UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
INSTITUTO DE CIÊNCIAS E TECNOLOGIA DAS ÁGUAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE

DARLISSON MESQUITA BATISTA

A ESTRUTURA FILOGENÉTICA DE COMUNIDADES DE ZINGIBERALES AMAZÔNICAS RESPONDE A GRADIENTES EDÁFICOS E CLIMÁTICOS

SANTARÉM - PA
2023

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade da Universidade Federal do Oeste do Pará, como requisito para obtenção de grau de Mestre em Biodiversidade.

Orientador: Profa. Dr. Thiago José de Carvalho André

Coorientadora: Prof. Drª. Amanda Frederico Mortati

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Mestrando

Dedico este trabalho aos meus amigos e especialmente a minha família.

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RESUMO

Observar e entender como as comunidades de plantas se constituem ao longo de um amplo espaço geográfico levando em consideração um ambiente altamente heterogêneo, que tem se mostrado um fator de extrema importância na origem e na manutenção de processos ecológicos e evolutivos, pode fornecer informações valiosas sobre como operam os processos de estruturação das comunidades. Nesse sentido, levantamos a seguinte questão: como os gradientes edáficos, climáticos e hidrológicos locais influenciam os padrões da estrutura filogenética das comunidades da ordem Zingiberales ao longo de toda a região Amazônica? Para isso, baixamos dados de ocorrência de Zingiberales ao longo de toda a região Amazônica do *Global Biodiversity Information Facility* (GBIF) e calculamos as métricas de diversidade filogenética: *Standardized effect size* (SES) de *mean pairwise distances* (SES.MPD), *mean nearest taxon distances* (SES.MNTD) e *Phylogenetic Diversity* (SES.PD). Em seguida, analisamos a influência dos gradientes edáficos, climáticos e hidrológicos sobre os padrões da estrutura filogenética das comunidades a partir das análises de modelos lineares. Solo e clima afetaram a diversidade e estrutura filogenética das comunidades. Comunidades com maior SES.PD estão presentes em regiões onde os solos são mais arenosos e possuem menor concentração de nitrogênio, e onde o clima apresenta menor precipitação anual. Houve um aumento do agrupamento filogenético nas regiões com temperatura média anual mais alta e com solos mais ácidos (SES.MPD), e em regiões de solos menos arenosos e argilosos (SES.MNTD). A condição hidrológica local não influenciou significativamente as relações filogenéticas das plantas em suas comunidades. Concluímos que os gradientes edáficos influenciam fortemente na diversidade e estrutura filogenética das comunidades de Zingiberales, tanto em uma escala de tempo evolutivo mais raso (SES.PD e SES.MNTD) quanto mais profunda (SES.MPD), reforçando ainda mais a importância da heterogeneidade edáfica, que impulsiona a distribuição dos padrões florísticos da região Amazônica. Além disso, também enfatizamos o fato de que nosso estudo abrangeu uma escala espacial continental e, provavelmente graças a esse fato, conseguimos identificar a influência do gradiente climático na estrutura filogenética das comunidades herbáceas amazônicas.

Palavras-Chave: Zingiberales. Ervas do sub-bosque. Ecologia Evolutiva. Gradientes edáficos. Gradientes climáticos.

ABSTRACT

Observing and understanding how plant communities are assembled over a wide geographic space, taking into account a highly heterogeneous environment, which has been shown to be an extremely important factor in the origin and maintenance of ecological and evolutionary processes, will provide valuable information on how to operate the assembly processes of communities. In this sense, we raise the following question: how do the local edaphic, climatic and hydrological gradients influence the patterns of the phylogenetic structure of the communities of the Zingiberales order throughout the entire Amazon region? For this, we downloaded occurrence data for Zingiberales throughout the entire Amazon region from the Global Biodiversity Information Facility (GBIF) and calculated the phylogenetic diversity metrics: Standardized effect size (SES) of mean pairwise distances (SES.MPD), mean nearest taxon distances (SES.MNTD) and Phylogenetic Diversity (SES.PD). And then we analyze the influence of edaphic, climatic and hydrological soil gradients on the patterns of the phylogenetic structure of the communities from the analysis of linear models. Thus, we observed that soil and climate affect the diversity and phylogenetic structure of communities. There are communities with higher SES.PD in regions where the soils are sandier and have a lower concentration of nitrogen and where the climate has less annual precipitation. We also observed an increase in phylogenetic grouping in regions with higher average annual temperature and more acidic soils (SES.MPD), and in regions with less sandy and clayey soils (SES.MNTD). The local hydrology condition did not significantly influence the phylogenetic relationships of plants in their communities. Therefore, we conclude that edaphic gradients strongly influence the diversity and phylogenetic structure of Zingiberales communities, both on a shallower (SES.PD and SES.MNTD) and deeper (SES.MPD) evolutionary time scale. Further reinforcing the importance of edaphic heterogeneity, which drives the distribution of floristic patterns in the Amazon region. In addition, we also emphasize the fact that our study covered a continental spatial scale and, probably thanks to this fact, we were able to identify the influence of the climate gradient on the phylogenetic structure of Amazonian herbaceous communities.

Keywords: Zingiberales. Understory herbs. Evolutionary Ecology. Edaphic gradients. Climate gradients.

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MPD – Distâncias médias entre pares da comunidade (do inglês *mean pairwise distances in communitie*)

MNTD – Distâncias médias dos táxons mais próximos da comunidade (do inglês *mean nearest taxon distances in communities*)

PD – Diversidade filogenética (do inglês *phylogenetic diversity*)

SES – Tamanho de efeito padronizado (do inglês *Standardized effect size*)

SES.MPD – Tamanho de efeito padronizado das distâncias médias entre pares da comunidade (do inglês *Standardized effect size of mean pairwise distances in communitie*)

SES.MNTD – Tamanho de efeito padronizado das distâncias médias dos táxons mais próximos da comunidade (do inglês *Standardized effect of mean nearest taxon distances in communities*)

SES.PD – Tamanho de efeito padronizado da diversidade filogenética (do inglês *Standardized effect size of phylogenetic diversity*)

GLM – Modelo Linear generalizado (do inglês *generalized linear model*)

GBIF – Banco de dados global de informações sobre biodiversidade (do inglês *Global Biodiversity Information Facility*)

SUMÁRIO

INTRODUÇÃO GERAL

A ESTRUTURA FILOGENÉTICA DE COMUNIDADES DE ZINGIBERALES AMAZÔNICAS RESPONDE A GRADIENTES EDÁFICOS E CLIMÁTICOS

Qual é o problema da pesquisa?

Ambientes que possuem grande variação em suas características físicas e químicas ao longo do espaço geográfico (gradiente ambiental) são grandes candidatos a possuírem uma enorme biodiversidade (Antonelli & Sanmartín, 2011; Chesson, 2000; Stein *et al.* 2014; Viana *et al.* 2021).

O gradiente ambiental climático pode ser considerado o principal motor que conduz os diferentes padrões de organização das comunidades vegetais em amplas escalas espaciais nos Neotrópicos (escala regional; Guevara Andino *et al.* 2021; Neves *et al.* 2020). Porém, quando observamos sob uma perspectiva geográfica local, as condições dos solos e também as condições hidrológicas são cotadas não apenas como os mais fortes geradores da biodiversidade, mas também sendo responsáveis por mantê-la (Kembel & Hubbell, 2006; Muscarella *et al.* 2019; Tuomisto *et al.* 2014).

Existem diferentes maneiras de tentar mensurar como e quando as diferentes condições ambientais influenciam na organização das comunidades biológicas locais, seja contando o número de espécies em um determinado local (riqueza de espécies) e em seguida vendo como esse número varia em resposta a diferentes medidas ambientais (ex: Drucker *et al.* 2008) ou até mesmo observando como essas medidas interferem nas características funcionais das espécies em uma comunidade (ex: Ackerly, 2003). Existem também outras formas de avaliar esse tipo de questão, como usar informações da história evolutiva das espécies (Losos, 2008).

Uma dessas abordagens é chamada de estrutura filogenética de comunidades (Webb *et al.* 2002), que quando aplicada, pode demonstrar dois padrões de relação de parentesco existentes em uma comunidade biológica: o agrupamento filogenético, quando as espécies possuem um elevado grau de parentesco evolutivo (Webb *et al.* 2002), e a sobredispersão filogenética, quando as espécies possuem um baixo grau de parentesco evolutivo (Webb *et al.* 2002). Dessa forma, utilizando esse método juntamente com dados ambientais disponíveis, podemos identificar se determinada faixa do gradiente ambiental pode influenciar nos padrões de estrutura filogenética das comunidades (Lehtonen *et al.* 2021).

As Zingiberales são um grupo de plantas terrestres tropicais encontradas em toda a Amazônia, e já demonstrou ser um excelente grupo para testar como a heterogeneidade ambiental influencia em sua organização, principalmente por conta de sua ampla distribuição espacial (Figueiredo *et al.* 2018, 2022). Nesse sentido, o presente trabalho pretendeu responder a seguinte questão: como os gradientes ambientais influenciam os padrões da estrutura filogenética observados nas comunidades de ervas Zingiberales ao longo da Amazônia?

Como a pesquisa foi realizada?

Baixamos informações de ocorrência das espécies de Zingiberales de toda a região amazônica do GBIF (para saber o significado dessa e de outras siglas, acesse a “lista de abreviaturas e siglas”) e em seguida essas informações foram transformadas em uma matriz de presença e ausência em grades com resolução de 1° x 1° (aproximadamente 111 km de arco na linha do equador).

