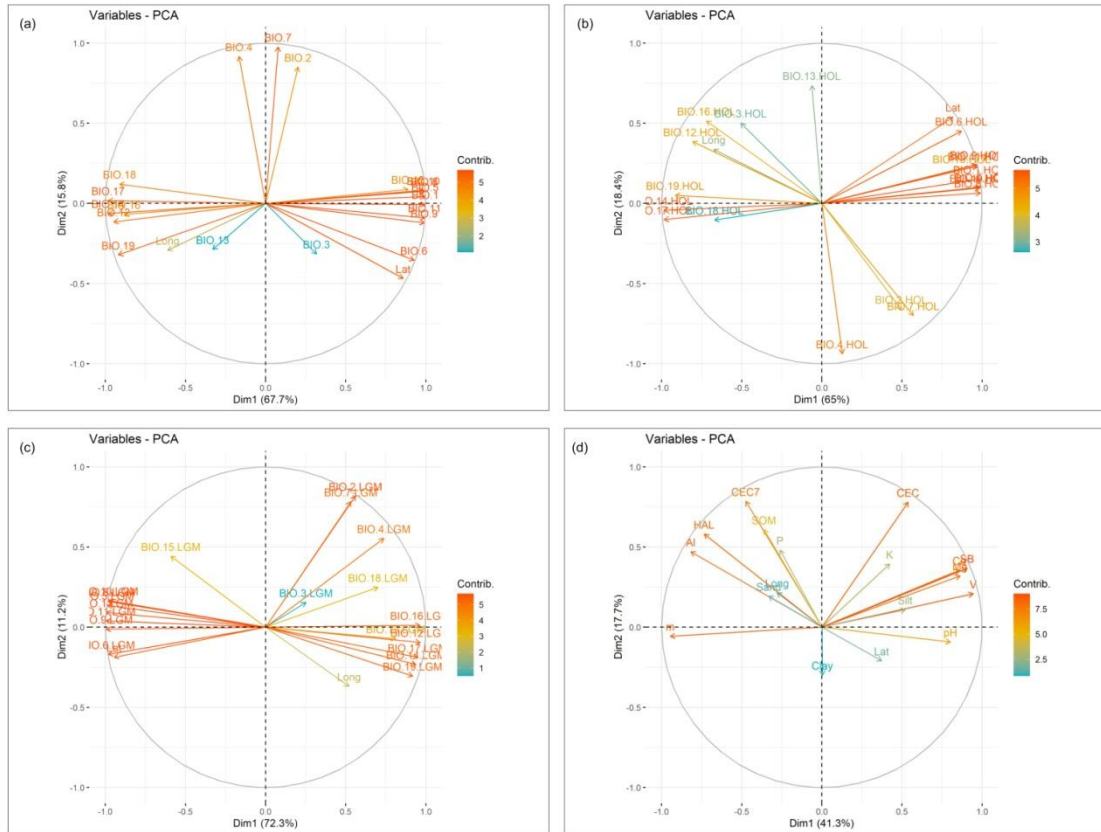
Figure 2: Relationship between spatial distance and turnover: (a) taxonomic – Bray-Curtis distance, (b) terminal clade – Comdistnt distance and (c) basal clade - Comdist distance.
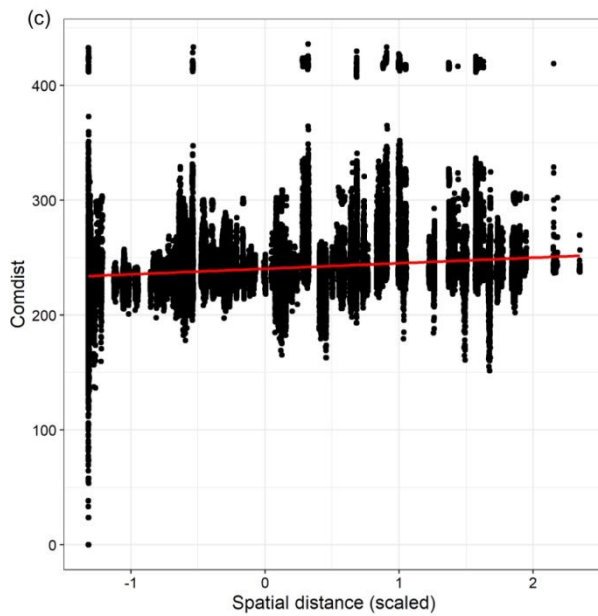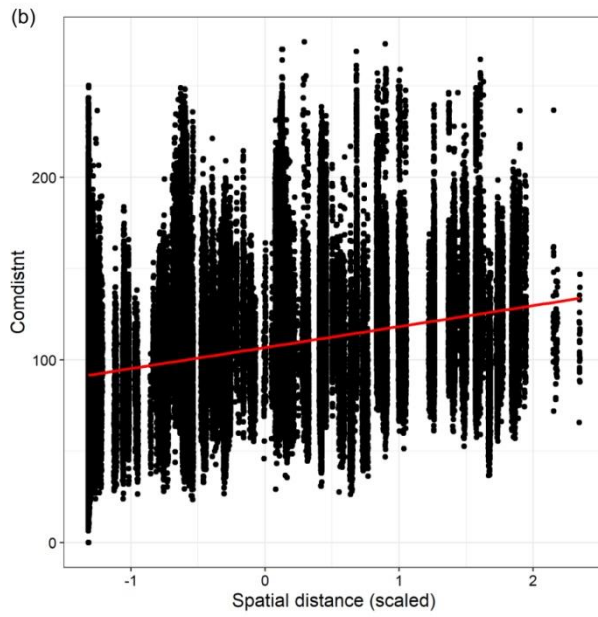
(a)

(b)

(c)

Figure 3: Direct effects of spatial distances and environmental variables on taxonomic turnover (Bray-Curtis distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.

(a)

CFI: 0.980 | SRMR: 0.030 | TLI: 0.950 | R-Square: 29.5%

(b)

CFI: 0.889 | SRMR: 0.079 | TLI: 0.724 | R-Square: 28.6%

(c)

CFI: 0.969 | SRMR: 0.033 | TLI: 0.923 | R-Square: 28.2%

Turnover metrics
Niche-based process
Neutral process
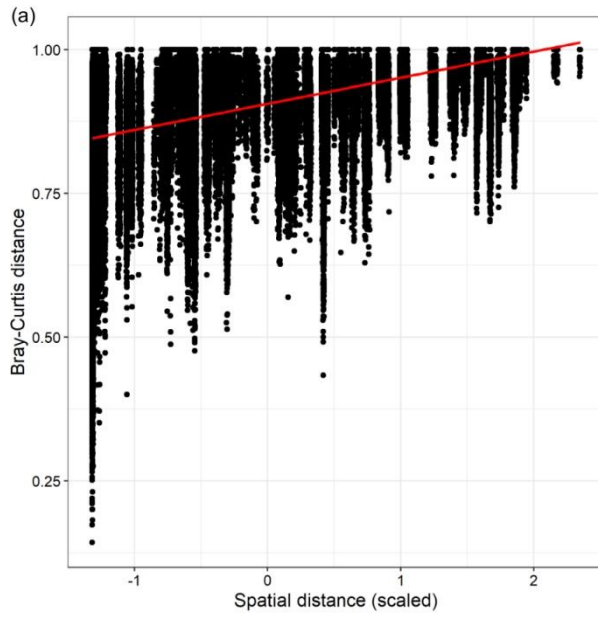Historical process
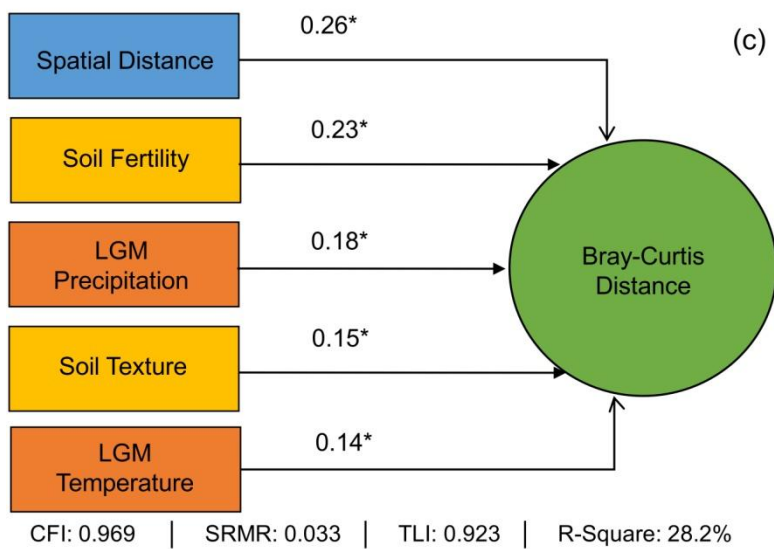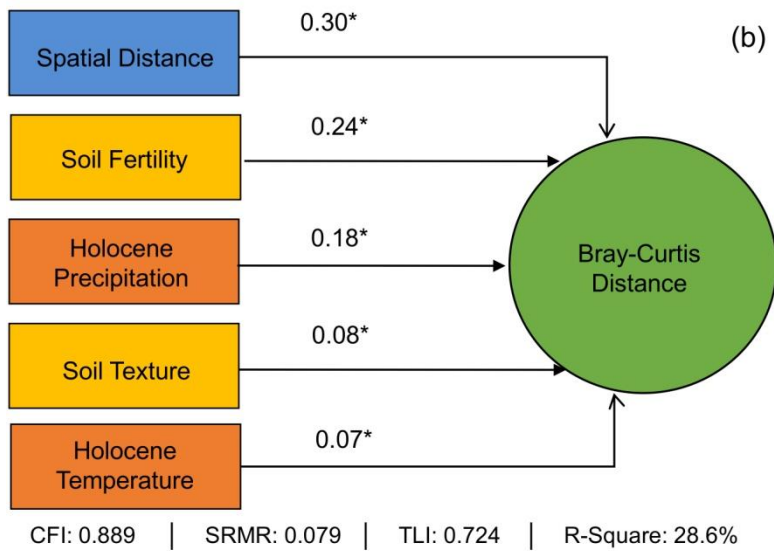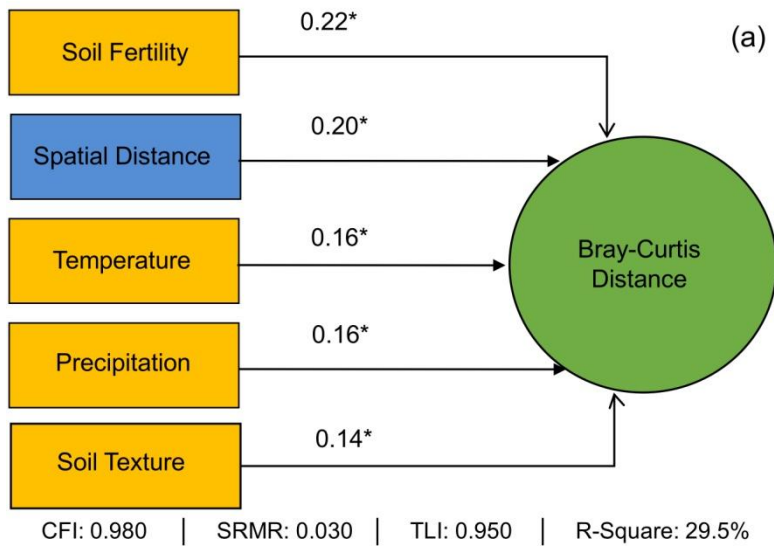* Significant if p ≤0.05
Direct effects

Figure 4: Direct effects of spatial distances and environmental variables on terminal clade turnover (Comdistnt distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Note: Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of environmental variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.

Figure 5: Direct effects of spatial distances and environmental variables on basal clade turnover (Comdist distance): a) Model with current climate data; b) Model with Mid-Holocene (HOL) climate data; c) Model with Last Glacial Maximum (LGM) climate data. Note: Values in parentheses represent the effect size of the variable. The arrow filled in black represents the direct effect of variables. Positive values show that the greater the effect of the variable, the greater the taxonomic dissimilarity, while negative values show that the greater the effect of the variable, the greater the taxonomic similarity. Effect significance is indicated by "*" if p ≤0.05. Legend: CIF - Comparative Fit Index; TLI - Tucker-Lewis Index; SRMR - Standardized Root Mean Square Residual.
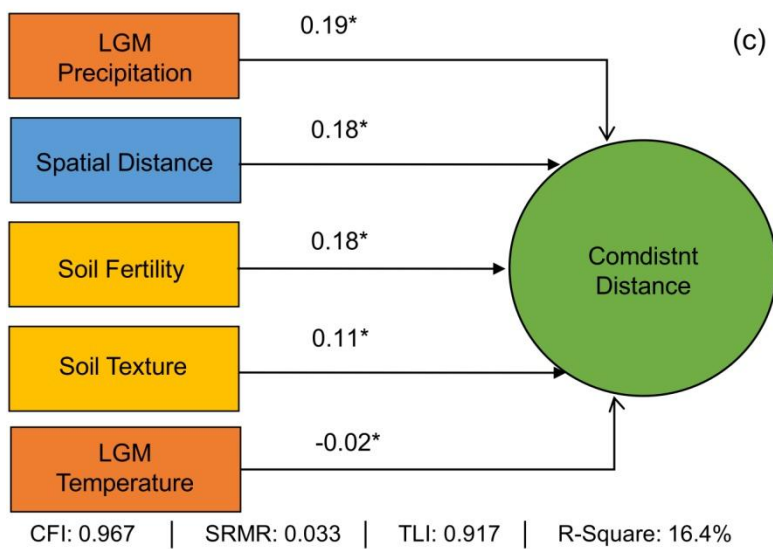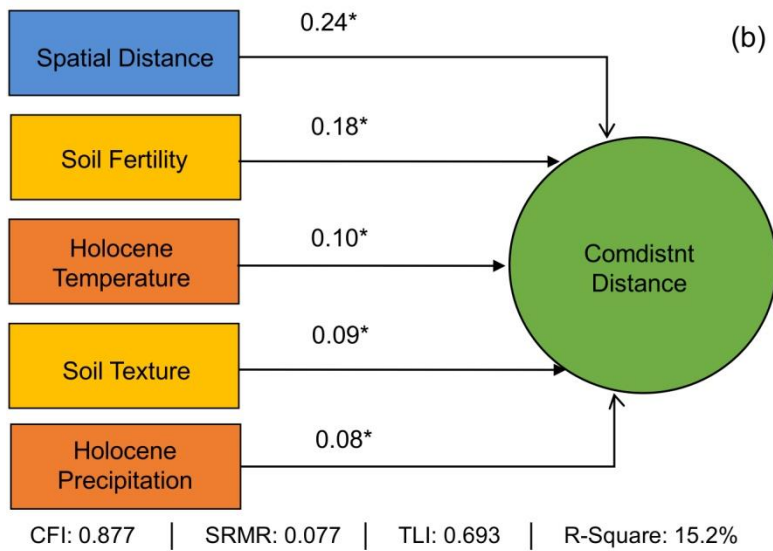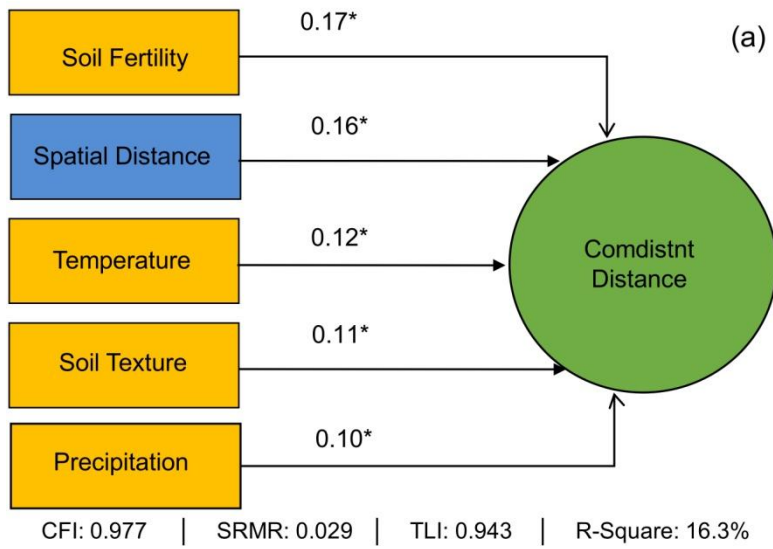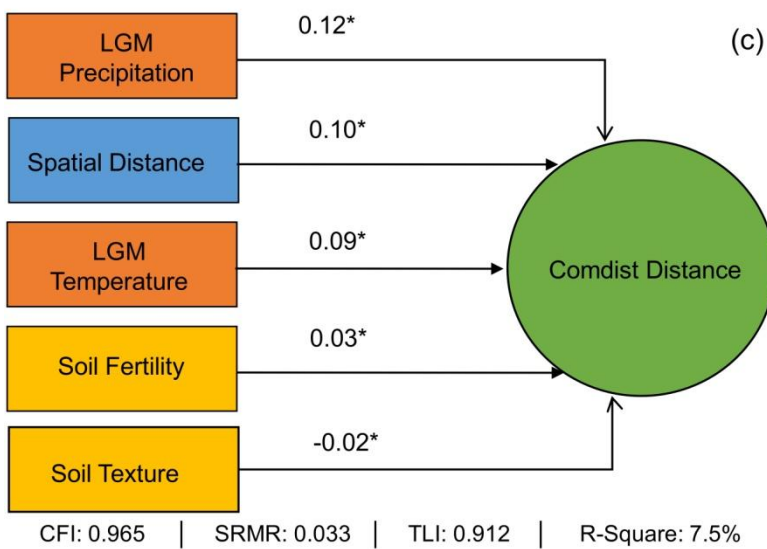
(a)

CFI: 0.975 | SRMR: 0.029 | TLI: 0.938 | R-Square: 7.4%

(b)

CFI: 0.870 | SRMR: 0.077 | TLI: 0.676 | R-Square: 8.4%

(c)

CFI: 0.965 | SRMR: 0.033 | TLI: 0.912 | R-Square: 7.5%

Supplementary material

Table S1 - Information about sites of Brazilian Atlantic rainforest used in the study.

Sites	Samp area (ha)	Lat	Long	Veg type	N of plots	Plot area (m²)
BOC-02	1.04	-22.217	-44.538	Omb	26	400
CRR-01	1.20	-21.612	-44.612	Semi	30	400
IBI-01	0.96	-21.71	-43.885	Omb	48	200
ING-01	1.00	-21.409	-44.892	Semi	25	400
ITM-01	1.00	-22.35	-44.794	Omb	25	400
ITT-01	0.94	-21.352	-44.609	Semi	42	225
ITT-02	0.84	-21.355	-44.615	Semi	28	300
LUM-01	1.28	-21.497	-44.913	Semi	32	400
MDD-01	1.59	-21.488	-44.376	Semi	70	225
MTR-01	1.20	-21.606	-44.556	Semi	30	400
SUB-01	2.00	-21.2214	-44.9631	Semi	49	400
SUB-02	5.04	-21.2278	-44.9639	Semi	126	400
SUB-03	1.12	-21.2737	-44.882	Semi	28	400
SUB-04	1.16	-21.2167	-44.9803	Semi	29	400

Note: Samp area: sampled area; lat: latitude; long: longitude; Veg type: Vegetation type; N of plots: number of plots; alt: altitude; Omb: Ombrophilic; Semi: Semideciduous.

Figure S1 - Contribution of each dimensions (axis) of the principal component analysis (PCA) in explaining the relationship between spatial variation (latitude and longitude) and current climatic data.
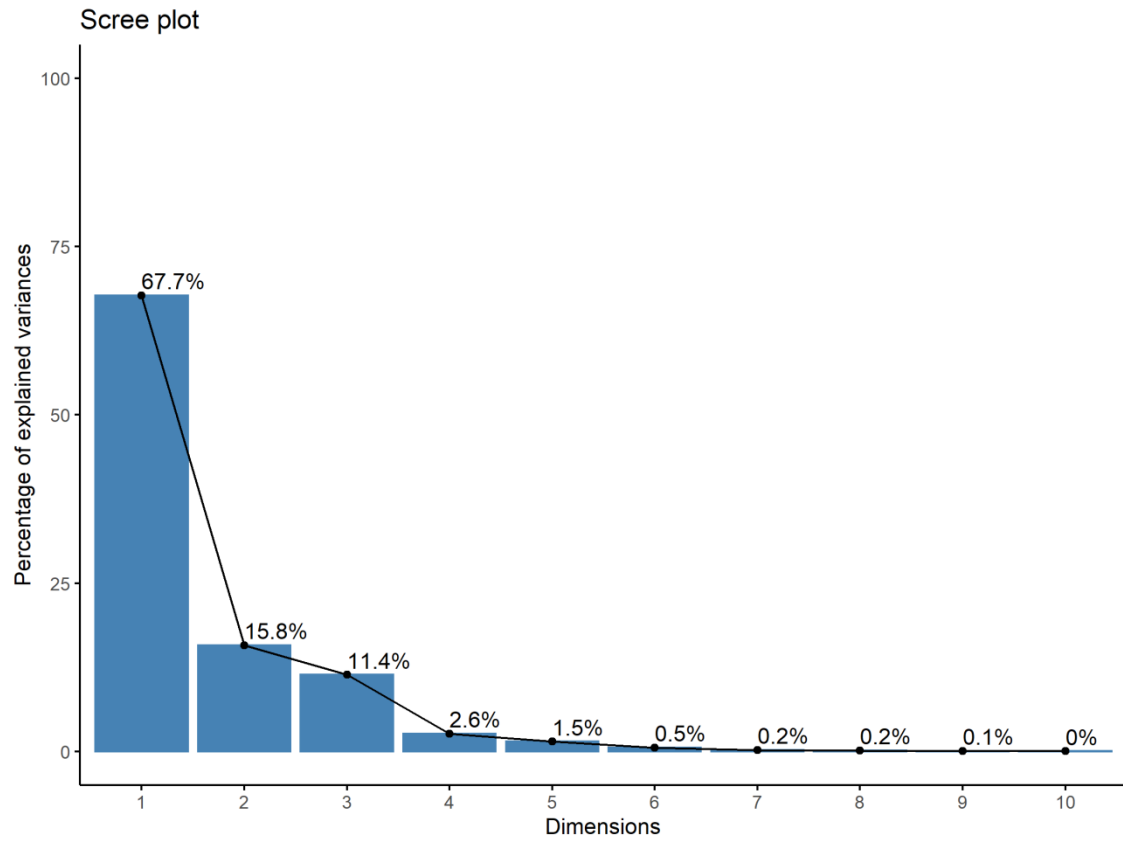
Table S2 - Information about the current climatic data used in the analysis of main components for each site of Brazilian Atlantic rainforest.