Esses dados de presença e ausência foram utilizados para medir a estrutura filogenética das comunidades. Utilizamos três abordagens para calcular a estrutura (PD, MPD e MNTD) e seus respectivos SES. PD é uma métrica que calcula a diversidade filogenética somando o comprimento dos ramos da filogenia para cada comunidade (Faith, 1992). O MPD obtém a diversidade filogenética calculando a distância média entre cada espécie da comunidade (Webb, 2000). Já o MNTD obtém calculando a distância média que separa cada espécie na comunidade de seu parente mais próximo (Webb, 2000). A filogenia de todas as espécies de Zingiberales amazônicas utilizada nas análises foi gerada no pacote *V.PhyloMaker* (Jin & Qian, 2019).

Em seguida, para sabermos se os gradientes ambientais influenciavam na estrutura filogenética das comunidades, nós medimos a relação entre as variáveis de estrutura filogenética e as variáveis ambientais climáticas (baixadas do WorldClim), do solo (baixadas do SoilGrid) e hidrológicas locais (disponibilizados por Fan et al. 2013 e Trabucco & Zomer, 2019), a partir de testes de regressão linear para múltiplas variáveis.

Todas as análises estatísticas e filogenéticas foram computadas em ambiente R versão 4.2.1 (R Core Team, 2022). Para uma visão metodológica completa verifique a seção “Material e métodos”.

Qual a importância da pesquisa?

Há muito tempo os pesquisadores vêm tentando encontrar uma justificativa que explique a grande biodiversidade existente nos Neotrópicos, em particular o que explicaria o fato de encontrarmos a maior número espécies de plantas nos Neotrópicos (Antonelli & Sanmartín, 2011). Muitas possíveis explicações surgiram nas últimas décadas, como a capacidade de dispersão das espécies (Antonelli & Sanmartín, 2011), conservadorismo de nicho ao longo da história evolutiva das espécies (Wiens & Donoghue, 2004), assim como a variação dos solos, precipitação, temperatura e heterogeneidade de habitat (Antonelli & Sanmartín, 2011). Acredito que esses mecanismos não atuam separadamente como caixinhas e sim a interação conjunta deles que promove e mantém essa grande diversidade de espécies que existe nos neotrópicos, dando maior destaque a alta variabilidade de habitats (Kembel & Hubbell, 2006; Muscarella *et al.* 2019; Tuomisto *et al.* 2014). Sendo assim, entender como a heterogeneidade ambiental atua sobre a organização das comunidades vegetais amazônicas levando em consideração as relações de parentesco entre as espécies, é crucial para nos ajudar a entender por que a diversidade de espécies de plantas é maior nos Neotrópicos, em especial na Amazônia (Antonelli & Sanmartín, 2011).

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Título original da pesquisa

Estrutura filogenética de comunidades de Zingiberales Amazônicas

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OBJETIVOS

Geral

Avaliar o efeito de gradientes ambientais na estrutura filogenética das comunidades de ervas terrestres rizomatosas da ordem Zingiberales na Amazônia

Específicos

- Avaliar o efeito de gradientes edáficos (concentração de cátions e textura do solo) na estrutura filogenética das comunidades de Zingiberales;
- Avaliar o efeito de condições climáticas (precipitação, temperatura) na estrutura filogenética das comunidades de Zingiberales;
- Avaliar o efeito de condições hidrológicas locais na estrutura filogenética das comunidades de Zingiberales

Hipóteses

(1) Encontraremos maior agrupamento filogenético em comunidades presentes nas porções do gradiente edáfico mais estressante, como solos arenosos e com baixa fertilidade, por conta da disponibilidade inadequada de recurso;

(2) encontraremos maior agrupamento filogenético no extremos climáticos (temperaturas mais frias e quentes) por conta do stress térmico;

(3) ambientes com maior escassez hídrica também terão espécies em suas comunidades mais próximas filogeneticamente causado pelo *stress* hídrico (baixa disponibilidade de recurso).

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CAPÍTULO ÚNICO

Artigo segue o modelo da *Journal of Vegetation Science*

1. Title

Phylogenetic structure of Amazonian ginger communities responds to edaphic and climatic gradients

2. Running title

Phylogenetic structure of Amazonian ginger communities

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6. Abstract and keywords

Question: How do edaphic, climatic and hydrological gradients influence the phylogenetic structure of the ginger communities throughout the Amazon region?

Methods: We compiled Zingiberales species occurrence data throughout Amazon region from the Global Biodiversity Information Facility (GBIF) and calculated phylogenetic diversity and structure metrics (standardized effect sizes (SES) of mean pairwise distances (SES.MPD), mean nearest taxon distances (SES.MNTD) and phylogenetic diversity (SES.PD)) for 1-degree cells (~111 km). The effects of edaphic, climatic and local hydrologic conditions gradients on the phylogenetic structure of the communities were analyzed using generalized linear models.

Results: We observed that soil and climate affected the diversity and phylogenetic structure of the Zingiberales communities. Communities with higher SES.PD were found on regions with predominantly sandier and low nitrogen soils, and lower annual precipitation. The phylogenetic clustering considering the entire phylogeny (SES.MPD) increased with higher average annual temperature and more acidic soils, and the clustering at lineages from more recent evolutionary history (SES.MNTD) varied with soil granulometry. No effect was detected for local hydrology at the 1-degree scale.

Conclusion: We found that edaphic and climate gradients strongly influence the diversity and phylogenetic structure of Zingiberales communities, both on a more recent (SES.PD and MNTD) and older (SES.MPD) evolutionary time scale, further reinforcing the importance of environmental heterogeneity on driving the distribution of floristic patterns in the Amazon region.

Keywords: Phylogenetic structure, understory herbs, Amazon, Community Ecology, Evolutionary Ecology, edaphic gradients, climatic gradients, depth of water table, HERBASE.

7. Main text

Introduction

Environmental heterogeneity is an important factor driving ecological and evolutionary processes that promote and maintain biodiversity (Antonelli & Sanmartín, 2011; Chesson, 2000; Stein et al., 2014; Viana et al., 2021). It has been shown that abiotic factors can generate spatial patterns of biological diversity in the Amazon region. However, most studies address local spatial scales and ignore plant species evolutionary relationships (Higgins et al., 2011; Lehtonen et al., 2021, 2015; Muscarella et al., 2019; Tuomisto et al., 2014), thus limiting knowledge about the importance of environmental heterogeneity, particularly in the phylogenetic structure of tropical plant communities at large spatial scale. Despite its recognized importance, few studies (eg: González-Caro et al., 2014; Guevara Andino et al., 2021) have simultaneously accessed edaphic, climatic and hydrological gradients at regional scales, mainly regarding their influence as filters on ecological and evolutionary processes.

The phylogenetic structure of communities can help explain how biological communities are currently organized from an evolutionary perspective, through processes responsible for the patterns of phylogenetic relatedness observed in communities (Cavender-Bares et al., 2009; Webb et al., 2002). Thus, wo main patterns can be observed in the phylogenetic structure of local communities: phylogenetic clustering and phylogenetic overdispersion (Kraft et al., 2007; Webb et al., 2002). If the niches and functional traits of the species are conserved in their evolutionary history, phylogenetic clustering can be observed when environmental filtering sorts species with functional traits adapted to these filters (Ackerly, 2003; Losos, 2008; Webb et al., 2002; Wiens & Graham, 2005). On the other hand, if phylogenetically close species conserve in their evolutionary lineages a shared similarity of niches and traits in scenarios of competition or density-dependent interactions (herbivore-pathogen specificity), a overlapping of their niches in the present leads to a pattern of phylogenetic overdispersion, i.e., assembly of communities mostly composed by phylogenetically distant species (Webb et al. al., 2002; Cavender-Bares et al., 2009). We can also observe phylogenetic overdispersion in cases of functional convergence through the action of environmental filters on large spatial scales (Cavender-Bares et al., 2004; Fine & Kembel, 2011) and in scenarios of facilitative interactions among species (Valiente-Banue & Verdú, 2007). When the ecological forces of factors like environmental filtering or interactions (e.g., competition) are weaker or counteract each other, local communities can present a random phylogenetic pattern, commonly caused by neutral processes, e.g., dispersion and by a combination of multiple processes (Cavender-Bares et al., 2009).

Amazonian soils are known to have high heterogeneity and variable levels in geographic space. Soils in the central and eastern regions are older and generally less fertile than soils in western Amazonia, which vary from extremely nutrient-poor white sands to well-drained, fertile soils (Quesada et al., 2011). This high edaphic heterogeneity has been the subject of several studies, for example, on Amazonian understory plant communities. Fertility gradients and soil texture were found to exert a strong influence on the phylogenetic structure of these communities (eg: Eiserhardt et al., 2013; Fine & Kembel, 2011; Guevara et al., 2016; Lehtonen et al., 2021, 2015; Muscarella et al., 2019; Villa et al., 2018). For instance, fern communities in lowland forests (non-flooded *terra firme* and white-sand *campinaranas*) of central Amazonia observed in habitats with richer soils exhibited higher degree of relatedness compared to those in habitats with poorer soils, indicating that soils with greater availability of nutrients are selecting species phylogenetically closer and adapted to such conditions (Lehtonen et al., 2015). Additionally, the upland palm communities located in western Amazon are phylogenetically clustered in areas with low soil fertility (Muscarella et al., 2019), in which case the low availability of resources in the soil would act as an environmental filter and select phylogenetically closer species.

Trends were also detected in the phylogenetic structure of communities along local hydrological gradients in neotropical forests, such as tree communities of the Barro Colorado Island in Panamá (Kembel & Hubbell, 2006), and palm communities in flooded forests in western Amazonia and from *terra firme* forests in central Amazonia (de Freitas et al., 2014; Muscarella et al., 2019). Muscarella et al. (2019) found that palm communities tend to be phylogenetically closer in soils that are subjected to flooding. Another important factor is the soil moisture due to the distance to the water table, which can affect the distribution of Amazonian plants, especially in the months of lower precipitation (Costa et al., 2023).

Soil fertility and texture, and local hydrology conditions alone do not explain plant distribution patterns. Climate is also an important factor that affects the diversity and composition of tropical plant communities (González-Caro et al., 2014; Guevara Andino et al., 2021; Neves et al., 2020), affecting the pedological processes themselves (Certini & Scalenghe, 2023; Phillips, 2017). Annual precipitation exerts a strong influence on the phylogenetic structure of communities. For instance, drier and rainy regions are related to the low phylogenetic diversity of local tree communities in South America (including the Amazon), suggesting that low availability or excess water may act as a filter and select species phylogenetically close and adapted to these conditions (Neves et al., 2020). Low temperatures have also been shown to cause phylogenetic clustering in Neotropical tree communities (González-Caro et al., 2014). These climatic effects on the ecological and evolutionary organization of plant communities can be clearer observed when the study area covers enough range of climate variation, which implies a large spatial scale (González-Caro et al., 2014; Guevara Andino et al., 2021; Neves et al., 2020).

Herbs are plants that do not have secondary growth, and therefore do not produce wood tissues. Terrestrial herb communities are formed by plants that germinate and spend their entire life cycle in the soil (Poulsen & Balslev, 1991) and help compose the understory. It is a species rich group, contributing up to 29% of the Amazonian plant species at the local scale (Gentry & Dodson, 1987). For instance, up to 96 species can be observed per hectare (Poulsen & Balslev, 1991). The spatial distribution of richness, composition and relative abundance of Amazonian Zingiberales, an ubiquitous lineage of herbs in the domain, is influenced by edaphic, topographic, climatic, hydrological and canopy cover gradients on local scales (e.g., Drucker et al., 2008; Figueiredo et al., 2018; Magalhães, 2010; Moulatlet et al., 2014; Santos, 2021). Environmental gradients not only interfere with the distribution of species, but also with the composition of the functional traits of Amazonian Zingiberales communities (Figueiredo, 2017). Thus, Zingiberales are an excellent model group to study the role of environmental heterogeneity in determining floristic patterns of the understory.

Despite the growing number of studies involving the phylogenetic structure of Amazonian plant communities in recent decades, the vast majority of them have sought to understand how environmental and historical factors drive the assembly of tree (e.g. Aldana et al., 2017; Cárdenas et al., 2017; Dexter et al., 2017; Fine & Kembel, 2011; González-Caro et al., 2021; Guevara et al., 2016) and palms communities (de Freitas et al., 2014; Eiserhardt et al., 2013; Muscarella et al., 2019). Few studies assessed the effect of these drivers on the species-rich tropical herbaceous substrate (Lehtonen et al., 2021, 2015). Consequently, we have a limited knowledge on how such communities are phylogenetically structured in relation across environmental gradients, particularly on broad spatial scales.

Here, we ask the following question: How do edaphic, climatic and hydrological gradients influence phylogenetic structure patterns of the ginger communities throughout the Amazon region? We hypothesized that the phylogenetic structure of Zingiberales communities is influenced by edaphic, climatic and hydrological conditions, as these conditions should affect the life cycle and metabolism of these herbs (Drucker et al., 2008; Figueiredo et al., 2022, 2018; Lehtonen et al., 2021, 2015; Moulatlet et al., 2014), and in extreme habitats they should act as environmental filters and select species phylogenetically close and adapted to these habitats and consequently cause phylogenetic groupings (Muscarella et al., 2019; Neves et al., 2020; Webb et al., 2002). Extreme habitats require adaptations that are defiant to evolve, so a lineage that is evolutionarily adapted to an extreme environment might end up producing other species in those habitats. On the other hand, a strong filter can eliminate many species from the regional pool and contribute to the coexistence of closely related species.

Material and methods

Study Area

Occurrence data for Zingiberales species were obtained from the Global Biodiversity Information Facility (GBIF; GBIF.org, 2022). Only species with native distribution in the Amazon region (Figure 1), included in the specialist-curated list of Amazonian plant species (Cardoso et al., 2017) as well as in the list of herb species occurring in more than 1,000 inventory plots in the Amazon, as part of the HERBASE project (Herbase, 2022) were considered in subsequent analyses. Occurrences that did not have available geographic coordinates were removed, in addition to those specimens that were not identified at the species level.

Occurrence data was transformed into matrices of presence and absence in grid-cells with a resolution of 1° x 1° (approximately 111 km of arc on the Equator), 0.5° x 0.5° (approximately 56 km), and 0 .1° x 0.1° (approximately 11 km) to test whether spatial scale influenced the phylogenetic structure of Amazonian Zingiberales. We classified the 1° x 1° cells as large scale, 0.5° x 0.5° as medium, and 0 .1° x 0.1° as small scale.

For this, we used the function "*lets.presab.points*" in the R package letsR (Vilela & Villalobos, 2015). Species richness (S) was spatialized for each cell on a map for the Amazon region (Eva et al., 2005), applying the "*plot*" function of letsR. We removed the cells that were centered outside of the boundaries of the Amazon region boundaries. We also excluded cells that only had one species per plot to avoid spurious low sample size effects and also because phylogenetic diversity indices produce null values when there is only one species in the community.

Environmental variables

To examine the relationship between environmental variables and the phylogenetic structure of Zingiberales in the Amazon region, we used three sets of environmental data (Climate, Soil and Local Hydrological Soil Conditions; Appendix S1) that were obtained from public available databases. The chosen variables represent environmental components widely recognized as determinants of the distribution and/or performance of tropical plant species (e.g., Clark et al., 1998; Johnson et al., 2017; Marca-Zevallos et al., 2022; Moulatlet et al., 2022; Murphy & Bowman, 2012; Tuomisto & Poulsen, 1996; van Schaik et al., 1993). We used five bioclimatic variables extracted from the WorldClim 2.1 climate database (Fick & Hijmans, 2017) with ~1,000 meters of resolution: mean annual temperature (BIO1), mean temperature of the warmest quarter (BIO10), mean temperature of the coldest quarter (BIO11), annual precipitation (BIO12) and precipitation of the driest quarter (BIO17). We obtained seven edaphic variables, at a resolution of 250 meters, from the SoilGrids 2.0 database created by ISRIC - World Soil Information (Poggio et al., 2021): soil cation exchange capacity (CEC), the proportion of clay particles in fine earth fraction (clay), total nitrogen (N), pH (phh2o), proportion of sand particles in the fine earth fraction (sand), soil organic carbon content in the fine earth fraction (SOC) and carbon stocks organic (OCS). Additionally, we obtained two local soil hydrological variables extracted from two different databases. The water table depth (WTD) was obtained from the layer provided by Fan et al. (2017, 2013) at ~1,000 meters resolution; and the variable soil water content (SWC) was extracted from the CGIAR database - Consortium for Spatial Information (Trabucco & Zomer, 2019) with a resolution of ~1,000 meters. To match the spatial resolutions of the grids used in this study, all 14 environmental variables were resampled using the bilinear interpolation method in the QGIS program version 3.22.7 (QGIS.org, 2022).

Phylogenetic Reconstruction

The monocot order Zingiberales Griseb. is a group of tropical terrestrial herbs comprising eight families (Cannaceae Juss; Costaceae Nakai; Heliconiaceae Nakai; Lowiaceae Ridl; Marantaceae R. Br; Musaceae Juss; Strelitziaceae Hutch and Zingiberaceae Martinov.), approximately 110 genera and more than 2600 species (Tropicos, Missouri Botanical Garden, accessed 05 Nov 2021 <https://tropicos.org>). It has a wide distribution in the Amazon region, with 6 families, 20 genera, and approximately 170 species (Cardoso et al., 2017), and can contribute with 14 to 40% of the species richness and 9 to 70% of the abundance among Amazonian terrestrial herbs (Costa, 2004; Drucker et al., 2008; Magalhães, 2010; Rodrigues et al., 2021; Santos, 2021).

We used the V.PhyloMaker package (Jin & Qian, 2019) to reconstruct a phylogenetic tree of Amazonian Zingiberales species based on the list of Amazonian species provided by Cardoso et al. (2017) and by Herbase (2022). V.PhyloMaker uses an updated and expanded version of the mega phylogeny GBOTB (GenBank taxa with a backbone provided by Open Tree of Life version 9.1) developed by Smith & Brown, (2018). The GBOTB.extended phylogeny is time-calibrated, including all extant families of seed plants (with 74,533 species), based on the APG IV system (Angiosperm Phylogeny Group 2016), thus being the largest dated phylogeny for vascular plants available (Jin & Qian, 2019). Species present in our dataset that are absent in the GBOTB.extended mega phylogeny were added to their respective genera using scenario 3, with the "*scenarios="S3"*" using the function *phylo.maker* implemented in V.PhyloMaker (Jin & Qian, 2019). To resolve existing polytomies in the generated phylogeny, we surveyed the literature to find available phylogenetic hypotheses that had included the species present in polytomous branches in our phylogeny (10 clades with polytomies; Appendix S2), following Milla (2020). In the 15 cases where we could not find published phylogenetic relationships, the resolution was based on taxonomic information (Appendix S3). All relationships were resolved manually based on the available phylogenetic and taxonomic information available using the phytools package, in R (Revell, 2012) with the "*drop.tip*" function to "disconnect" the polytomic branch and the "*bind.tip*" function to "rebind" it to a given branch. For the additional 38 species (Figure 2), it was not possible to find published phylogenetic hypotheses or taxonomic revisions, and they were then maintained as basal polytomies in their respective genera.