Site	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19
BOC-02	16.5	12.5	64	212.9	24.6	5.2	19.4	18.8	13.5	18.9	13.5	1664	302	20	75	855	77	760	77
CRR-01	16.3	12.4	68	186.1	24.1	5.9	18.2	18.3	13.8	18.3	13.6	1757	338	19	76	907	71	788	86
IBI-01	16.4	10.8	65	180.8	24.1	7.6	16.5	18.4	14.0	18.5	13.9	1694	309	22	73	850	78	747	94
ING-01	19.9	12.5	66	199.2	28.1	9.4	18.8	22.0	17.3	22.0	17.0	1461	298	13	78	754	53	634	70
ITM-01	15.6	12.7	64	215.6	23.7	4.0	19.7	18.0	12.6	18.0	12.6	1751	319	22	75	903	86	812	86
ITT-01	19.6	12.4	67	196.7	27.5	9.2	18.3	21.6	16.8	21.6	16.7	1566	323	14	80	817	54	687	69
ITT-02	19.6	12.4	67	196.2	27.5	9.2	18.3	21.6	16.8	21.6	16.7	1568	323	14	80	818	54	688	69
LUM-01	19.6	12.7	66	203.3	27.9	8.9	19.0	21.8	16.9	21.8	16.7	1459	295	14	78	751	54	711	71
MDD-01	19.6	12.2	65	206.5	27.7	9.1	18.6	21.8	16.8	22.0	16.8	1512	301	14	78	780	53	668	71
MTR-01	17.6	12.5	66	196.5	25.6	7.0	18.6	19.7	14.9	19.7	14.8	1645	322	16	77	853	63	735	78
SUB-01	19.8	12.0	66	185.2	28.0	9.9	18.1	21.7	17.6	21.7	17.2	1534	316	13	80	803	53	674	70
SUB-02	19.9	12.0	66	186.1	28.1	10.0	18.1	21.7	17.6	21.7	17.2	1518	312	13	79	793	53	666	70
SUB-03	20.3	12.2	66	190.6	28.4	10.0	18.4	22.2	17.8	22.2	17.5	1493	308	13	79	777	52	649	69
SUB-04	20.1	12.0	66	186.9	28.3	10.2	18.1	21.9	17.9	21.9	17.4	1495	306	12	79	780	52	655	69

Note: BIO.1 = annual mean temperature, BIO.2 = mean diurnal range, BIO.3 = isothermality, BIO.4 = temperature seasonality, BIO.5 = maximum temperature of the warmest month, BIO.6 = minimum temperature of the coldest month, BIO.7 = annual temperature range, BIO.8 = mean temperature of the wettest quarter, BIO.9 = mean temperature of the driest quarter, BIO.10 = mean temperature of the warmest quarter, BIO.11 = mean temperature of the coldest quarter, BIO.12 = annual precipitation, BIO.13 = precipitation of the wettest month, BIO.14 = precipitation of the driest month, BIO.15 = precipitation seasonality (coefficient of variation of annual monthly precipitation), BIO.16 = precipitation of the wettest quarter, BIO.17 = precipitation of the driest quarter, BIO.18 = precipitation of the warmest quarter, and BIO.19 = precipitation of the coldest quarter.

Figure S2 - Contribution of each dimensions (axis) of the principal component analysis (PCA) in explaining the relationship between spatial variation (latitude and longitude) and Mid-Holocene climatic data.
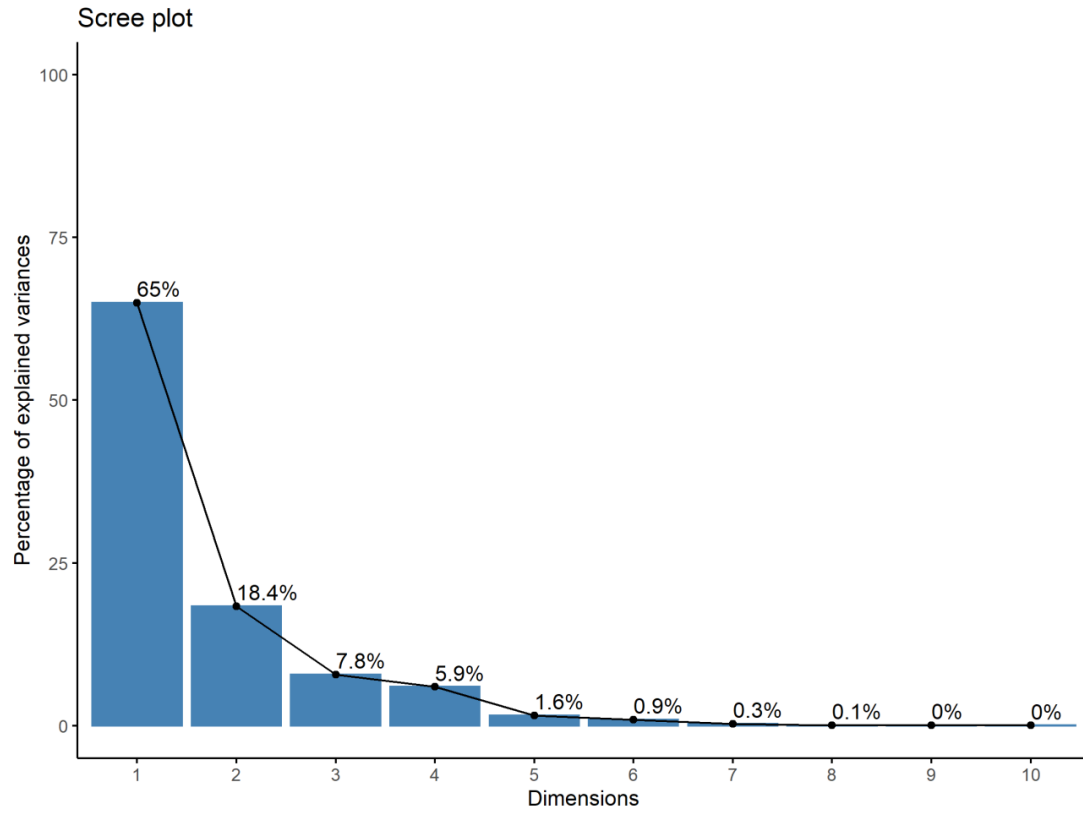
Table S3 - Information about the Mid-Holocene (HOL) climatic data used in the analysis of main components for each site of Brazilian Atlantic rainforest.

Site	BIO.1 HOL	BIO.2 HOL	BIO.3 HOL	BIO.4 HOL	BIO.5 HOL	BIO.6 HOL	BIO.7 HOL	BIO.8 HOL	BIO.9 HOL	BIO.10 HOL	BIO.11 HOL	BIO.12 HOL	BIO.13 HOL	BIO.14 HOL	BIO.15 HOL	BIO.16 HOL	BIO.17 HOL	BIO.18 HOL	BIO.19 HOL
BOC-02	16	13.2	68	178.6	24.0	4.6	19.4	17.4	13.6	17.9	13.3	2064	366	23	69	994	99	844	123
CRR-01	16.2	13.2	69	152.9	24.6	5.7	18.9	17.1	14.3	17.7	13.7	2267	414	22	70	1084	95	918	127
IBI-01	16.2	11.6	71	144.0	23.6	7.3	16.3	17.2	14.5	17.8	14	2192	390	26	69	1062	104	865	133
ING-01	19.8	13.5	68	167.3	28.6	9.0	19.7	20.9	18.0	21.3	17.1	1934	369	15	71	945	71	758	109
ITM-01	15	13.3	68	181.0	22.8	3.3	19.5	16.8	12.5	16.9	12.2	2151	371	26	69	1033	111	892	130
ITT-01	19.5	13.3	70	161.7	27.8	8.9	18.9	20.5	17.4	21.0	16.9	2061	403	16	73	1021	72	818	104
ITT-02	19.5	13.3	70	161.4	27.8	8.9	18.9	20.5	17.4	21.0	16.9	2063	403	16	73	1022	72	819	104
LUM-01	19.5	13.7	68	170.4	28.4	8.5	19.9	20.7	17.6	21.1	16.8	1914	362	16	71	931	71	752	109
MDD-01	19.5	13.1	69	167.3	27.7	8.9	18.8	20.6	17.3	21.3	16.9	1981	378	17	72	975	72	789	106
MTR-01	17.5	13.3	70	160.3	25.8	6.8	19.0	18.5	15.4	19.1	14.9	2122	395	19	71	1028	85	856	115
SUB-01	19.8	13.0	67	159.0	28.7	9.5	19.2	20.7	18.3	21.0	17.3	2059	397	15	72	1008	71	820	111
SUB-02	19.8	13.0	68	158.2	28.7	9.6	19.1	20.8	18.4	21.1	17.4	2038	392	15	72	997	71	578	111
SUB-03	20.2	13.2	68	160.3	29.0	9.6	19.4	21.2	18.5	21.5	17.6	1988	384	15	72	980	69	782	108
SUB-04	20.1	13.0	67	159.7	29.0	9.8	19.2	21.0	18.7	21.4	17.6	2009	385	14	72	983	70	586	110

Note: BIO.1 = annual mean temperature, BIO.2 = mean diurnal range, BIO.3 = isothermality, BIO.4 = temperature seasonality, BIO.5 = maximum temperature of the warmest month, BIO.6 = minimum temperature of the coldest month, BIO.7 = annual temperature range, BIO.8 = mean temperature of the wettest quarter, BIO.9 = mean temperature of the driest quarter, BIO.10 = mean temperature of the warmest quarter, BIO.11 = mean temperature of the coldest quarter, BIO.12 = annual precipitation, BIO.13 = precipitation of the wettest month, BIO.14 = precipitation of the driest month, BIO.15 = precipitation seasonality (coefficient of variation of annual monthly precipitation), BIO.16 = precipitation of the wettest quarter, BIO.17 = precipitation of the driest quarter, BIO.18 = precipitation of the warmest quarter, and BIO.19 = precipitation of the coldest quarter.