Phylogenetic diversity and structure

To assess the phylogenetic diversity and structure of communities, we used three metrics that incorporate knowledge about evolutionary history in quantifying the diversity of biological communities (Faith, 1992; Webb et al., 2002): Faith's phylogenetic diversity (PD; Faith, 1992), mean pairwise phylogenetic distance (MPD; Webb, 2000) and mean nearest neighbor distance (MNTD; Webb, 2000). PD is the sum of the branch lengths of a phylogenetic tree (Faith, 1992), which is commonly correlated with species richness (Lehtonen et al., 2015). It is considered a terminal metric and more sensitive to phylogenetic relatedness at branch tips (Mazel et al., 2016). The MPD quantifies the mean phylogenetic distance of between each pair of species in the community, and then indicates the average phylogenetic distance between all taxa, from the deepest to the shallowest nodes of the phylogeny (Webb, 2000), which can be interpreted as a baseline metric (Mazel et al., 2016). The MNTD, on the other hand, estimates the distances between each species and its closest relative, thus being more sensitive to capturing relationships in more recent evolutionary history (Webb, 2000) and, like PD, can be considered a terminal metric (Mazel et al., 2016). We compared the observed values of PD, MPD and MNTD with null expectations generated by random selection of species. For this, we calculated the standardized effect size of the PD, MPD and MNTD metrics (SES.PD, SES.MPD and SES.MNND) as follows:

$$SES = \frac{(\chi OBS - \chi Nul)}{SDNul}$$

Where χOBS is the observed value of PD, MPD or MNTD, χNul is the average of the of the random communities and SDNul is the standard deviation of the of the random communities. To reach the null values, we used the independentswap model (randomizes the community data matrix with the independent swap algorithm), as it maintains the frequency of occurrence and species richness in the communities, performing 9999 randomizations and 10000 iterations using the picante package (Kembel et al., 2010). SES.MPD and SES.MNTD are equivalent to -1 times the Net Relatedness Index (NRI; Webb, 2000) and the Nearest Taxon Index (NTI; Webb, 2000), respectively. We generated the standardized effect size of the PD metric to avoid possible bias derived from the common correlation between PD and species richness (Lehtonen et al., 2015). Positive values of SES.PD, SES.MPD, and SES.MNTD indicate that the species are more phylogenetically distant than expected by chance (i.e., overdispersion), while negative values indicate that the species are closer phylogenetically than expected by chance (i.e., clustering). Further, for SES.PD, significant negative values indicate lower phylogenetic diversity and positive values indicate higher phylogenetic diversity.

Statistical analysis

The effect of phylogenetic resolution on the observed results of the phylogenetic diversity and structure of communities was tested through correlations of the results of the metrics SES.PD, SES.MPD, and SES.MNTD, obtained from a phylogeny with resolved polytomies using published phylogenetic hypotheses and taxonomic revisions (Appendix S4), and from the phylogeny that had part of its polytomies resolved using only published phylogenetic hypotheses (Appendix S5). For this, we used Spearman's correlation test with the "*chart.Correlation*" function in the PerformanceAnalytics package (Peterson et al., 2022). As the correlation coefficients had values > 0.96 between each phylogenetic resolution for each metric (Appendix S6), we chose to proceed with further analysis considering the results of the phylogenetic structure produced by the phylogeny resolved from published phylogenetic hypotheses and taxonomic revisions.

To investigate whether the phylogenetic structure of the Amazonian Zingiberales communities is affected by the spatial sampling scale (cell resolution), we compared the means of the phylogenetic metrics (SES.PD, SES.MPD and SES.MNTD) among the spatial scales (1º x 1º - large, 0.5º x 0.5º - medium, and 0.1º x 0.1º - small) using the non-parametric Kruskal-Wallis test (McKight & Najab, 2010).

To test whether environmental gradients influence the structure and phylogenetic diversity of Zingiberales communities, we used generalized linear models (GLMs). For this, we considered the variables representing climate, soil and local hydrologic conditions as predictors and the phylogenetic metrics as dependent variables. For this purpose, we first verified the existence of collinearity between the predictor variables (Zuur et al., 2010), from the Spearman correlation coefficient with the "*chart.Correlation*" function in the PerformanceAnalytics package (Peterson et al., 2022). When the correlation coefficients showed values ≥ 0.7 between two variables, one was excluded and the other was selected. In total, seven variables were excluded after the correlation test (Appendix S7). Additionally, to exclude any trace of collinearity, we evaluated the Variance Inflation Factor (VIF) using the "*vif* " function of the CAR package (Fox & Weisberg, 2011), excluding those variables with values of VIF ≥ 5. Seven independent variables remained (Table 1). For the residuals to have a better fit and respect the assumptions of variance homoscedasticity, normality and linearity for the linear regression analyses (Zuur et al., 2010), we selected the best normalization method using the "*bestNormalize*" function of the bestNormalize package (Peterson, 2022). The variables SES.MPD, SES.PD, BIO1, BIO12, N, phh2o, and WTD were normalized using the Ordered Quantile technique with the "*orderNorm*" function. Ordered Quantile is a classification-based method, where values are mapped to their percentile, and then mapped to the same percentile from the normal distribution (Peterson & Cavanaugh, 2020). Clay and sand variables were normalized using the Box-Cox method with the "*boxcox*" function. Box-Cox is a power transformation technique, which stabilizes the variance, making the data closer to the normal distribution (Box & Cox, 1964). Both transformations were performed in the bestNormalize package (Peterson, 2022). The SES.MNTD variable met the assumptions of normality without the need of transformation. After this process, we ran the analyzes with Gaussian distribution for each dependent variable and the seven selected predictors (Table 1). We then performed an automated model selection procedure (Anderson & Burnham, 2002; Wagenmakers & Farrell, 2004) based on the corrected Akaike information criterion (AICc; Wagenmakers & Farrell, 2004), using the "*dredge*" function in the MuMIn package (Barton, 2009; Appendix S8). From the set of candidate models generated, we selected the ones with best-fitting considering values of delta AICc < 2 and averaged the models (Anderson & Burnham, 2002) with the function "*model.avg*" (package MuMIn; Barton, 2009). Additionally, we obtained the importance of each variable for the model using the "*sw*" function (MuMIn; Barton, 2009), using delta AICc < 2 as a criterion. All statistical and phylogenetic analyzes were computed in an R version 4.2 (R Core Team, 2022).

Results

In the GBIF records we found 24,291 occurrences of herbs of the order Zingiberales for the Amazon region, belonging to 186 species (Appendix S9). The richest family was Marantaceae, with 113 species (60.75%), followed by Costaceae (29 spp; 15.5%), Heliconiaceae (25 spp; 13.44%), Zingiberaceae (16 spp; 8.6%), Cannaceae (2 spp; 1.1%) and Strelitziaceae (1 sp; 0.5%).

Five hundred and thirty-seven cells with a resolution of 1° x 1° were initially generated (Figure 1). After removing cells with their centers outside the limits of the Amazon and with one species, 460 cells with 186 species remained (Appendix S10). We also generated 1,305 cells of 0.5° x 0.5°, which after eliminating marginal cells with centers outside the Amazon limits and with less than two species, resulted in 968 pixels, preserving the number of species (186; Appendix S10). In cells of 0.1° x 0.1°, which had 3,945 cells and after removals, 2,174 cells remained, resulting in 184 species (Appendix S10).

The phylogeny generated by merging the species lists for the Amazon by Cardoso et al. (2017) and the Herbase database resulted in 190 terminal taxa (Figure 2).

We found non-significant differences in SES.PD (P = 0.7; Figure 3), SES.MPD (P = 0.08; Figure 4) and SES.MNTD (P = 0.84; Figure 4) for the communities of Zingiberales among the different spatial scales studied: large (1° x 1°), medium (0.5° x 0.5°) and small (0.1° x 0.1°). For this reason, we focused on the results of linear regression analyses for the 1° x 1° scale, to address macro scale relationships.

The phylogenetic diversity (SES.PD) of Zingiberales in the Amazon was affected by edaphic and climatic gradients (Table 2; Figure 5). SES.PD values ranged from -3.61 to 2.88 (mean: -0.26; standard deviation: 1.05; Appendix S11), where negative values indicate phylogenetic clustering and positive values, phylogenetic overdispersion. We observed an increase in the phylogenetic diversity in regions where soils are sandier (Table 2; Figure 5), and decrease of this diversity in regions with lower nitrogen concentration and also in drier regions (lower annual precipitation) (Table 2; Figure 5).

The phylogenetic structure of communities was also influenced by environmental gradients

(Table 4; Figure 6). SES.MPD values ranged from -6.74 to 1.65 (mean: -0.25; standard deviation: 1.37; Appendix S11). Negative values indicate phylogenetic clustering considering the phylogeny as a whole, and positive values indicate phylogenetic overdispersion. The SES.MNTD values ranged from -2.88 to 3.31 (mean: -0.178; standard deviation: 1; Appendix S11). Here, negative values indicate phylogenetic clustering toward terminal phylogenetic relationships and positive values indicate phylogenetic overdispersion. We observed an increase in the phylogenetic clustering in regions with higher average annual temperatures and more acidic soils (SES.MPD) (Table 4; figure 6), and in regions with less sandy soils and also in regions with less clayey soils (SES.MNTD) (Table 4; figure 6).