Figure S3 - Contribution of each dimensions (axis) of the principal component analysis (PCA) in explaining the relationship between spatial variation (latitude and longitude) and Last Glacial Maximum climatic data.
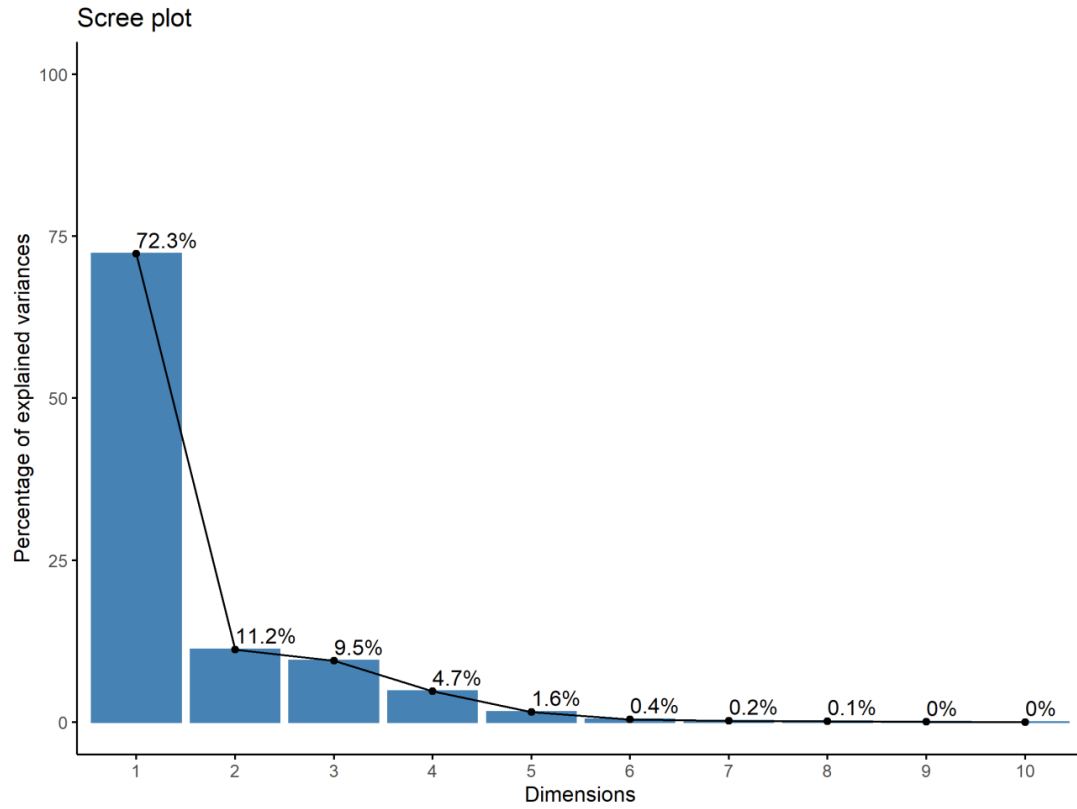
Table S4 - Information about the Last Glacial Maximum (LGM) climatic data used in the analysis of main components for each site of Brazilian Atlantic rainforest.

Site	BIO.1 LGM	BIO.2 LGM	BIO.3 LGM	BIO.4 LGM	BIO.5 LGM	BIO.6 LGM	BIO.7 LGM	BIO.8 LGM	BIO.9 LGM	BIO.10 LGM	BIO.11 LGM	BIO.12 LGM	BIO.13 LGM	BIO.14 LGM	BIO.15 LGM	BIO.16 LGM	BIO.17 LGM	BIO.18 LGM	BIO.19 LGM
BOC-02	12.7	13.7	6.6	208.8	21.6	1.0	20.6	15.1	9.9	15.1	9.7	1927	346	31	71	960	111	960	127
CRR-01	13.6	13.1	6.9	181.4	22	3.2	18.8	15.7	11.4	15.7	11.0	1935	355	26	72	960	99	960	121
IBI-01	13.5	12	6.7	177.4	21.9	4.1	17.8	15.6	11.3	15.6	10.9	1916	346	31	70	924	108	817	129
ING-01	16.7	12.9	6.7	180.4	25.2	6.1	19.1	18.7	14.5	18.7	14.0	1658	314	21	71	815	82	815	107
ITM-01	11.9	13.7	6.6	213.5	20.7	0.0	20.6	14.4	9.0	14.4	8.9	2002	339	36	70	993	127	993	139
ITT-01	16.4	12.9	6.8	182.2	24.8	6.0	18.8	18.5	14.1	18.5	13.8	1765	338	19	73	875	83	875	107
ITT-02	16.4	12.9	6.8	182.2	24.8	6.0	18.8	18.5	14.1	18.5	13.8	1765	338	19	73	875	83	875	107
LUM-01	16.3	13.1	6.7	185.3	24.9	5.5	19.4	18.4	14.0	18.4	13.5	1669	315	22	71	823	83	823	107
MDD-01	16.2	12.9	6.7	190.8	24.8	5.8	19.0	18.4	13.7	18.5	13.5	1735	324	19	73	852	81	754	107
MTR-01	14.2	13.1	6.9	183.5	22.6	3.7	19.0	16.3	11.9	16.3	11.5	1886	349	26	72	937	96	884	117
SUB-01	16.8	12.3	6.6	168.9	25.3	6.9	18.4	18.6	15.0	18.6	14.3	1676	316	20	72	826	84	826	110
SUB-02	16.8	12.3	6.6	168.9	25.3	6.9	18.4	18.6	15.0	18.6	14.3	1676	316	20	72	826	84	826	110
SUB-03	16.9	12.6	6.7	170.9	25.3	6.6	18.7	18.8	14.9	18.8	14.3	1693	323	21	72	837	82	837	108
SUB-04	16.8	12.3	6.6	168.8	25.3	6.9	18.4	18.6	15.0	18.6	14.3	1683	317	20	72	829	84	821	110

Note: BIO.1 = annual mean temperature, BIO.2 = mean diurnal range, BIO.3 = isothermality, BIO.4 = temperature seasonality, BIO.5 = maximum temperature of the warmest month, BIO.6 = minimum temperature of the coldest month, BIO.7 = annual temperature range, BIO.8 = mean temperature of the wettest quarter, BIO.9 = mean temperature of the driest quarter, BIO.10 = mean temperature of the warmest quarter, BIO.11 = mean temperature of the coldest quarter, BIO.12 = annual precipitation, BIO.13 = precipitation of the wettest month, BIO.14 = precipitation of the driest month, BIO.15 = precipitation seasonality (coefficient of variation of annual monthly precipitation), BIO.16 = precipitation of the wettest quarter, BIO.17 = precipitation of the driest quarter, BIO.18 = precipitation of the warmest quarter, and BIO.19 = precipitation of the coldest quarter.

Figure S4 - Contribution of each dimensions (axis) of the principal component analysis (PCA) in explaining the relationship between spatial variation (latitude and longitude) soil data.
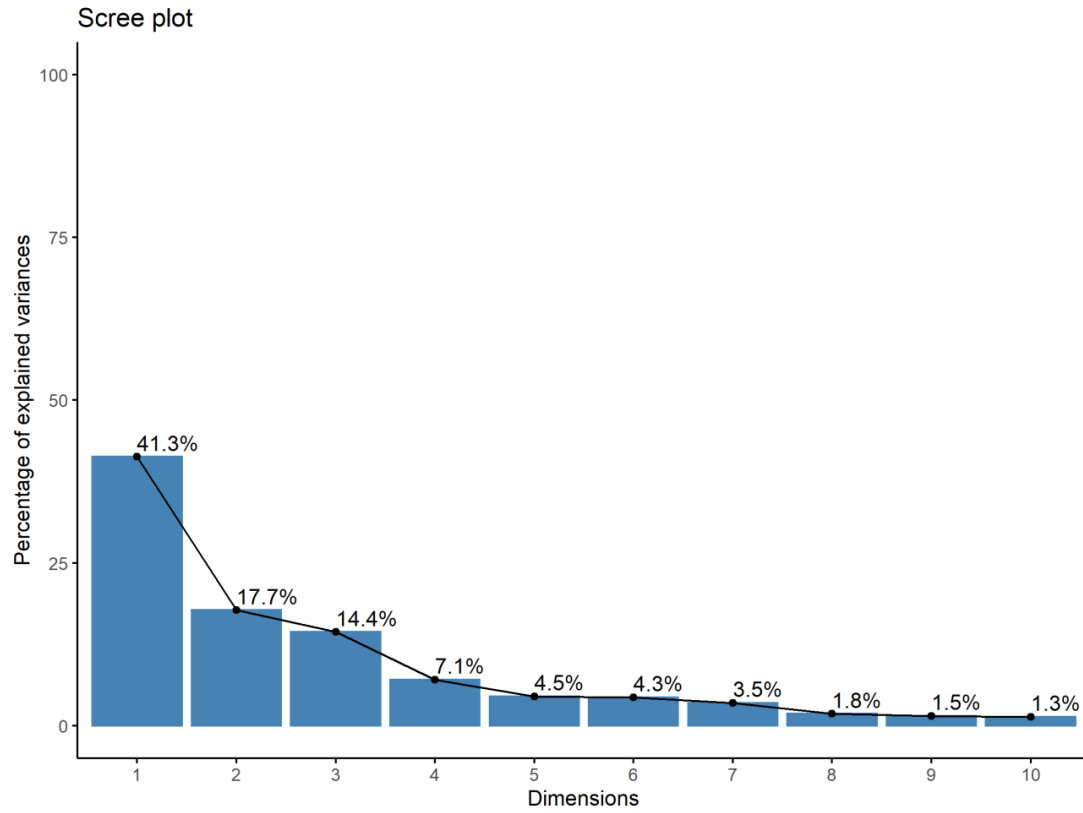
Table S5 - Information about the soil data used in the principal component analysis for each site of Brazilian Atlantic rainforest used in the study.