Discussion

Our findings demonstrated that soil and climate affected the phylogenetic diversity and structure of ginger communities, causing both clustering and phylogenetic overdispersion. However, the local hydrology conditions did not significantly influence the phylogenetic relationships of Amazonian Zingiberales at the large scale. Thus, we showed that soil, along with climate, plays an important role in organizing evolutionary relationships in rhizomatous terrestrial herb communities, possibly acting as environmental filters along the Amazon region. The non-significant differences we found in the phylogenetic structure of Zingiberales' communities across different spatial scales, contrasts with previous findings for tropical forests (Kembel & Hubbell, 2006; Okuno et al., 2022). Among the possible explanations for this finding, we stress the size of the study areas. In other published results, the smallest scale is generally 10 x 10 meters and the broadest 100 x 100 meters (Kembel & Hubbell, 2006; Okuno et al., 2022), while in our present study they were ~11 x 11 km and ~111 x 111 km, respectively. Soils with a more alkaline pH and higher clay concentration are more fertile (Fine & Kembel, 2011; Quesada et al., 2011). Therefore, when the pH is more acidic and less clayey, soils that are poorer in nutrients are expected, which may be related to greater abiotic stress. Our findings show that these edaphic characteristics are causing phylogenetic clustering in Amazonian Zingiberales communities, both for more basal relationships, considering the phylogeny as a whole (SES.MPD; Webb, 2000), and for more recent divergences in evolutionary history (SES. MNTD; Webb, 2000), suggesting that low resource availability acts as an environmental filter and selects species that are phylogenetically closer and adapted to these types of environments. If species niches are conserved in their evolutionary lineages, these results indicate that edaphic filters leading to poor and harsh conditions are selecting phylogenetically close species adapted to them, as closely related species tend to be ecologically similar (Ackerly, 2003; Losos, 2008; Wiens & Graham, 2005). As we see plant communities occurring in more clayey soils and with more alkaline pH, we notice an increase in phylogenetic overdispersion, possibly caused by the increase in resource availability, favoring the co-occurrence of less related species. Similar results were also found in palm communities (Lehtonen et al., 2021; Muscarella et al., 2019) and Amazonian trees (Fine & Kembel, 2011). Therefore, our results highlight and reinforce the importance and influence of the availability of nutrients in the soil on the structure of Amazonian plant communities (e.g., Figueiredo et al., 2022, 2018; Lehtonen et al., 2021, 2015; Muscarella et al., 2019; Tuomisto et al., 2014).

Considering also a scenario of effects of environmental filtering on species from convergent clades, i.e., trait similarities independent of common ancestry, we can expect the assembly of communities phylogenetically overdispersed (Cavender-Bares et al., 2004; Kraft et al., 2007; Webb et al., 2002), which could be among the possible explanations for the observed pattern of increase in SES.MNTD values in response to the increase in sand concentration. It suggests that taxa from clades sharing more recent evolutionary history under similar environmental constraints might have converged to inhabit sandier soils. Similar results have already been seen for tree communities found in white sand ecosystems in western Amazonia (Fine &

Kembel, 2011). Although the sandy soils are poor in nutrients and considered a stressful environment for several plant species (see Adeney et al., 2016, for a review of this type of ecosystem), Zingiberales communities found in more sandy soils may might have evolved their niches to avoid competition for limited resources available in less sandy and possibly more fertile soils, such as in non-flooded *terra firme* habitats (Fine et al., 2005; Fine & Kembel, 2011). Alternatively, phylogenetic overdispersion found in soils with higher concentrations of sand might be an adaptive response to water resources. Several Amazonian white sand ecosystems have enormous amounts of available water content, such as in humid grasslands, mainly caused by insufficient water drainage, which leads to shallow and (or) seasonally flooded water tables (Adeney, 2009; Adeney et al., 2016). These environmental conditions can be considered optimal for groups adapted to such conditions. In fact, Zingiberales are more diverse in poorly drained valleys (Drucker et al., 2008).

We observed a decrease in phylogenetic diversity due to the increase in soil nitrogen. This pattern may have arisen due to the recent rapid diversification of phylogenetically close clades with a strategy of rapid acquisitive growth, which had their radiation favored by fertile soils of recent Andean orogeny (Figueiredo et al., 2022). Thus, we have co-occurrence of phylogenetically close species towards the tips of the phylogeny (Mazel et al., 2016), which tend to decrease the PD as compared to the co-occurrence of species belonging to older lineages with longer branch lengths that are present in older soils and with lower nitrogen concentrations. As PD measures branching length to estimate phylogenetic diversity, this could explain why there is a higher SES.PD in nitrogen-poor soils. In the same sense, Zingiberales not adapted to the gradient ranges with lower nitrogen concentration remain in the gradient portions with higher concentrations, as these soils are more conducive to plant development, due to the importance of this nutrient in the growth of plant structures and in the reduction of abiotic stress (reviewed by Ye et al. 2022).

Climate also proved to be an important predictor for the patterns found in the phylogenetic diversity and structure of Zingiberales communities, with species that are phylogenetically closer (SES.MPD) in warmer environments, and in environments with higher annual precipitation (SES.PD). This is congruent with tropical predominance of Zingiberales and their origin in humid and warm climates during the Cretaceous (Chen & Smith, 2013; Deng et al., 2016; Kress & Specht, 2006; Strömberg, 2004). Thus, the drier and colder regions possibly impose a physiological barrier and prevent the colonization of species not adapted to this type of environment. Alternatively, the negative influence of increased precipitation on phylogenetic diversity may be the result of recent diversification that occurred in some clades of Zingiberales belonging to the more humid neotropical regions (André et al., 2016; Figueiredo et al., 2022; Särkinen et al., 2007). This could have caused shorter branches at the ends of the phylogeny, given that the SES.PD is strongly influenced by terminal relationships (Mazel et al., 2016), which corroborates recent findings for tree communities in humid regions of South America (Neves et al., 2020).

To the best of our knowledge, this is the first study demonstrating the influence of climate on the phylogenetic structure of Amazonian herb communities. Previous results have concentrated sampling efforts on more restricted Amazonian scales, therefore experiencing a limited range of climate variation (Lehtonen et al., 2015). Climate is an important predictor for understanding patterns of phylogenetic structure of plant communities in the Neotropics (González-Caro et al., 2014; Neves et al., 2020), including phylogenetic and taxonomic turnover at broad spatial scales (Guevara Andino et al. al., 2021). In our research, we collected data on the occurrence of Zingiberales throughout the entire Amazon region, including regions close to the Andes mountains range, with colder temperatures (Segovia et al., 2020). Corroborating our findings, Guevara Andino et al. (2021), studying tree communities on a broader scale in the Ecuadorian Amazon, highlighted that climate is an important predictor of phylogenetic turnover at large scales and a weak predictor at finer spatial scales.

The depth of the water table did not influence on the diversity or the phylogenetic structure of the Amazonian Zingiberales communities. We are aware that the depth of the water table has great importance on the distribution of plant communities (Costa et al., 2023). A probable explanation for this possibly relates to the spatial scale considered here, where in a broader scale, variation within local conditions could hide the true relation in the scale in which plants interact with soil water. Additionally, herb roots penetrate only the most superficial part of the soil (Fan et al., 2017), and thus, may not be directly influenced by the water table, which is much deeper than these roots, even in places where it is more superficial (Fan et al., 2017). Zingiberales could obtain water from the shallowest layers of the soil, as in regions close to watercourses (Drucker et al., 2008) and also in humid soils under the direct influence of precipitation. It is also worth mentioning that the variable soil water content is strongly correlated with annual precipitation in Amazonia (Appendix S7). In this way, the water present in the most superficial layers of the soil maintained by the rain can have great importance in the distribution of the Amazonian Zingiberales.

Many studies have attempted to identify patterns in the phylogenetic structure of plant communities in the Amazon (e.g., Campos et al., 2022; Cárdenas et al., 2017; Eiserhardt et al., 2013; Fine & Kembel, 2011; Guevara et al., 2016; Lehtonen et al., 2021, 2015; Muscarella et al., 2019; Villa et al., 2018), but focused on more restricted spatial scales. The few research in the Neotropics that concentrated their studies on broader spatial scales (González-Caro et al., 2014; Guevara Andino et al., 2021), demonstrated that not only edaphic gradients, but climate gradients also exert a strong influence on the phylogenetic structure of tropical plant communities (González-Caro et al., 2014; Guevara Andino et al., 2021). However, these discoveries were until then restricted to tree communities. Our research was also the first to assess evolutionary relationships in terrestrial herb communities throughout the Amazonian territory. We encourage further studies to use functional traits to identify which ones would be related to the patterns observed in the present study, as well as to test whether there is phylogenetic niche conservatism in the Zingiberales lineage.

Conclusion

Not only do edaphic resources influence the diversity and phylogenetic structure of Zingiberales communities, but climate also proved to be an important predictor, both on a shallower (SES.PD and SES.MNTD) and deeper (SES.MPD) evolutionary time scale. Our results help to further reinforce the importance of soil in the evolution of Amazonian plant communities, especially understory herbs, highlighting that the availability of nutrients is an important driver in the distribution of floristic patterns in the region. We observed that certain edaphic and climatic conditions can filter lineages with potential physiological restrictions to occupy portions of the environmental gradient. The depth of the water table is not an important predictor of the phylogenetic structure of the Zingiberales communities at larger scales.

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9. Author contributions

DMB, TA and FRCC conceived the research idea; DMB downloaded and screened the GBIF occurrence data as well as the environmental variables; Herbase data was collected by TA, AFM, FRCC, TEA, PPPA, CRB, DPD, RLP, MAL, JLLM, AGM, IESM, GMM, ECP, EQV, JGS, MS, DST, HT and TVA; DMB, TA and AFM performed statistical analyses; DMB, TA, AFM and FRCC wrote the article; all authors discussed the results, reviewed and approved the manuscript.