Site	pH	P	K	Ca	Mg	Al	H+AL	SB	CEC	CEC7	V	m	SOM	Sand	Silt	Clay
BOC-02	4.40±0.17	1.78±0.50	14.73±7.35	0.34±0.11	0.12±0.04	1.79±0.40	10.76±1.83	0.48±0.15	2.27±0.39	11.24±1.81	4.56±1.72	77.69±7.78	3.56±0.78	51.15±4.14	12.23±3.28	36.62±5.46
CRR-01	4.10±0.25	3.63±1.07	56.97±19.43	0.29±0.07	0.10±0.02	3.34±0.95	19.09±5.69	0.54±0.10	3.88±0.93	19.63±5.67	3.11±1.49	84.91±5.84	5.94±1.90	64.13±8.84	12.87±6.94	23.00±6.25
IBI-01	4.25±0.46	4.39±3.06	39.54±28.13	0.60±0.47	0.28±0.27	2.02±0.78	12.41±3.80	0.95±0.79	2.94±0.98	13.34±3.69	7.46±6.82	69.26±16.05	5.70±2.90	69.06±13.98	13.73±12.37	17.69±7.08
ING-01	5.00±0.22	1.76±1.09	53.76±19.19	1.1±0.91	0.66±0.61	1.05±0.58	7.87±2.78	1.90±1.47	2.94±1.10	9.78±1.94	20.56±15.08	41.43±24.37	3.70±1.46	49.08±18.16	23.96±10.50	26.96±9.42
ITM-01	4.08±0.15	1.76±0.34	54.64±12.37	0.1±0.00	0.10±0.00	2.44±0.41	16.34±2.63	0.33±0.05	2.78±0.43	16.58±2.70	2.09±0.29	87.54±1.60	5.08±0.92	37.08±7.44	11.6±3.00	51.32±5.55
ITT-01	4.68±0.33	2.88±0.89	93.64±45.33	1.05±0.99	0.61±0.69	1.88±0.78	9.60±2.12	1.90±1.54	3.78±1.01	11.50±2.07	16.33±12.01	53.90±23.83	4.44±1.03	34.45±3.14	31.33±2.28	34.19±4.63
ITT-02	4.14±0.24	1.93±0.79	47.89±12.23	0.30±0.13	0.12±0.05	1.81±0.62	11.58±2.97	0.55±0.17	2.38±0.64	12.12±2.98	4.79±1.53	75.55±7.03	3.67±0.63	30.01±5.07	22.52±3.27	46.89±5.97
LUM-01	5.03±0.65	1.44±0.72	79.97±60.36	1.39±1.14	0.71±0.61	0.98±0.83	9.27±3.39	2.30±1.79	3.28±1.33	11.57±2.71	20.73±16.01	36.39±27.51	3.38±1.08	33.59±12.34	35.84±7.14	30.56±8.24
MDD-01	5.06±0.23	2.37±0.89	29.54±11.18	0.52±0.48	0.22±0.19	1.01±0.38	7.56±1.81	0.85±0.72	1.83±0.46	8.39±1.28	10.95±11.38	59.07±24.24	3.02±0.74	46.49±18.48	25.03±14.50	28.20±6.05
MTR-01	4.31±0.49	2.49±0.81	62.87±19.57	0.69±0.95	0.26±0.31	2.47±1.50	16.10±10.08	1.10±1.29	3.57±0.92	17.2±9.37	10.35±13.99	68.92±33.38	4.43±1.83	67.23±8.19	11.77±6.19	21.00±4.28
SUB-01	4.65±0.54	1.12±0.33	58.41±31.34	1.42±1.21	0.87±0.69	0.86±0.63	5.25±1.61	2.44±1.90	3.25±1.43	7.69±1.16	30.51±20.49	34.08±26.71	2.55±0.67	50.16±9.30	15.82±5.71	34.02±8.75
SUB-02	4.18±0.13	2.13±0.50	36.76±14.3	0.39±0.12	0.11±0.03	1.80±0.29	11.51±1.42	0.60±0.17	2.41±0.29	12.11±1.38	5.10±1.74	74.79±7.02	5.69±0.74	27.51±8.57	13.10±9.06	59.40±8.62
SUB-03	4.60±0.35	1.39±0.50	36.25±12.66	1.75±2.23	0.60±0.54	1.29±0.53	9.45±2.90	2.46±2.50	3.75±2.19	12.95±2.61	17.47±14.08	44.64±24.08	3.97±0.59	33.32±11.95	30.25±7.83	36.43±6.76
SUB-04	5.09±0.41	1.17±0.38	52.28±27.15	2.76±1.75	1.69±1.16	0.61±0.58	6.42±1.91	4.58±2.81	5.19±2.35	11±1.74	39.76±20.98	20.25±25.03	4.12±0.80	21.66±8.29	26.62±5.35	51.72±7.59

Note: P = phosphorus (mg/cm³), K = potassium (mg/cm³), Ca = calcium (cmol/dm³), Mg = magnesium (cmol/dm³), Al = aluminium (cmol/dm³), H+Al = potential acidity, SB = sum of bases, effective CEC = cation exchange capacity, CEC7 = cation exchange capacity at pH 7.0, m = aluminium saturation, V = base saturation.

ARTIGO 2 - Taxonomic identity, but not evolutionary relatedness, determines carbon stocks uptake in tropical forests

(artigo redigido conforme norma do *Journal of Applied Ecology* a qual será submetido)

Taxonomic identity, but not evolutionary relatedness, determines carbon stocks uptake in tropical forests

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Abstract

1. Carbon stock and uptake are among the main ecosystem services provided by tropical forests. However, deforestation and climate change threaten to drastically change their role on carbon cycle. The evolution of tree traits associated with carbon fluxes and storage may have left a signature in the phylogeny, and therefore the degree of trait conservatism may be relevant to better understand these aspects of the carbon cycle.

2. Based on the assumption that taxa tend to retain their ancestor state characteristics and using forest inventory data from 30 tropical forest sites (33.86 ha), we explored the role of main ecological drivers (taxonomic vs. environmental effects) and the evolutionary legacy on carbon stock (ton/ha) and uptake (ton/ha/year).

3. Our assessment suggests that variations in carbon stock and uptake by individual trees were mostly determined by taxonomic identity (28.7% and 26.7%, respectively) rather than environmental factors (7.1% and 8.9%, respectively), but evolutionary relatedness did not predict similarities among species.

4. Synthesis and applications. Our results indicate that the ability of species to process and store carbon depend on their intrinsic characteristics, although these are not shared among closely related *taxa*. Climate projections predict the loss of species unable to adapt to novel conditions, which, in light of our results, could impact tropical carbon dynamics. Although evolutionary relatedness does not predict similarity in terms of function at the scale of our study (suggesting lability of traits related to carbon storage), species losses indicate that environmental changes are beyond species' ability to adapt to current and predicted changes. In this case, it is necessary to intensify initiatives towards decreasing deforestation and tropical forest degradation and to restore degraded tropical ecosystems.

Key-words: phylogenetic signal; divergence and evolutionary convergence; environmental factors; biodiversity attributes; trait lability.

1 Introduction

Tropical forests are among the main terrestrial carbon sinks, accounting for 32% of global primary productivity and half of the global aboveground carbon stocks (Field et al., 1998; Lewis et al., 2009; Martin et al., 2018; Pan et al., 2011). Tropical forest carbon stocks are spatially structured and mainly determined by environmental conditions that influence tree establishment and development (Poorter et al., 2017; Unger et al., 2012; Sullivan et al., 2017). Therefore, tree growth, productivity and, consequently, carbon stock and uptake by tropical trees are expected to increase with increasing resource availability (e.g., annual precipitation and soil fertility) (Baraloto et al., 2011; Le Toan et al., 2011; Poorter et al., 2015; Quesada et al., 2012).

Other than their direct effects, environmental conditions also play an indirect role on the spatial variation of carbon stocks and uptake through their effects on biodiversity attributes, such as taxonomic, functional and phylogenetic diversity, which vary widely along environmental gradients (Poorter et al., 2015; Van der Sande et al., 2017). These biodiversity attributes are linked to species' resource use and, therefore, have important direct and indirect effects on tropical forest carbon dynamics. Each biodiversity attribute translates into different ecological information and influences forest carbon dynamics in different ways (Ali et al., 2019; Van der Sande et al. 2017). For example, tree carbon concentration depends on intrinsic functional characteristics related to atmospheric carbon acquisition and allocation (e.g., leaf area and wood density) (Capellesso et al., 2020; Fauset et al., 2015; Wu et al., 2017). As a result, species contribute differently to carbon stocks and uptake in tropical forests,

highlighting the role of taxonomic identity on carbon dynamics (Blasko et al., 2020; Zhang et al., 2009).

Besides taxonomic identity, evolutionary relatedness between *taxa* may also provide insight on the ability of trees to process and store carbon, after all, the tendency of related species to share ecological characteristics is a widely known pattern in ecology (Losos, 2008). Thus, biodiversity attributes associated with individual tree taxonomic identity and evolutionary relatedness between species are promising, considering their potential to synthesize other variables (Blasko et al., 2020). Taxonomic identity, for example, synthesizes functional and evolutionary differences through differentiation in species, genera and families (Fyllas et al., 2009). Along with it, information on relatedness between species allows functional differences to be combined with evolutionary distances and the assessment of patterns of evolutionary convergence and divergence. This approach provides a more comprehensive understanding of species responses to environmental variations (Ackerly, 2009; Liu et al., 2015).

Understanding how these drivers (environmental conditions, taxonomic identity and, evolutionary relatedness) shape current carbon stocks and carbon uptake helps predict how they may behave in the future. This is especially relevant with the ongoing changes in tropical forest carbon dynamics in response to the increasing concentrations of carbon in the atmosphere and associated climatic changes (Brienen et al., 2015; IPCC, 2007; Maia, Santos, et al., 2020). For example, while CO_2 fertilization has been stimulating tree growth and carbon sequestration in some moist tropical forests (Malhi & Grace, 2000; Mitchard, 2018), in others, climate changes resulting from the same phenomenon has been increasing tree mortality (McDowell et al., 2020; Mitchard 2018; Rowland et al., 2015) and species losses (Bunker et al., 2005; Esquivel-Muelbert et al., 2019; Van Der Sande et al., 2017). Altogether,

this imbalance between tree growth and mortality has converted some tropical forests from carbon sinks to carbon sources (Brienen et al., 2015; Maia, Santos, et al., 2020).

To avoid these negative feedbacks and mitigate climate change, ecosystem functions related to carbon dynamics have become a central issue of public policies focused on tropical forest conservation (Bu et al., 2019). Examples include the United Nations Organization's REDD + (Reducing Emissions from Deforestation and Degradation) and the New York Declaration for Global Forest Restoration, both of which aim to reduce carbon emissions related to deforestation and forest degradation. However, the success of these initiatives depends on knowledge about environmental effects and processes underpinning temporal variations of tropical forest carbon dynamics (Baker et al., 2010). This information provides basis for effective strategies towards preserving and promoting carbon sequestration in tropical forest ecosystems. Therefore, investigations spanning broad temporal intervals (to identify temporal patterns) and broad taxonomic variation (to assess effects of taxonomic identity and evolutionary relatedness) provide relevant intellectual resources for effective policies.

Here, we used data on carbon stock and uptake by tropical trees in 30 repeatedly measured tropical forest sites (with two to eight inventories each and total area sampled of 33.86 ha) to explore the roles of taxonomic identity and shared evolutionary history in the final expression of these two ecosystem services. This is a unique dataset covering a wide latitudinal (approximately 1,000 km) and environmental gradient that covers three tropical vegetation types: deciduous, semi-deciduous and cloud forests. Using these data, we first compared the role of taxonomic identity vs environmental factors in determining carbon stock and uptake by species populations along the climatic gradient. First, we specifically assessed the ability of individual trees to store and absorb carbon based on their taxonomic identity (species, genus and family) and the local conditions where they occur (site and vegetation

type). Second, we investigated the evolutionary fingerprint on carbon stock and uptake in tropical forest genera by quantifying the extent of phylogenetic signal using a genus-level molecular phylogeny by Neves et al. (2020). Thirdly, we assessed whether the final expression of the two ecosystem services is influenced by relatedness (e.g., whether closely related genera have similar values) and discussed the role of heritability on ecosystem service provision.