10. Data availability statement

Raw occurrence data for species of the order Zingiberales downloaded from GBIF are available at https://doi.org/10.15468/dl.dty2qu. The other data used and generated can be found in the supplementary material of this work. Additional data related to this manuscript can be requested from the corresponding author.

11. Information Support

Appendix S1: Matrix containing the environmental data used in the work.

Appendix S2: Phylogeny containing all polytomies generated by V.PhyloMaker.

Appendix S3: R Script used to solve the polytomies of the Zingiberales phylogeny.

Appendix S4: Phylogeny with polytomies solved using published phylogenetic hypotheses and taxonomic reviews.

Appendix S5: Phylogeny with part of its polytomies resolved using only published phylogenetic hypotheses.

Appendix S6: Matrix containing the results of the correlations obtained for each metric generated for each phylogeny.

Appendix S7: Matrix containing the results of the correlation test between environmental variables.

Appendix S8: Matrix containing all possible models generated by the MuMIn package.

Appendix S9: Matrix containing data on occurrences of herbs of the order Zingiberales for the Amazon region.

Appendix S10: Matrix containing the presence and absence data for each Zingiberales community generated for each of the three resolutions (1° x 1°, 0.5° x 0.5°, 0.1° x 0.1°).

Appendix S11: Matrix containing the results of the phylogenetic structure analyses.

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13 Table

Table 1. Climatic, edaphic and hydrological soil variables selected to test the influence of environmental gradients on the structure and phylogenetic diversity of Zingiberales from the Amazonian understory.

Variables	Description of variables	Conventional units	Resolution original
BIO1	Annual Mean Temperature	°C	~1000 m
BIO12	Annual Precipitation	mm	~1000 m
Sand	Proportion of sand particles in the fine earth fraction	g/100g (%)	250 m
phh2o	Soil pH	pH	250 m
N	Total nitrogen	g/kg	250 m
clay	Proportion of clay particles in the fine earth fraction	g/100g (%)	250 m
WTD	Depth of the water table	m	~500 m

Table 2. Full average model results for the standardized effect size of Phylogenetic Diversity (SES.PD), based on the generalized linear model with the Gaussian family.*

SES.PD	**Estimate**	**Standard error**	**Z**	**p**	**Importance**
Intercept	0.000002	0.04	0	0.99	-
Proportion of clay	0.06	0.05	1.13	0.25	0.75
Proportion of sand	0.15	0.05	2.79	P<0.01	1
Annual Precipitation	-0.12	0.05	2.36	P<0.05	1
Nitrogen	-0.14	0.05	2.61	P<0.01	1
Annual Mean Temperature	-0.006	0.02	0.24	0.8	0.18
pH	-0.003	0.02	0.13	0.89	0.15

* Model selection was based on the corrected Akaike information criterion (AICc). Only models with delta AICc < 2 were selected for full mean. The importance of the variables was generated using the same criterion (delta AICc < 2).

Table 3. Full average model results for the standardized effect size of Mean Nearest Neighbor Distance (SES.MNTD) and standardized effect size of Mean Pairwise Distance (SES.MPD), based on the generalized linear model with the Gaussian family *.

SES.MPD	**Estimate**	**Standard error**	**Z**	**P**	**Importance**
Intercept	-0.00007	0.04	0.002	0.99	
Annual Precipitation	-0.05	0.06	0.89	0.37	0.61
Annual Mean Temperature	-0.12	0.05	2.16	< 0.05	1
pH	0.17	0.06	2.63	< 0.01	1
Nitrogen	-0.019	0.04	0.46	0.64	0.34
Depth of the water table	0.005	0.03	0.18	0.85	0.14
SES.MNTD					
Intercept	-0.17	0.04	3.94	< 0.001	
Proportion of clay	0.12	0.05	2.37	< 0.05	1
Proportion of sand	0.22	0.06	3.61	< 0.001	1
Annual Precipitation	-0.14	0.08	1.65	0.09	0.82
pH	-0.12	0.08	1.52	0.12	0.82
Nitrogen	-0.04	0.06	0.63	0.52	0.40
Depth of the water table	0.009	0.03	0.27	0.78	0.16
Annual Mean Temperature	0.002	0.02	0.095	0.92	0.11

* Model selection was based on the corrected Akaike information criterion (AICc). Only models with delta AICc < 2 were selected for full mean. The importance of the variables was generated using the same criterion (delta AICc < 2).

14 Figures

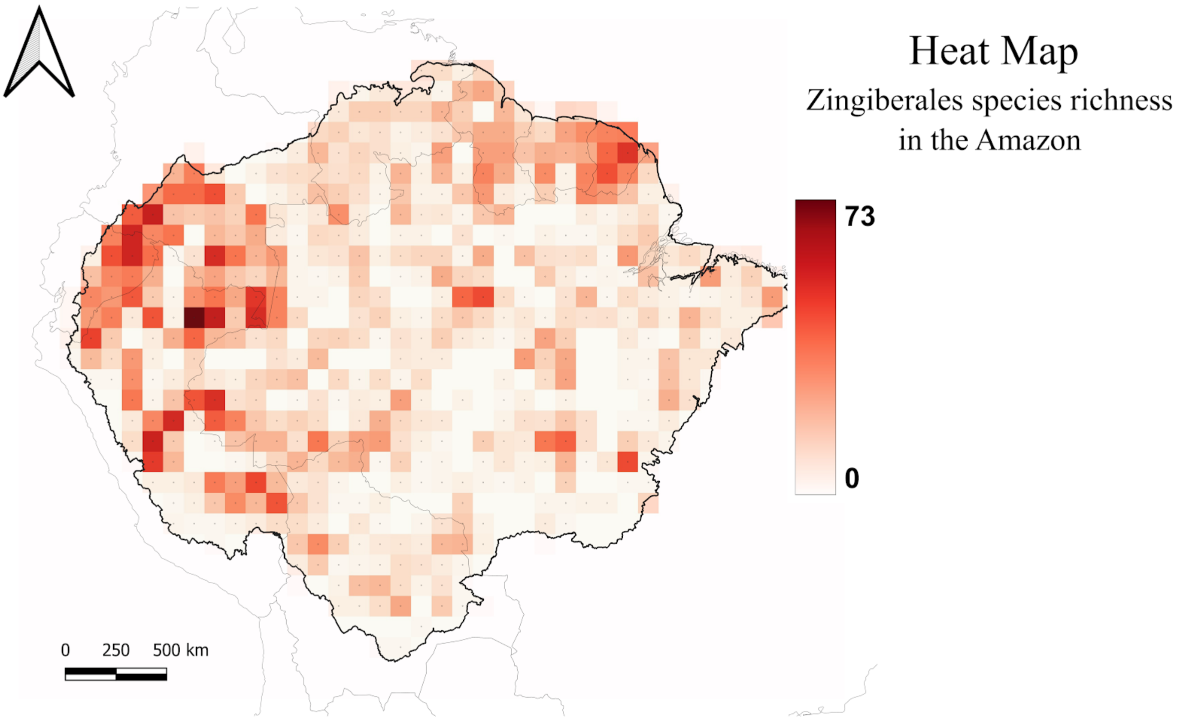

Figure 1. Heat map indicating species richness belonging to the order Zingiberales throughout the Amazon region. The grids have a resolution of 1° x 1° (approximately 111 km of arc at the equator). Occurrence data were downloaded from GBIF (Global Biodiversity Information Facility). The warmer the grid color (red), the greater the species richness.

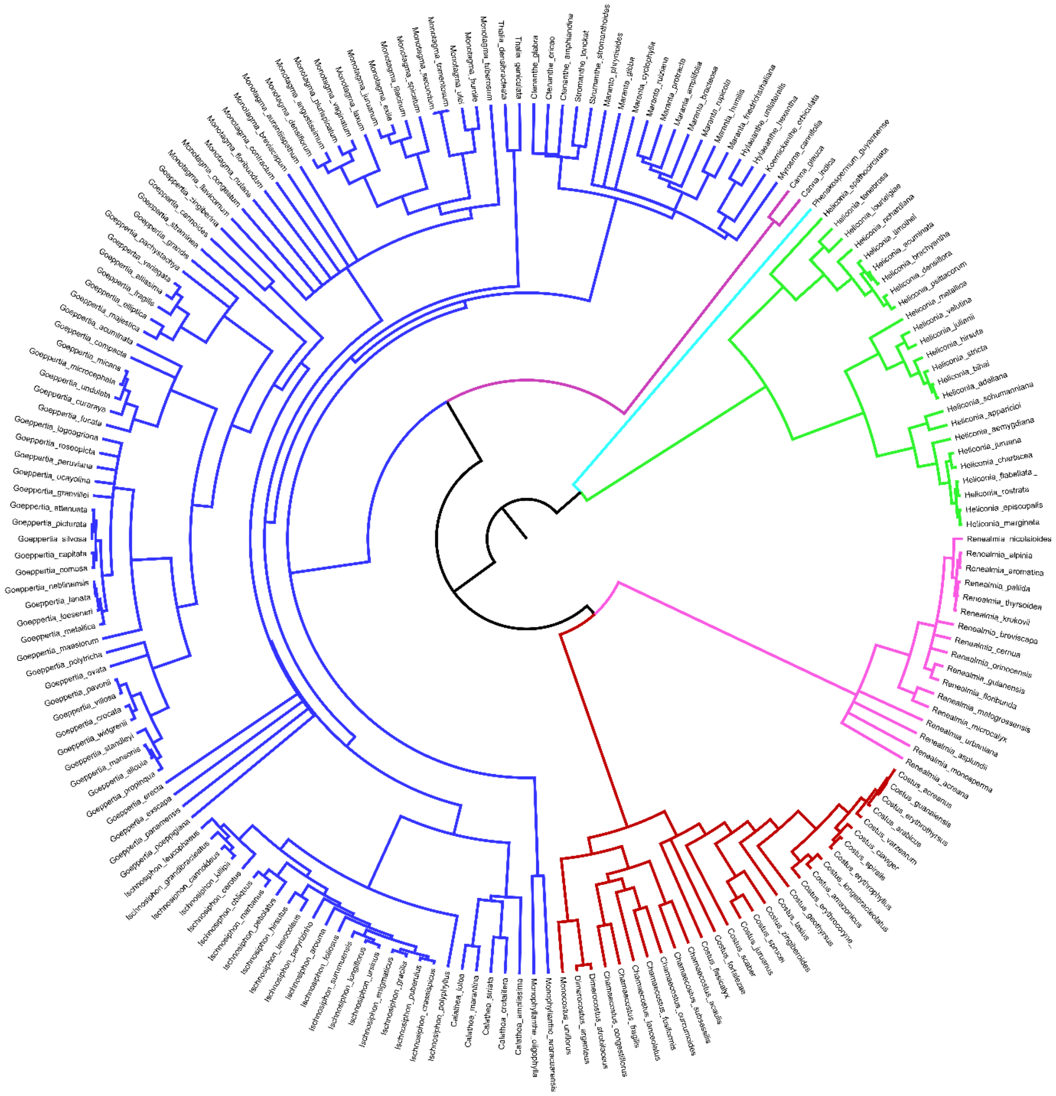

Figure 2. Phylogenetic tree generated in V.PhyloMaker for 190 species of Amazonian Zingiberales. The colors on the branches indicate the families belonging to the Zingiberales group: Marantaceae (dark blue); Costaceae (brown); Heliconiaceae (green); Cannaceae (purple); Zingiberaceae (rose); and in light blue is the sole representative of the Strelitziaceae in the Neotropics, *Phenakospermum guyannense*.

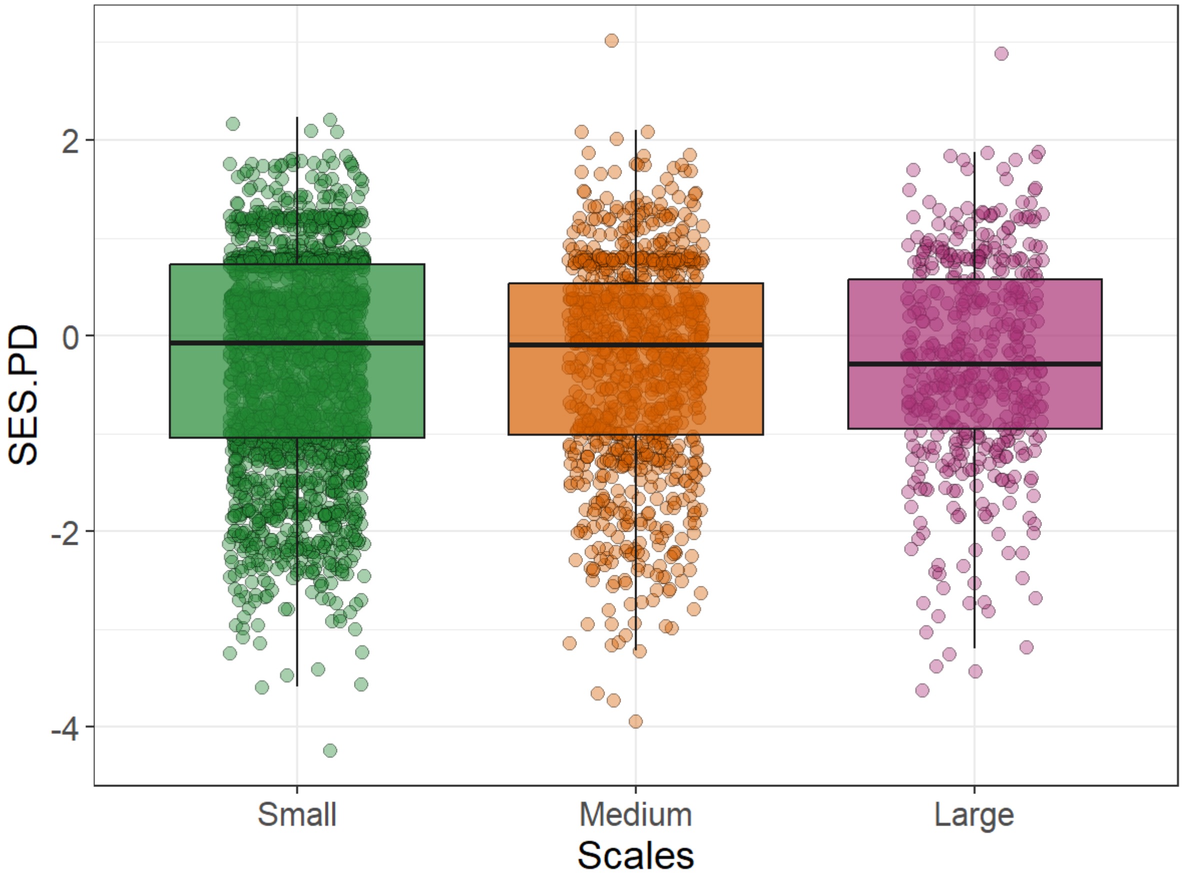

Figure 3. Comparison of standardized effect size of Phylogenetic Diversity (SES.PD) among different spatial scales: small (0.1 ° x 0.1°), medium (0.5° x 0.5°) and large (1° x 1°).

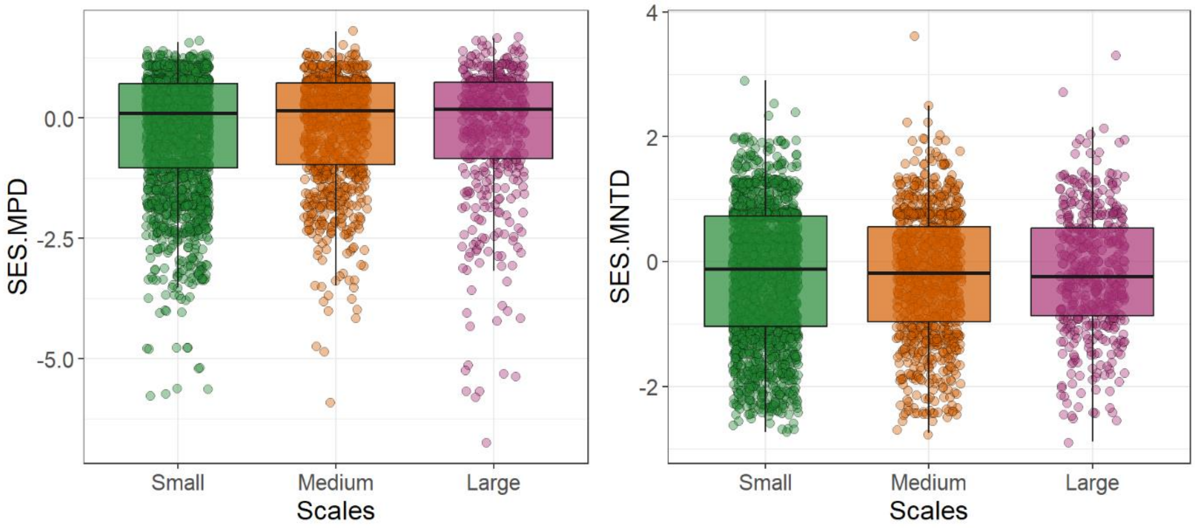

Figure 4. Comparison of standardized effect size of Mean Pairwise Distance (SES.MPD) and the standardized effect size of Mean Nearest Neighbor Distance (SES.MNTD) among different scales: small (0.1 ° x 0.1°), medium (0.5° x 0.5°) and large (1° x 1°).