2 Material and Methods

2.1 Study áreas

We used tree community data from 30 repeatedly measured forest sites (total area of 33.86 ha) located in the Brazilian states of Minas Gerais and Bahia (Figure 1). Altitudes vary between 447 and 1490 meters above sea level (Table S1). Regional climate is classified as Koppen Cwa (humid subtropical climate, with dry winters and temperate summers) and As (tropical climate, with dry summers) (Alvares et al., 2013).

Our sampling covers three vegetation types distinguished by deciduousness and climate: (a) deciduous forests associated with Caatinga phytogeographic domain, with more than 50% of canopy deciduousness during the dry season and under the driest and warmest climate in our dataset (Santos et al., 2012; Fig 1); (b) semideciduous forests associated with the Atlantic Forest phytogeographic domain, with 20-50% of canopy deciduousness during the dry season and under an intermediate climate (Neves et al., 2017; Fig 1); (c) cloud forests, also associated with the Atlantic Forest domain, are floristically similar to rain forests, have little deciduousness, and occur under the coldest and wettest climate in the dataset (Neves et al., 2017; Fig 1). All sites are mixed-age forests with similar conservation status, with no indication of human disturbance.
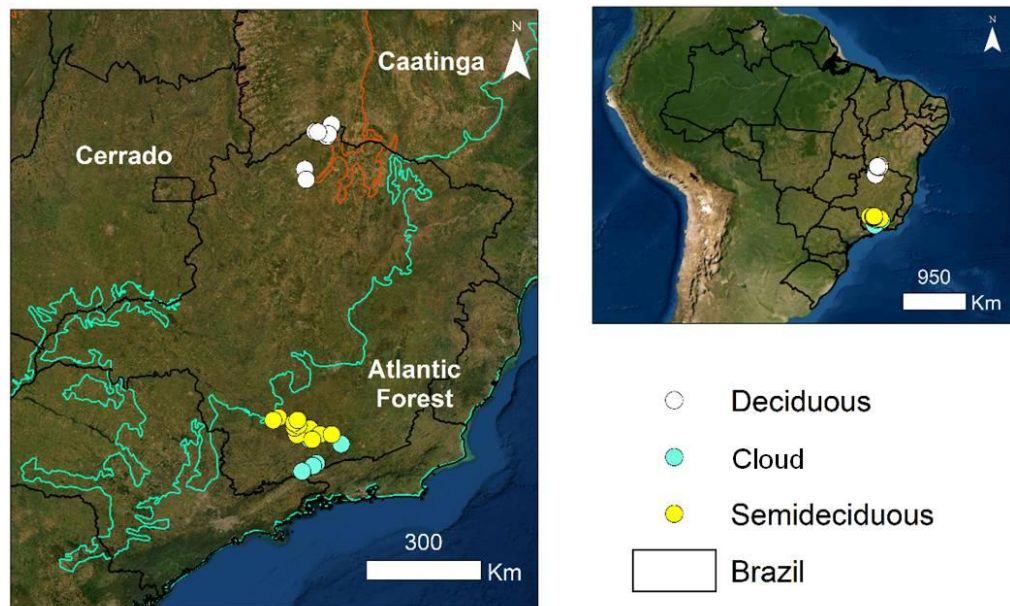
Figure 1: Location of 30 tropical forest sites in the states of Minas Gerais and Bahia, Brazil, and their position relative to South America and Brazilian phytogeographic domains.

2.2 Data collection

Forest structure data were repeatedly collected from our study sites between 1987 and 2020. In total, 119 measurements were performed (2 to 8 inventories *per* site), with 88 intervals between measurements and census interval length (among different sites and of the same site over time) varying between 2 to 10 years (mean 5 years). In the first inventory year, permanent sampling units were established at each site (sampling intensity varies from 5 to 126 plots). From our 30 forest sites sampled, 9 (30%) are classified as deciduous forest (7.56 ha), 16 (53.3%) as semideciduous forest (21.70 ha) and 5 (16.7%) as evergreen forest (4.60 ha) (Table S1).

Within plots, we measured and identified all individual trees with diameter at breast height DBH ≥ 5 cm at the species level. For multi-stemmed trees, the inclusion method was based on the square diameter of the tree, namely the quadratic DBH or DBHq. When the

DBHq of a multi-stemmed tree reached the minimum inclusion criteria, the diameter of each individual stem was recorded, even if below the threshold. At time intervals, we returned to the plots of each site and re-measured all living individuals, record the dead and measured individuals, which met the inclusion criteria in the interval (recruits).

Plants were identified by specialists in the field or by herbarium visits and followed the taxonomic nomenclature of the Angiosperm Phylogeny Group (APG IV, 2016). Name standardization followed REFLORA (2020), through the *flora* package (Carvalho, 2016), implemented in the software R (R Core Team, 2020). Forest inventory data for the 30 sites is stored in the ForestPlots.net database (Lopez-Gonzalez et al., 2011; Lopez-Gonzalez et al. 2012; see site codes in Table S1). A total of 62,139 individual trees, 832 species, 324 genera and 87 plant families were sampled.

2.3 Carbon variables obtaining

With the data from the multiple forest inventories, we calculated the aboveground woody biomass (AGWB) of each individual tree using the modified pantropical equation by Chave et al. (2014) that does not require tree height data. The equation estimates tree AGWB using tree DBH, species' average wood density obtained from Zanne (2009) (genus or family averages are used when wood density is unavailable for species and the average of the parcel when the family average is unavailable), and a bioclimatic stressor variable E. This bioclimatic variable compensates for the lack of height data through its relationship with climatic water deficit, is based on plot geographic location and derived from the WorldClim database. We converted each tree's AGWB into carbon stock by multiplying AGWB by a constant 0.456, estimated as the average carbon concentration in tropical angiosperm tissues (Martin et al. 2018). We used the package *BIOMASS* (Rejou-Mechaine et al., 2017) implemented in software R (R Core Team, 2020).

Based on carbon stock of each tree, we calculated two variables at the population level (i.e., for each species occurring at each site): average carbon stock (ton/ha) and average carbon uptake (ton/ha/year). Average carbon stock was the average carbon retained by a given species in a given site across all measurement years (standardized by sample size). Carbon uptake was the amount of carbon incremented by growth of surviving trees and recruits of a given species in a given site after each measurement interval (standardized by sample size and interval length). We corrected for potential bias in interval length following Talbot et al. (2014). We calculated average carbon uptake by each population in each site by averaging uptake values recorded after each interval. Thus, the final variables indicated (i) the average carbon stock of each population (species *per* site) over measured period and (ii) the average carbon uptake by each population (species *per* site) between measurements.

Final sample consisted of 3707 populations of 768 species, 306 genera and 83 plant families. We removed dead individuals, in order to avoid the influence of mortality stochasticity. Thus, only surviving individuals were used in all inventories. We also excluded families Cyatheaceae and Arecaceae, removed from the dataset that do not have secondary growth and trees lacking botanical identification.

2.4 Data analysis

2.4.1 Taxonomic vs environmental effects on carbon stock and uptake

To compare the relative influence of taxonomic identity and environmental factors (site and the vegetation type) on carbon stocks and uptake by each population (species *per* site), we used linear mixed effects models and variance partitioning analysis. We built a global model for each response variable (Gaussian residuals distribution) as a function of two

groups of random variables: (i) site and vegetation type (to quantify site environmental effects) and (ii) species, genus and family (to quantify taxonomic effects) (Equation 1).

Equation 1:

$$Carbon\ variable \sim 1 + (1|Site) + (1|Vegetation\ type) + (1|Family) + (1|Genus) + (1|Species)$$

From models' results, we performed a variance partitioning analysis to assess the proportion of variance explained by random effects of each set of variables (environmental and taxonomic) on carbon stock and uptake (Fyllas et al., 2009; Oliveras et al., 2020). We also evaluated the contribution of each random factor by analyzing the impact of its removal from the global model, based on Akaike information criterion of second order (AICc). We thus compared the AICc of global models with the absence of environmental factors (site and vegetation type) and absence of taxonomic factors (family, genus and species). We emphasize that this approach does not include evolutionary relatedness between species, genera or families. It indicates to what extent taxonomic identity alone influences tropical trees carbon stocks and uptake.

2.4.2 Evolutionary fingerprint on carbon stock and uptake

Moving beyond taxonomic effects, we also evaluated the evolutionary fingerprint on genus-level carbon stocks and uptake. Evolutionary fingerprint analysis was conducted at the genus level due to the resolution of the phylogeny (Neves et al. 2020). The decision to use a well-resolved genus phylogeny (e.g., instead of a mega-tree approach) aimed to avoid polytomies and reduce uncertainty below the family and genus levels, known for

compromising the reliability of phylogenetic signal estimations (Molina-Venegas & Rodríguez, 2017).

To synthesize a unique value per *taxon* (in this case, at the genus level in the sites), we averaged the values of carbon stocks and uptake by each sampled genus in each sampled population in the sites. We applied natural logarithm to these variables to meet the normality assumption required for analysis. Phylogenetic signal for the two variables was estimated using Pagel's λ (Freckleton et al., 2002; Pagel, 1999), which is considered a more appropriate measure when phylogeny is incomplete (Molina-Venegas & Rodríguez, 2017). Pagel's λ compares the traits distribution on a phylogeny with that expected under a Brownian Motion model of evolution (BM), whereby traits drift randomly across evolutionary time. A value of λ = 0 indicates lack of phylogenetic signal and complete independence between *taxa* trait values and evolutionary relatedness; λ = 1 indicates a perfect fit to BM model (Freckleton et al., 2002); and 0 < λ <1 indicates that trait values are similar between closely related *taxa*, but less than expected under BM (i.e., likely driven by other evolutionary processes than random drift) (Crisp & Cook, 2012). Significance of λ values was quantified by comparing the likelihood of the observed λ value with the likelihood of a model that assumes complete phylogenetic independence among trait values (λ = 0). We conducted all phylogenetic analyses using functions from the packages *phytools* (Revell, 2012), *ape* (Paradis et al., 2004) and *geiger* (Harmon et al., 2008) implemented in R (R Core Team, 2020).

3 Results

3.1 Taxonomic vs environmental effects on carbon stock and uptake

Our results show that the ecological drivers (taxonomy and environmental factors) explain 35.8% of the variation in the carbon stocks (ton/ha) and 35.6% of the uptake

(ton/ha/year). Variations in carbon stocks and uptake of tree species populations are mostly determined by taxonomy (family, genus and species) when compared to environmental factors (site and vegetation type). Taxonomy accounts for, respectively, 28.7% and 26.7% of variation in carbon stock and uptake, whereas environmental factors account for solely 7.1 and 8.9%, respectively (Figure 2; Table S2). This result is supported by greater contribution of taxonomic compared to environmental factors in reducing the AICc of global models for each response variable. For both carbon stocks and uptake, the removal of taxonomic factors increased AICc in almost three-folds when compare with the increase related to the removal of environmental factors (Table 1; Figure S1). Thus, among the ecological drivers analyzed, the ability of a population to store and absorb carbon largely depends on its taxonomic identity.
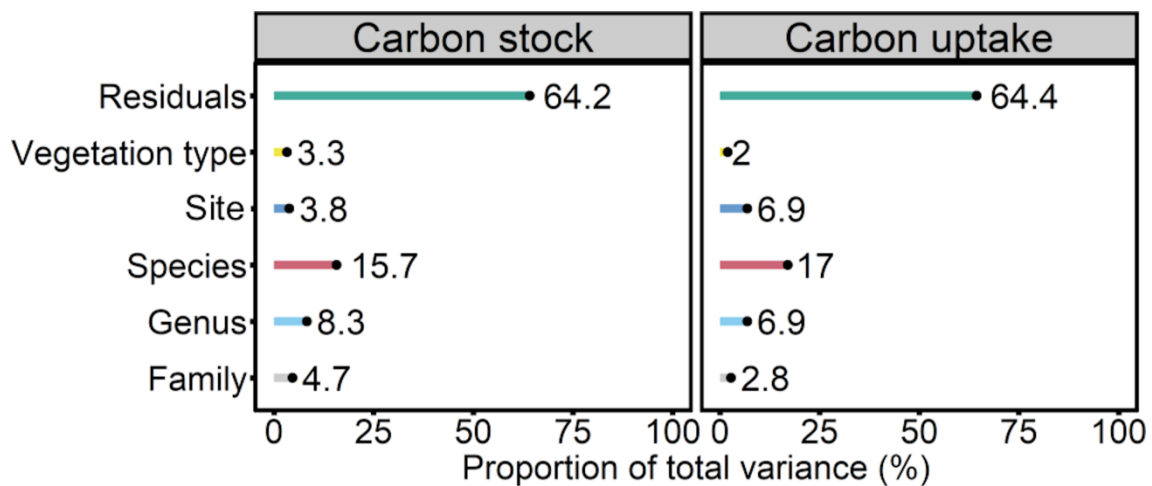

Figure 2: Results of the variance partitioning analysis of environmental effects (site and vegetation type) vs. taxonomic effects (family, genus and species) on the variation of carbon stock and uptake in 30 tropical forest sites in central-eastern Brazil.

Table 1: Full results in second-order Akaike information (AICc) for each model with absent of each random effect.

Variables	Models	AIC	Delta AIC
Carbon stock	Full model	16530.2	-
	Model without taxonomic effect	17162.7	632.52
	Model without site effect	16757.7	227.48
Carbon uptake	Full model	14228.1	-
	Model without taxonomic effect	14746.8	518.69
	Model without site effect	14453.6	225.48

3.2 Evolutionary fingerprint on carbon stock and uptake

Phylogenetic signal analysis showed non-significant λ values for carbon stock (λ = 0.0306; p-value = 0.6763) and carbon uptake (λ = 0.0207; p-value = 0.8079), suggesting phylogenetic independence in the variation of these traits. That is, closely related genera do not necessarily store (Fig. 4) or absorb (Fig. 5) similar amounts of carbon. For example, evolutionarily related genera within Euphorbiaceae (*Manihot* vs. *Cnidoscolus* show very contrasting carbon stock patterns (Fig. 4), whereas within Bignoniaceae (*Cybistax* vs. *Zeyheria)* show very distinct ability in carbon uptake (Fig. 5).
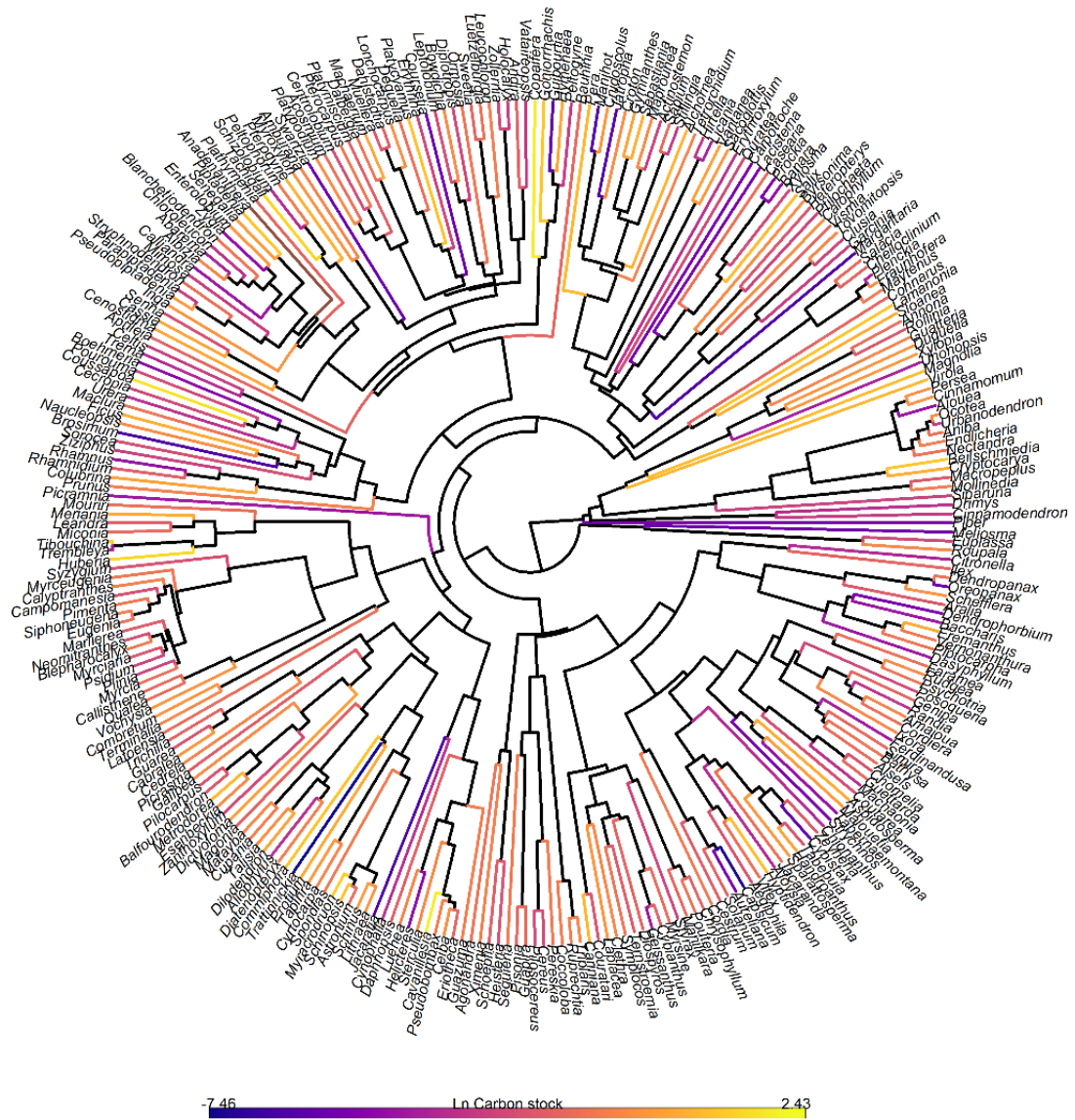
Figure 4: Phylogeny of 306 tropical forests genera with branches colored according to natural logarithm (ln) of carbon stock.
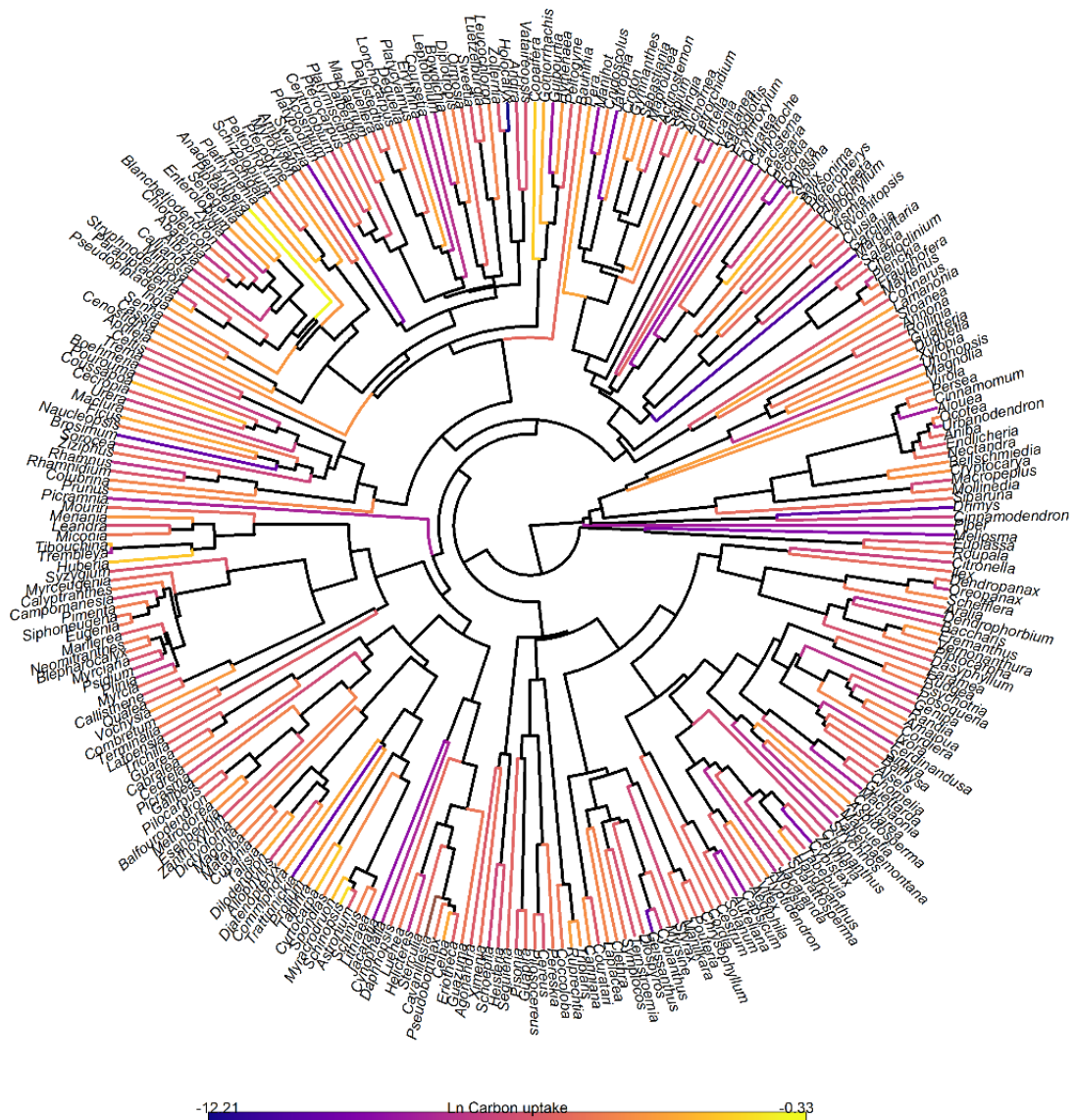
Figure 5: Phylogeny of 306 tropical tree genera with branches colored according to natural logarithm (ln) of carbon uptake.

4 Discussion

We found that two vital ecosystem services: carbon stock and uptake are mainly determined by taxonomic identity, and to a much lesser extent, by environmental factors. In contrast, the amount of evolutionary history shared among related genera, is not associated with their ability to process and store carbon (i.e. lack of phylogenetic signal).

4.1 Taxonomic vs environmental effects on carbon stock and uptake

There is a stronger effect of taxonomic identity (mainly species) on carbon stock and uptake, compared to site environmental factors. Thus, although the effect of environmental variables on carbon stock and uptake is well known (Ali et al. 2019; Maia, Souza, et al., 2020), their variation among populations along the environmental gradient is more strongly associated with species-specific intrinsic characteristics. This suggests that species' ability to store and absorb carbon can be understood as an intrinsic characteristic that varies in response to the environment, thought within a range of variation predetermined by the functional limits inherited in associated traits (e.g., wood density and photosynthesis-related traits). Thus, due to variability in characteristics between species, species contribute differently to aboveground carbon stock and uptake, with some species storing and absorbing more carbon than others (Fauset et al., 2015; Stephenson et al., 2014; Tilman et al., 2014).

Our results also point to the importance of abiotic ecological filters, which select the final set of species from the communities within the regional species pool (Cadotte & Tucker, 2017). The set of species capable of surviving and establishing in our sites determine community function related to carbon stock and uptake. That is, although environmental conditions (represented by site and vegetation type) had weak direct effects on carbon stocks and uptake of established populations, their indirect effects (through species selection) should also be considered (Cadotte & Tukcer, 2017; Gianasi et al., 2020; Poorter et al., 2015). In turn, (i) environment determines the set of species able to colonize a given site, (ii) different sites have different sets of species, (iii) species differ in resource use and contribute differently to local carbon stocks and uptake. Therefore, sites under different environmental conditions display different ecosystem-level function related to carbon dynamics. In a context of major environmental changes, patterns of species occurrence and abundance may alter significantly, which may impact site-level contribution to carbon dynamics.

4.2 Evolutionary fingerprint on carbon stock and uptake

Absence of phylogenetic signal suggests that carbon stocks and uptake, as final expressions of a set of traits, are not determined by relatedness between genera: closely related genera do not have similar abilities to process and store carbon. Thus, the provision of these ecosystem services occurs in a phylogenetically independent way (Blomberg et al., 2003; Kraft et al., 2007; Losos, 2008). Absence of phylogenetic signal is commonly interpreted as a sign of convergent evolution, meaning that distantly related lineages display similar traits (Losos, 2008; Webb et al., 2002). Evolutionary convergence emerges when distantly related lineages suffer similar evolution pressure, which promotes the adaptation to similar (convergent) traits over evolutionary time in response to a given condition (Ackerly, 2009; Liu et al., 2015). Our database includes an environmental gradient of climate and soil that conditions the occurrence of different forest habitats, such as moist and dry forests. Within these habitats, phylogenetically distant genera may occur, but may have experienced similar environmental pressures, which has promoted convergent evolution of essential characteristics for survival and success in a given habitat. As an example we have the genera *Pereskia* (Cactaceae) and *Luetzelburgia* (Fabaceae) which are phylogenetically distant and occur only in the deciduous forests of the database (Figure 4, 5).

Likewise, related genera may have gone through contrasting conditions throughout their evolutionary history, in order to diverge in their carbon stock and uptake capacity. This other interpretation of the absence of a phylogenetic signal and is associated with the evolutionary lability of a trait (Blomberg et al., 2003; Gittleman et al., 1996), that suggests the occurrence of rapid and repeated evolutionary changes in traits, which can be conditioned by different evolutionary processes, such as the displacement of characters (Losos, 2000; Schluter, 2000). Thus, when taxa are established in environments where a given characteristic is no longer advantageous, this trait can be quickly lost (Crisp & Cook, 2012), increasing the

likelihood of observing great trait differentiation between related genera (Donovan et al., 2014). This is what may have happened with the genera *Vataireopsis* and *Holocalyx*, both Fabaceae and phylogenetically closes, but that occur in different habitats, being Vataireopsis in cloud forests and Holocalyx in deciduous forests (Figure 4, 5). This differentiation is also related to the time of evolutionary divergence: the longer the time, the lower the ecological similarity between related species (Cavender-Bares et al., 2006; Losos, 2008; Silvertown et al., 2006), such as observed in the Fabaceae genera *Peltogyne* and *Apuleia*. Both occur in semideciduous forests, but have a long differentiation time within the Fabaceae group in the database (Figure 4, 5). In this case, ancient evolutionary divergence of traits associated with carbon stock and uptake may have led to the differentiation between sister *taxa*.

4.3 General Implications

The significant role of taxonomic identity reinforces the concern about the impacts of climate change on forest function. Conservative predictions of the effects of climate change indicate that climate will be unsuitable for a large portion of plant species all over the world: no species is likely to expand its climatic niche by 2080, and of these, 57% will lose half of their climatic niche (Warren et al., 2013). Tropical forest carbon dynamics could be significantly affected by this species loss, especially if they constitute the small percentage that drives most of the tropical carbon stocks; for instance, half of the Amazon carbon stock is controlled by 1% of the species (Fauset et al., 2015), while in Brazilian dry forests, half of the regional biomass stock is concentrated in 4% of the genera (Aguiar-Campos et al., 2021). Apparent evolutionary lability of biological traits involved in carbon dynamics indicate potential adaptability of species to environmental changes (Donovan et al., 2014), such as exhibiting plastic responses, genetic adaptations, or geographic changes to track ideal conditions (Williams et al., 2008). But, these evolutionary capacities occur over the long term

and the impacts of climate change (e.g., species loss) suggest that changes in environmental conditions are occurring at a rate beyond the ability of species to show these responses (Williams et al., 2008).

In addition, the forests that we analyzed have already begun to function as carbon sources because of increasing tree mortality and decreasing tree recruitment (Maia et al., 2020). As concentrations of atmospheric CO_2 and climate change are expected to continue to rise in the coming decades (IPCC, 2014), initiatives towards reducing deforestation and restoring degraded tropical lands (as proposed by REDD + and the New York Declaration on Forests) needs to intensify. Thus, as tropical trees are the main providers of carbon uptake, their maintenance also requires the conservation of current vegetation remnants and the improvement of fragment connectivity to facilitate species migration to tracking suitable environmental conditions (Dawson et al., 2011; Mitchard, 2018; Poorter et al. 2016). In addition, the fact that the lineages are diverse in the expression of carbon stocks suggests the primordial need for conservation of different sites, because the greater the number of sites, the more different lineages will be conserved.

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Supplementary material

Table S1: Basic information of the 30 sites of collection used in this study. The codes for sites presented are the respective codes on ForestPlot system (https://www.forestplots.net/).

FP code	Vegetation type	Sample area (ha)	Latitude	Longitude	N census
BAH-07	Deciduous	192	-14.4705	-44.1884	2
BON-01	Deciduous	37.8	-15.3116	-44.7349	3
DEC-01	Deciduous	59	-14.4138	-44.1627	5
DEC-02	Deciduous	134.4	-15.5502	-44.701	3
DEC-03	Deciduous	16	-14.5447	-44.2105	4
DEC-04	Deciduous	8	-14.2663	-44.1068	2
DEC-05	Deciduous	4.8	-14.4315	-44.4911	5
DEC-06	Deciduous	40.32	-14.4919	-44.1841	5
MON-01	Deciduous	54	-14.4401	-44.4246	2
BOC-01	Cloud	26.4	-22.1617	-44.4658	2
BOC-02	Cloud	193.44	-22.2175	-44.5389	4
CRR-01	Cloud	164.4	-21.6121	-44.612	4
IBI-01	Cloud	161.28	-21.7103	-43.8855	5
ITM-01	Cloud	144	-22.3501	-44.7946	2
COQ-01	Semideciduous	137.6	-21.0946	-45.3482	3
COQ-02	Semideciduous	176	-21.1553	-45.4714	3
ING-01	Semideciduous	169	-21.4098	-44.8929	5
ITT-01	Semideciduous	151.2	-21.3526	-44.609	5
ITT-02	Semideciduous	129.36	-21.3556	-44.6155	5
LUM-01	Semideciduous	239.36	-21.4977	-44.9134	4
MDD-01	Semideciduous	202.8825	-21.4885	-44.3762	7
MTR-01	Semideciduous	246	-21.6069	-44.5569	3
PIE-01	Semideciduous	234	-21.4884	-44.1006	3
POC-01	Semideciduous	89.7	-21.3292	-44.9717	3
POC-03	Semideciduous	193.8	-21.3292	-44.9717	4
SUB-01	Semideciduous	380	-21.2214	-44.9631	4
SUB-02	Semideciduous	1098.72	-21.2278	-44.9639	8
SUB-03	Semideciduous	202.72	-21.2737	-44.882	5
SUB-04	Semideciduous	199.52	-21.2167	-44.9803	4
SUB-05	Semideciduous	85.8	-21.15	-44.8999	5

Table S2: Proportion of variance explained by each random factor in the generalized linear mixed models for each carbon variable.

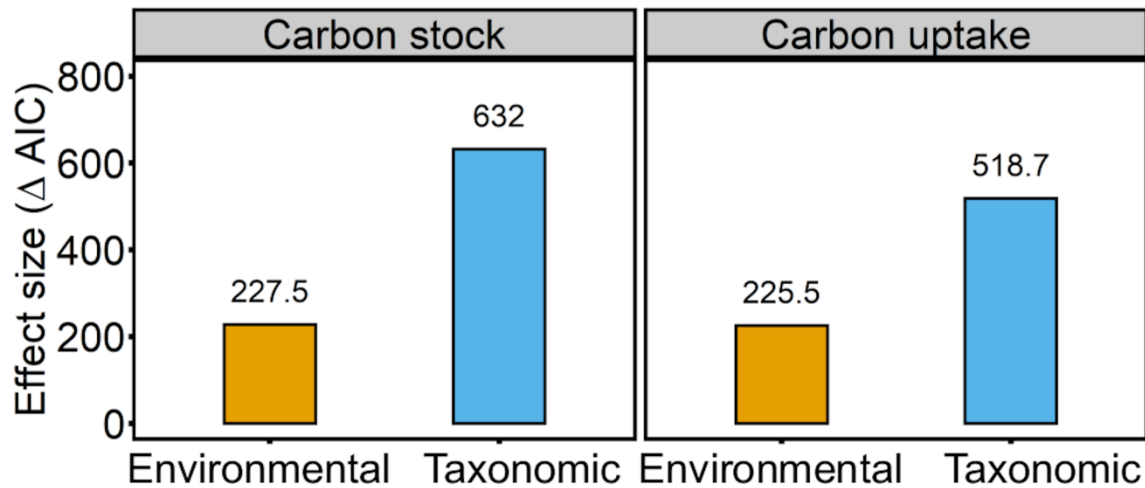| Random factor	% of variance - Carbon stock	% of variance - Carbon uptake
Family	4.70	2.81
Genus	8.30	6.90
Species	15.70	17.04
Vegetation type	3.27	1.95
Plot	3.84	6.90
Residuals	64.19	64.40

Figure S1: Impact of removing environmental and taxonomic factors on the AICc of global models for carbon stock and uptake in 30 tropical forest sites in central-eastern Brazil.