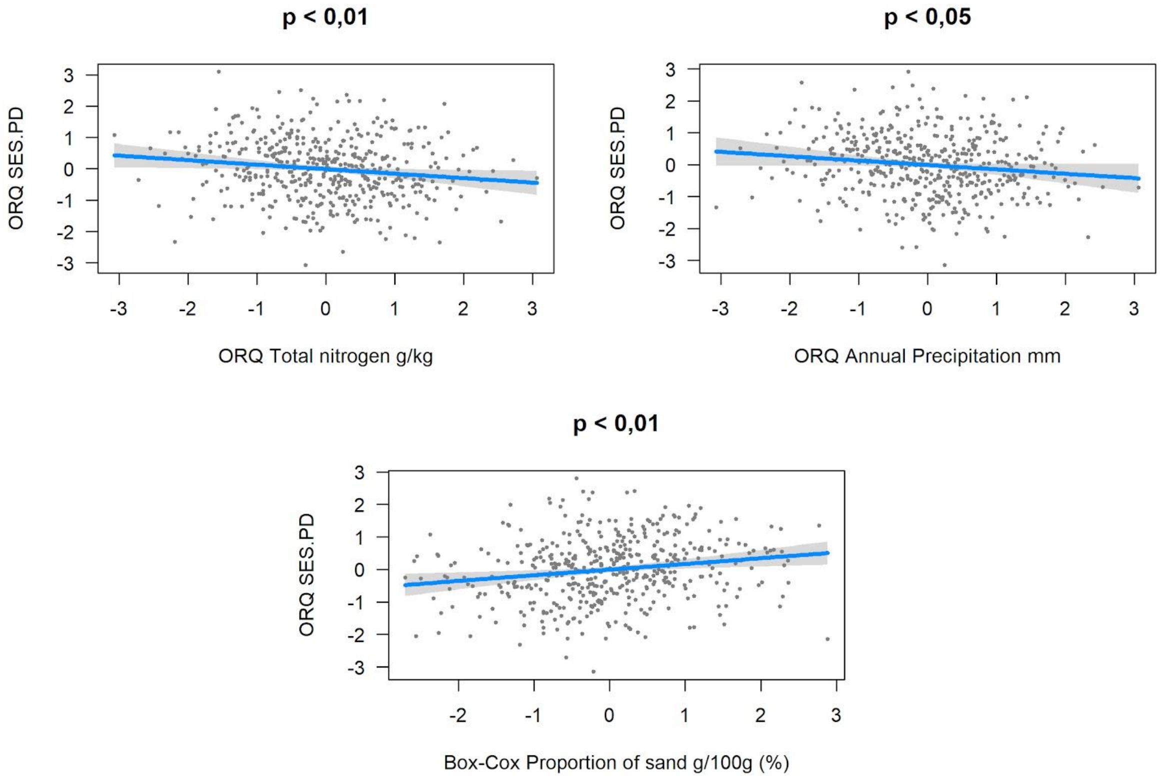

Figure 5. Relationship between the standardized effect size of Phylogenetic Diversity (SES.PD) and the environmental variables. SES.PD, annual precipitation and total nitrogen were transformed with the Ordered Quantile (ORQ) method. The proportion of sand was transformed with the Box-Cox method. P values were generated from the average of the best selected models based on delta AICc < 2.

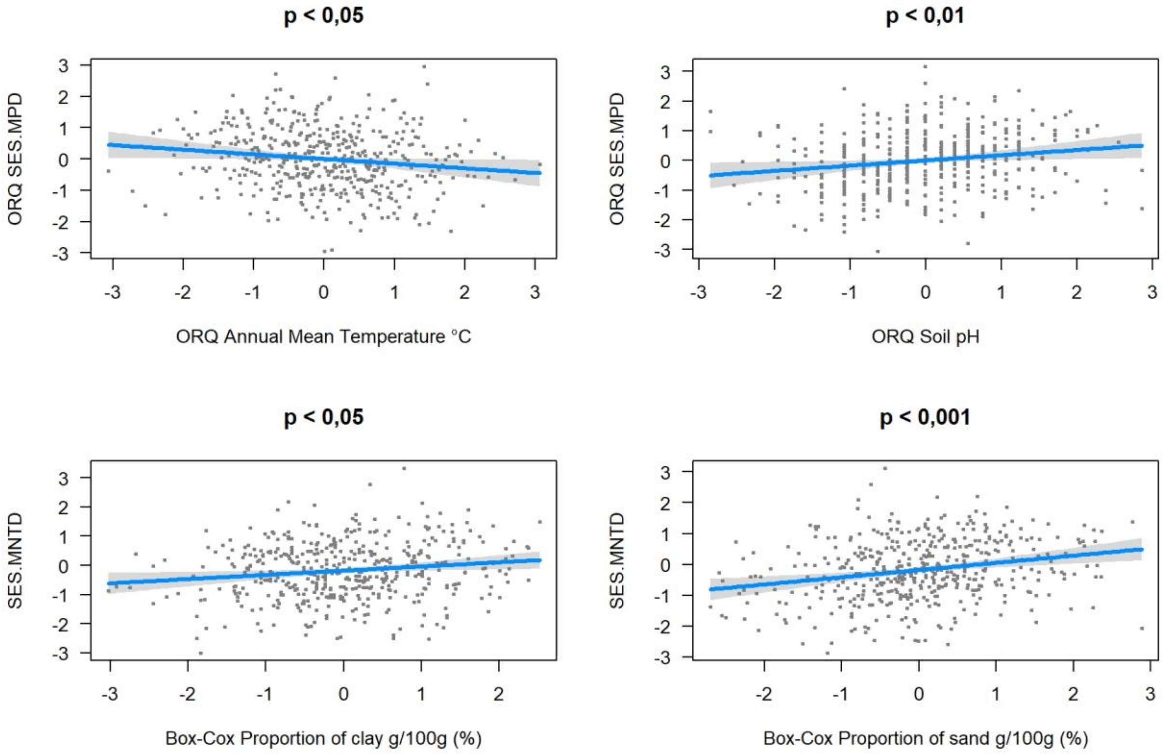

Figure 6. Relation of standardized effect size of Mean Pairwise Distance (SES.MPD) and standardized effect size of Mean Nearest Neighbor Distance (SES.MNTD) with environmental variables. SES.MPD, mean annual temperature and soil pH were transformed with the Ordered Quantile (ORQ) method. Clay proportion and sand proportion were transformed with the Box-Cox method. P values were generated from the average of the best selected models based on delta AICc < 2.

Comentários à coordenação do PPGBEES:

A dissertação aqui mencionada e avaliada possui excelentes e novas informações sobre evolução vegetal em ecossistemas Amazônicos, com potencial para publicação em revista de relevante impacto. Portanto, o discente deve também receber todo suporte e incentivo possível do programa para que esse trabalho seja publicado o mais breve possível. Eu fiz comentários ao longo da dissertação, a ser quando julgarem adequado, compartilhar com o discente e seu orientador, objetivando contribuir e auxiliar em polimentos no texto que contribuam para publicação mais rápida.

Avaliação final do projeto de dissertação de mestrado

I - Aprovada (x)

Aprovada: indica que o revisor aprova a dissertação sem ou com correções. Na existência de correções, estas devem ser indicadas nos comentários à coordenação e/ou no próprio documento da dissertação.

IV - Reprovada ( )

Reprovada: indica que a dissertação não é adequada.

Nome do membro da banca: Écio Souza Diniz

Data: 21/06/2023

Assinatura: Écio Souza Diniz

Comentários à coordenação do PPGBEES:

A dissertação do Darlisson Mesquita aborda a relação entre variação ambiental e estrutura filogenética de comunidades de ervas Zingiberales na Amazônia, utilizando dados disponíveis online, envolvendo a construção de hipóteses filogenéticas e manipulação de dados espaciais, climáticos, hidrológicos e edáficos. Contém uma introdução geral em português e um manuscrito em inglês que tem a colaboração de 20 autores. O manuscrito tem um inglês de excelente qualidade e envolve análises estatísticas complexas. É um trabalho de alta qualidade para uma dissertação de mestrado, considerando minha experiência com estudantes na pós do INPA, e o manuscrito está perto de pronto para ser submetido, embora a meu ver deveria incorporar alguns aspectos teóricos e analíticos que eu sugeri diretamente no texto da dissertação.

Vejo com satisfação que o trabalho do aluno tenha envolvido tanta gente, entendo que muitos indiretamente disponibilizando dados. Acho que isso demonstra que o aluno foi inserido numa grande rede de pesquisa e essas colaborações são fundamentais na formação de um cientista.

Avaliação final do projeto de dissertação de mestrado

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Reprovada: indica que a dissertação não é adequada.

Nome do membro da banca: **Alberto Vicentini**

Data: 01/07/2023

Assinatura:

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Data: 01/07/2023 10:35:38-0300
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Comentários à coordenação do PPGBEES:

A dissertação apresentada trata de tema relevante e apresenta resultados que contribuirão para a discussão da temática (fatores que influenciam na diversidade filogenética de comunidades de plantas amazônicas). Os resultados apresentados são inovadores, por utilizarem um conjunto de dados robusto, apoiado em bases taxonômicas confiáveis, por tratarem de métricas filogenéticas para linhagens de ervas amazônicas e por buscarem correlacionar fatores não antes utilizados.

As análises empregadas são adequadas e o texto apresentado encontra-se bem amadurecido, e certamente será aceito para publicação em periódico no estrato pretendido.

Cabe citar que é importante para o programa e para o contexto Amazônico que um discente lidere um trabalho que envolva um conjunto de pesquisadores, vislumbrando que ele possa interagir com eles após a experiência do mestrado.

Considerando que a dissertação está bem escrita e a mensagem central do texto é clara, são apresentadas algumas sugestões diretamente no arquivo anexo para melhoria do texto, em especial em relação a esclarecer algumas partes da discussão e utilizar termos que possam ser mais prontamente compreendidos pelo leitor.

Sugere-se que as figuras sejam mais citadas no texto, valorizando-as. Para tal, sugere-se que sejam atribuídas letras àquelas figuras que contam com mais de um elemento, para que eles possam ser citados individualmente.

Avaliação final do projeto de dissertação de mestrado

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Reprovada: indica que a dissertação não é adequada.

Nome do membro da banca: Leandro Lacerda Giacomin

Data: 1 de julho de 2023

Assinatura: Leandro L. Giacomin

Comentários à coordenação do PPGBEES:

A formação de um mestre é mais do que a produção de uma dissertação ou de um artigo científico, e o discente em questão é um exemplo disso. Darlisson aprendeu sobre as espécies que estudou, sobre filogenia, sobre as análises, sobre o R e sobre ajudar os colegas. Há ajustes que precisam ser feitos em sua dissertação para publicação de um artigo científico consistente, mas tudo que está escrito ali é fruto de muito trabalho e dedicação do aluno e de seus orientadores. Parabéns!
Deixo meus pequenos comentários no texto.

Avaliação final do projeto de dissertação de mestrado

I - Aprovada (x)

Aprovada: indica que o revisor aprova a dissertação sem ou com correções. Na existência de correções, estas devem ser indicadas nos comentários à coordenação e/ou no próprio documento da dissertação.

IV - Reprovada (   )

Reprovada: indica que a dissertação não é adequada.

Nome do membro da banca: Rodrigo Ferreira Fadini

Data: 20/06/2023

Assinatura: