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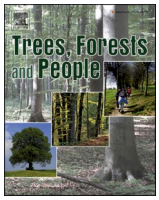

Unveiling anthropogenic disturbance effects on tropical tree communities: clade-based insights across elevations

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ABSTRACT

Community assemblies in tropical forests are influenced by both environmental filtering and anthropogenic disturbance processes, posing significant challenges in ecological research. To disentangle these complex effects, we applied species-level and phylogenetic approaches to a dataset of 14,500 tree individuals from 310 species across eight communities in the Brazilian Atlantic Forest, including both undisturbed and selectively logged plots along an elevational gradient. Using rarefaction and ordination analyses, and node-based assessments of species distributions—with and without tree ferns—we investigated how selective logging influences community assembly across elevations and whether its effects vary among evolutionary lineages. Selective logging had a stronger impact on tree communities at lower elevations, suggesting that their species assembly and phylogenetic structure are more susceptible to the same anthropogenic disturbance in montane communities. Regarding clade-based perspective, Cyatheaceae and Magnoliids were over-represented in montane forests and Fabidae and Myrtaceae in submontane forests, yet disturbance markedly reduced Fabidae in submontane areas, decreased Magnoliids in both forest types, and led to a significant decline of Myrtaceae in disturbed montane forests. In general, we underscore that species clades varied in their responses to environmental and anthropogenic filters, highlighting the necessity for clade-specific analyses to enhance our understanding of community assembly processes and improve conservation strategies. By recognizing the differential responses of tree species clades, conservation efforts can be better tailored to address the unique challenges faced by different species and clades. This approach can contribute to more effective and sustainable management of tropical forest ecosystems in the face of ongoing environmental and anthropogenic changes.

1. Introduction

Both environmental filtering and anthropogenic disturbances influence community assemblies, shaping species composition and diversity within ecosystems. Environmental filters, such as climate, soil type, and topography, determine the abiotic conditions that species must tolerate to establish and persist in a given habitat (Götzenberger et al., 2012; Mayfield and Levine, 2010). Moreover, anthropogenic disturbances, such as selective logging and habitat fragmentation can significantly alter these natural assemblies by introducing novel pressures and modifying existing environmental conditions (Haddad et al., 2015; Newbold et al., 2015). These disturbances often lead to changes in species distributions, reductions in biodiversity, and shifts in the resident community structure, which can have profound implications for ecosystem functioning and resilience (Cardinale et al., 2012; Fahrig 2003). Understanding the interplay between filters and anthropogenic disturbances is crucial for predicting how diverse communities will respond to ongoing environmental changes and for developing effective

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conservation strategies (Dawson et al., 2011; Gerhold et al., 2015; Hishe et al., 2021; Mason et al., 2005).

Studies on the ecological and evolutionary similarity of co-occurring species provide key insights into the interconnected processes shaping species community assemblies (Ackerly, 2003; Götzenberger et al., 2012; Neves et al., 2020; Swenson, 2013; Webb et al., 2002). However, disentangling the complex effects of selective logging across elevational gradients in tropical forests remains an open question in the fields of ecology and conservation. Changes in species distribution and diversity in tropical forests are influenced by environmental filters that lead to limiting similarity among species (Hooper et al., 2005). Elevation gradients significantly shape these patterns, as variations in temperature and rainfall create distinct microclimates and habitats (Körner, 2007). In mountain ranges, along with elevational variations, the atmospheric pressure, temperature, solar radiation, and UV-B radiation are abiotic factors related to altitude in mountainous regions, and precipitation, wind speed, and seasonality are indirectly related factors (Körner, 2007). Additionally, biotic interactions, such as competition and mutualism, vary with elevation, further affecting community assembly (Callaway, 1998; Fontaine et al., 2011).

The effects of environmental filtering might be coupled with the presence and intensity of disturbances, such as increased anthropogenic impacts, in structuring vegetation communities, thereby modifying species occurrence and diversity in tropical forests (Gibson et al., 2011; Putz et al., 2012). Abiotic filters are determinant across habitats at broad spatial scales, while limiting similarity affected by disturbances tends to dominate within habitats at smaller spatial scales (Götzenberger et al., 2012). Abiotic filters often create a clustered pattern in the phylogenetic structure of plant communities due to the grouping of species with similar survival and dispersion strategies. In contrast, disturbances can promote plant species diversity by slowing or preventing competitive exclusion (Crawley, 2004). Disturbances of anthropogenic origin under these conditions are expected to be peaked, with maximum diversity being observed under intermediate disturbance levels (Connell, 1978; Huston, 1979). However, the effect of environmental filtering on assembly rules might overshadow the disturbance effect, making it less apparent (de Bello et al., 2012).

Selective logging for timber extraction is one major anthropogenic disturbance that affects tropical forests, which can lead to changes in species composition and community structure, loss of species diversity, and a tendency to produce a clustered phylogenetic pattern in tree communities, also affecting the recovery capacity of disturbed areas (Berenguer et al., 2014; Ding et al., 2012; Hirota et al., 2011; Whitfeld et al., 2012). Selective logging is a common management strategy employed by local human communities for resource exploitation and is permitted in many tropical forest areas (Matricardi et al., 2010; Ribeiro et al., 2009; Verissimo et al., 1992). However, the intricate dynamics of tropical forests, combining environmental filters and disturbances, can obscure the understanding of ecological processes that arise from the phylogenetic diversity and structure of their communities (Baraloto et al., 2012; Kembel and Hubbell, 2006; Mayfield and Levine, 2010). Rapid advancements in research fields that integrate species distributions and evolutionary relationships have significantly improved our understanding of the processes underlying assembly rules (Swenson, 2013). Combined metrics evaluate each phylogenetic node by comparing descendant clade distributions to a null model, effectively exploring node allopatry and macroevolutionary patterns (Borregaard et al., 2014).

Beyond the challenge of disentangling the effects of environmental filtering and disturbances, the plant clades used in analysis can influence results on species diversity and the phylogenetic structure of plant communities (Cadotte et al., 2009; Srivastava et al., 2012; Swenson et al., 2007; Vamosi et al., 2009; Ndiribe et al., 2013). Specially, the inclusion of lineages belonging to non-flowering plant clades such as ferns, when constructing a phylogenetic tree, can significantly alter the results of phylogenetic diversity and structure (Chave et al., 2007; Worthy et al., 2019). Indeed, when vegetation sampling is narrowly defined by researchers (i.e., not including specific clades such as tree ferns), different outcomes and conclusions may arise (Worthy et al., 2019; Münkemüller et al., 2020). Therefore, the scale at which communities are defined taxonomically is an important step in estimating phylogenetic diversity and structure of communities, which can lead to contradictory results (Cavender-Bares et al., 2006, 2009; Worthy et al., 2019). To test the hypothesis that local assemblages result from a series of abiotic and biotic filters applied to regional species pools, and that these filters leave predictable signals in observed diversity patterns, it is essential to include greater phylogenetic diversity (Cavender-Bares et al., 2006; Worthy et al., 2019; Münkemüller et al., 2020).

Here, we evaluated the effects of anthropogenic disturbances on tropical tree communities at different elevations. Selective logging in the area ceased in the mid-1970s with the establishment of the national park (Joly et al., 2012), allowing us to assess the historical effects of these disturbances. Specifically, we assessed how selective logging impacts species-level and phylogenetic diversity and composition, species distributions, and phylogenetic structure, as well as its overall effects on community assembly along an elevational gradient in the southeastern Brazilian Atlantic Forest. We also examined whether these effects vary by clades used in ecological and evolutionary analyses and explored phylogenetic regionalization tools to provide a framework for applied questions in ecology and conservation. We postulated a more pronounced negative impact of anthropogenic disturbance on species distribution, and consequently on species composition and phylogenetic structure, in tree communities at lower elevations compared to higher ones. This expectation is based on the generally higher species richness found in low-elevation tropical forests, which is often associated with more favorable climatic conditions and greater resource availability (Homeier et al., 2010; Sanchez et al., 2013). Additionally, we hypothesized that the impacts of elevational and selective logging filters on community assemblies will be influenced by the clades analyzed, where the exclusion of non-flowering plant clades can overshadow the effects of these filters (Stadler et al., 2017; Zheng et al., 2022). We also expected that phylogenetic regionalization would reveal distinct spatial phylogenetic patterns that can be used to identify priority areas for conservation, particularly in regions where anthropogenic disturbances intersect with high species and phylogenetic diversity (Winter et al., 2013).

2. Material and methods

2.1. Study area

The present study site is in the *Parque Estadual da Serra do Mar* (23°58′ S, 46°38′ W)., a state non-take protected area located in the São Paulo state coast, in Southeast Brazil, that covers about 330.000 hectares mainly of forests in the mountain range of Serra do Mar, comprising one of the biggest remnants of the Atlantic Forest (Rezende et al., 2018). It ranges sea level up to 1200 m a.s.l. The predominant climate, according to the Köppen classification in the lowlands is Cfa and in the mountain region is Cfb, with a temperature and precipitation average of 20,8 °C and 2224 in the lowlands, and 16.7 °C and 1778 mm in the mountains (Alvares et al., 2013), respectively. The vegetation types vary from Mangroves, Restingas, to Ombrophilous Dense Forest, with different formations according with the elevational range (IBGE, 2012). The fog is nearly daily above 500 m a.s.l. (pers. obs.). In general, soils present low fertility and nutrients, with high levels of aluminum (Sousa Neto et al., 2011).

We analyzed eight plots (communities) of 10,000 m^2 each (Fig. 1), divided into 100 sub-plots of 100 m^2 in the *Parque Estadual da Serra do Mar*. The plots (herein tree communities) were placed in two elevational ranges comprising two vegetation types: four hectares are located in the submontane Forest, with elevation ranging from 150 m to 350 m, and four plots in the montane Forest, with elevation around 1000 m (IBGE,

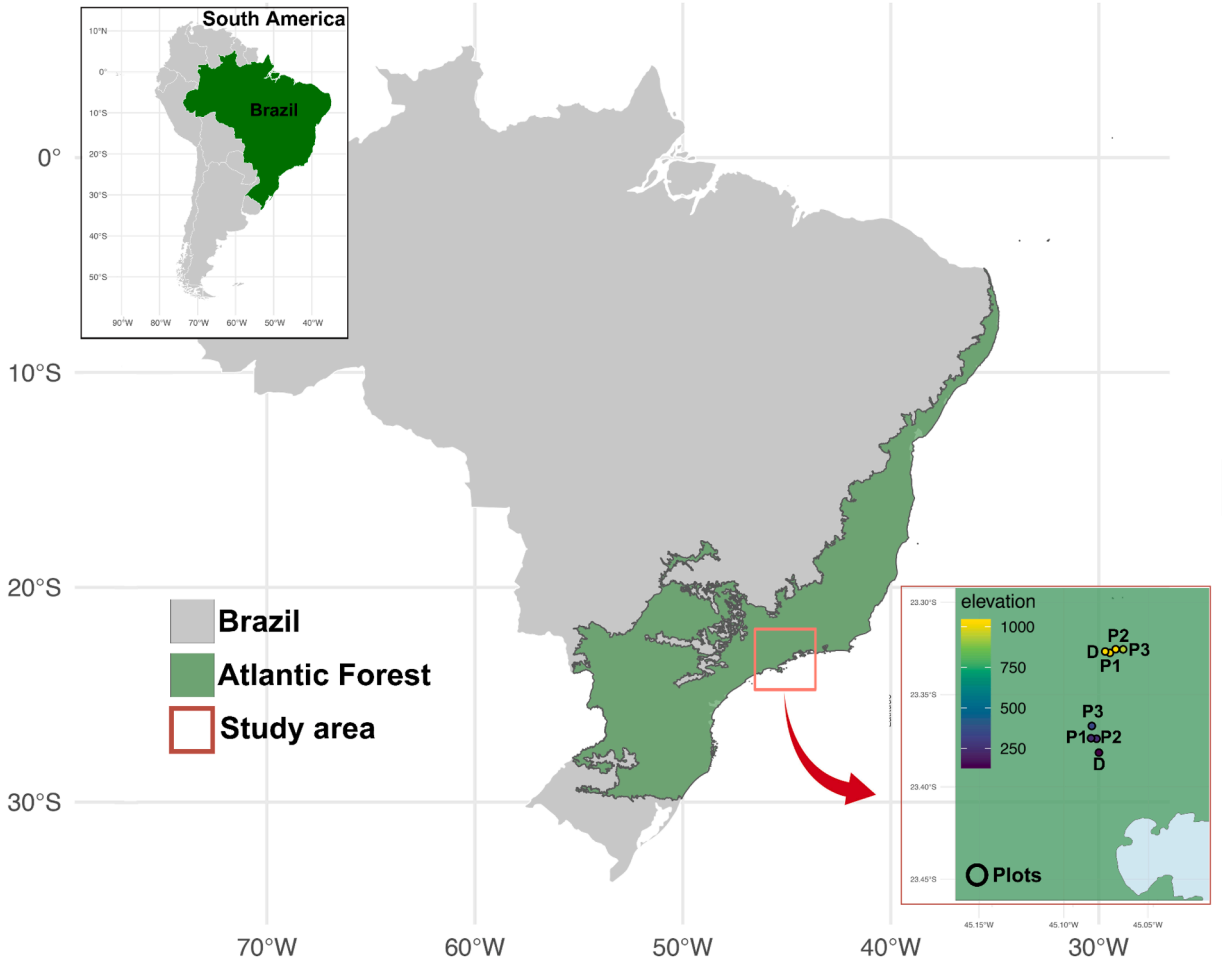

Fig. 1. Map of the study area and distribution of study plots (10,000 m^2each) in the Atlantic Forest, southeastern Brazil. The tree communities were distributed in relation to the selective logging disturbance (referred with 'D') or without this disturbance (referred as preserved with 'P') in two elevation ranges (submontane and montane forests).

2012). In each elevation range, we analyzed three undisturbed plots (Eisenlohr et al., 2013) and one plot that suffered selective logging (hereafter disturbed) in 1976 (Padgurschi et al., 2011; Ramos et al., 2011). We identified all tree individuals in each of the eight tree communities, those with perimeter at breast height equal or higher than 15 cm, including palms and tree ferns (Cyatheaceae) species (Joly et al., 2012). All botanical material was placed in the UEC, IAC and HRCB herbaria (acronyms according with Index Herbariorum (2024) continuously updated).

2.2. Data analysis

We initially investigated the floristic relationships among subplots of the tree communities using ordination analyses through non-metric multidimensional scaling (NMDS; McCune and Grace, 2002) and assessed its overall significance through an analysis of similarities (ANOSIM; Clarke, 1993). NMDS was performed with the Bray-Curtis dissimilarity index, excluding 83 singletons (species found at a single plot) to reduce noise and improve the accuracy of the ordination analysis (Lepš and Šmilauer, 2003). Additionally, we plotted the convex hull area of the two disturbed communities on the ordination graphs. The convex hull represents the area occupied by subplots of these two communities within the space delimited by all subplots, effectively serving as the 'multivariate equivalent of range' (Cornwell et al., 2006). To assess species diversity in each community, we generated rarefaction curves using the 'iNEXT' function from the package of the same name (Hsieh et al., 2016). We set the endpoint for rarefaction at 2500 to analyze the expected species richness at this standardized sampling effort.

To investigate how elevation and anthropogenic disturbances shape tree community phylogenetic structure, we first constructed a phylogenetic tree for all sampled species (Appendix S1) using the mega-tree approach in the 'V.PhyloMaker' R package (Jin and Qian, 2019). 'V. PhyloMaker' inserts genera and species onto a dated, family-level backbone supertree of vascular plants based on their taxonomic placement (Jin and Qian, 2019). We then added information on family and genus with good resolution further published for Fabaceae (Doyle et al., 2000), Lauraceae (Chanderbali et al., 2001), and Myrtaceae (Lucas et al., 2007). We then generated phylogenetic trees employed the 'phylo.maker' function, using the phylogenetic hypotheses (scenario 'S3' in the function) where tips of new genera or species not included in the mega-tree are bound to the midpoint of the family or genus branch, representing the branch between the family and genus root node and the basal node (Jin and Qian, 2019).

The phylogenetic relationships between subplots of tree communities at different altitudes and management regimes were assessed by employing a phylogenetic ordination using the 'evoPCA$_{Hellinger}$' function from the 'adiv' package (Pavoine, 2024). This method incorporates both community composition and phylogenetic information. The 'evoPCA-$_{Hellinger}$' function adapts Principal Component Analysis (PCA) to analyze phylogenetic diversity patterns in communities by using evolutionary main components based on Hellinger's distance (Pavoine, 2016). In this

analysis, the plots are mapped onto the axes based on their phylogenetic compositions (see Pavoine, 2016). Additionally, we plotted the convex hull area of the two disturbed communities in the phylogenetic ordination graphs.

The effects of elevation and selective logging on the phylogenetic structure of tree communities were evaluated using the nearest relative index (NRI). NRI is calculated by standardizing the mean phylogenetic distance (MPD; Swenson, 2014) using the independent swap algorithm (Gotelli, 2000). NRI is an ecological metric for quantifying and testing the phylogenetic structure of communities (Webb et al., 2002). It is calculated as $NRI = -1x\frac{MPDobs-MPDrnd}{sdMPDrnd}$, with *MPDobs* being the mean distance observed in each sub-plot; *MPDrnd* is the mean value from 1000 randomly generated assemblages; and *sdMPDrnd* is the standard deviations of the mean distance of null communities. Null models were constructed by fixing species and individual number per community, while randomizing phtylogenetic relationships among taxa. We calculated NRI 1000 times to construct a probability distribution of NRIs and their p-values, ensuring the robustness of the phylogenetic structure patterns of the communities.

To assess the phylogenetic spatial structure and identify nodes responsible for significant geographical shifts in species distributions, we employed two indices: the Specific Over-representation Score (SOS) and the Geographical Node Divergence (GND) (Borregaard et al., 2014). The SOS quantifies clade over-representation by evaluating each node in the phylogeny and comparing the species richness of sister clades against a null model. This results in a matrix of SOS values for each combination of nodes and communities. The GND summarizes all SOS values across occupied plots, providing a comprehensive measure of phylogenetic spatial structure and species co-occurrence. We used a cut-off value of 0.8 to select the nodes with the highest degrees of allopatry.

For all analyses (excluding GND and SOS analyses), we conducted evaluations both including and excluding tree fern species (Cyatheaceae), with a significance level set at 0.05 for all tests. Species classification followed the Angiosperm Phylogeny Group system (Chase et al., 2016) and the Pteridophytes Phylogeny Group system (Schuettpelz et al., 2016).

3. Results

3.1. Floristic composition

We sampled 14,577 tree individuals from 310 species across 59 families (Appendix S1). Among all communities, Arecaceae exhibited the highest abundance, accounting for 19.4 % of the individuals, while Myrtaceae demonstrated the highest richness, comprising 29.3 % or 63 species. In the two elevation ranges surveyed, the preserved montane communities displayed the greatest tree abundance with 5364 individuals (Appendix S2), whereas the preserved submontane communities exhibited the highest species richness with 217 species. In contrast, among the disturbed areas, the disturbed montane community showed the lowest abundance with 1623 individuals, and the disturbed submontane community had the lowest richness with 95 species.

In the submontane plots, family richness ranged from 37 families in the selectively logged community to 46 in the preserved plots (Appendix S1). In contrast, montane communities showed only slight variation, with 35 families in the disturbed plot and 38 in the preserved plots. In the disturbed submontane community, Rubiaceae was dominant, particularly *Bathysa australis*, which reached 357 individuals, followed by Fabaceae, notably *Lonchocarpus cultratus* with 158 individuals. In preserved submontane plots, Arecaceae, especially *Euterpe edulis*, with up to 226 individuals in a single plot, and Chrysobalanaceae, mainly *Licania hoehnei*, were the most abundant families. Montane plots, regardless of disturbance, were characterized by a high proportion of tree ferns (Cyatheaceae), with *Cyathea dichromatolepis* reaching up to 40 individuals. Particularly, the highest overall abundance of tree ferns was found in the disturbed submontane plot, where *Alsophila sternbergii* accounted for 235 individuals. Lastly, both disturbed and preserved montane plots showed higher representation of Magnoliids, particularly species and genera within Lauraceae, compared to submontane plots.

3.2. Effects of elevation and selective logging on species and phylogenetic structure

The ordination analysis of both species (Fig. 2a and b) and phylogenetic (Fig. 2c and d) composition effectively distinguished subplots among vegetation types associated with different elevations. All ordinations yielded consistent results, with NMDS stress values below 0.2 and PCA inertias above 0.2. ANOSIM analysis confirmed the differences in species and phylogenetic composition among communities, with or without tree ferns ($p < 0.01$ for all analyses). However, clear discrimination between disturbed areas was only observed for species composition within submontane communities (Fig. 2).

We observed a trend towards lower species richness in disturbed areas, regardless of whether tree ferns were included in the analyses (Fig. 3a and b). In submontane forests (Fig. 3a), the rarefaction curves for preserved communities lie consistently above those for the logged plot across all sample sizes, reflecting a significant decline in species richness after selective logging (non-overlapping 95 % confidence intervals; $p < 0.05$). By contrast, montane forests (Fig. 3b) show highly similar rarefaction results for preserved and disturbed plots, with overlapping confidence bands and no significant difference in Hill species numbers ($p > 0.05$). The differences in species richness between disturbed and undisturbed plots were more pronounced in submontane forests, where one community exhibited the highest richness. Regarding the phylogenetic structures of communities, elevation tended to cause a clustered structure (Fig. 3c and d) and a random structure in preserved Submontane forests. Selective logging had varying effects on the phylogenetic structure of disturbed areas, depending on the inclusion of tree ferns in the analyses. Including Cyatheaceae in the NRI results revealed a significant clustering effect on the phylogenetic structure ($p > 0.95$) in selectively logged Submontane forests, which was not observed when this clade was excluded from the analyses.

3.3. Elevation and anthropogenic disturbance impacts on phylogenetic spatial distribution

Four nodes in the phylogenetic tree showed high node allopatry (cut-off 0.8, Fig. 4). Node A separated tree ferns (positive scores) from angiosperms (negative scores). Node B separated Magnoliids (positive) from Eudicotyledoneae and Monocotyledoneae (negative). Node C separated Fabidae (positive) from Malvidae (negative). Node D separated Myrtaceae (positive) from other clades (negative).

The most allopatric nodes showed relationships with elevation, and three of them were associated with disturbance (Fig. 5). Overall, the spatial pattern of SOS values indicated elevational divergences among nodes: Cyatheaceae and Magnoliids (Fig. 5a and b) were over-represented in montane forest communities, while Fabidae and Myrtaceae (Fig. 5c and d) were over-represented in submontane forest communities. However, SOS scores varied within plots of the same forest type depending on the presence or absence of disturbance. This variation led to different effects on the spatial structure of Magnoliids, Fabidae, and Myrtaceae.

The most prominent effect of disturbance on clade over-representation was observed for Fabidae within submontane communities. Disturbed areas showed an under-representation of this clade, in contrast to preserved communities in the same forest type. Magnoliids were under-represented in both submontane and montane disturbed communities, with the lowest values in submontane area. Regarding Myrtaceae, disturbance also led to an under-representation of species in this family, with a more pronounced effect in montane disturbed

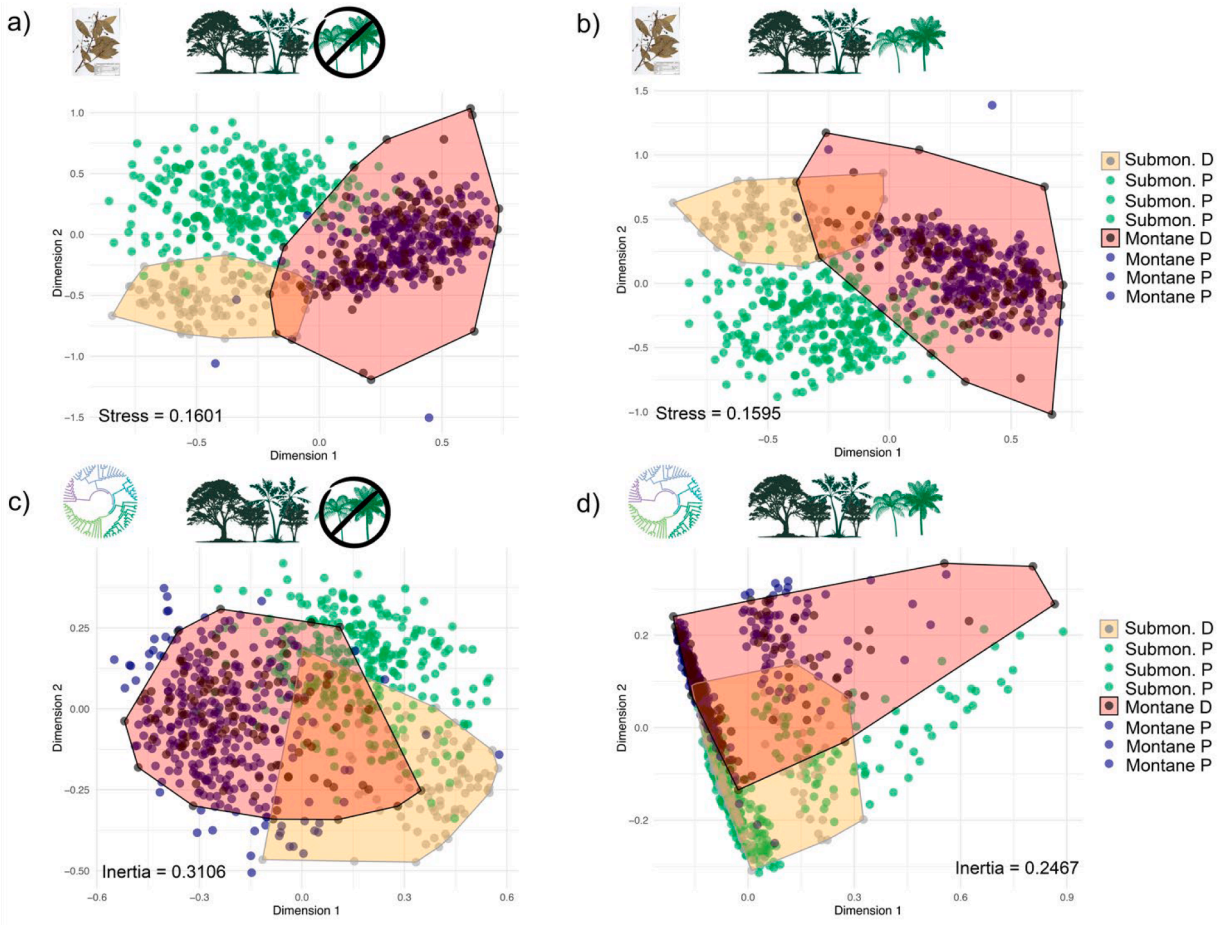

Fig. 2. The effects of elevation and anthropogenic disturbance (D, referring to selective logging; P, referring to preserved forest) on species (a and b) and phylogenetic (c and d) composition analyzed for eight tree communities in submontane and montane forests of the Atlantic Forest, southeastern Brazil. NMDS analyses were conducted excluding (a and c) or including (b and d) tree ferns. Convex hulls of subplots in disturbed communities are depicted by shaded areas. Submon – submontane.

communities.

4. Discussion

Applying ecological and evolutionary approaches to investigate species composition and diversity holds a great potential in determining the processes underlying the diversity and assembly of communities, especially in highly diverse tropical forests (Cadotte and Tucker, 2017; Swenson, 2013). In this study, we found that environmental filters related to elevation and selective logging interact in their effects on tree community assemblies. Our results show that the impact of selective logging is not consistent across elevations, even when the same disturbance occurred simultaneously in time. Instead, it interacts with environmental filtering in distinct ways, influencing both species composition and phylogenetic structure. Species and phylogenetic compositions changed among forest types at different elevations, with lower species richness in disturbed areas. Also, both factors related to elevation and anthropogenic disturbance significantly affected phylogenetic structure. However, the exclusion of tree ferns overshadows the effects of anthropogenic disturbances in tree communities at lower elevations. Concurrently, the elevation filter overshadowed the impact of selective logging, which was more pronounced in submontane forests, where the disturbed area presented less species of the most allopatric nodes of the tree communities. Furthermore, we highlight the varying sensitivity of different clades to environmental and anthropogenic filters between and within forest types. Our findings not only inform us about the effects of anthropogenic disturbances on community diversity and structure, but they also contain important information about how taxonomic scaling and environmental complexity may influence the diversity and assembly of Neotropical Forest communities.

4.1. Species distribution and phylogenetic changes with elevation and logging

Elevational gradients are known to impose strong environmental filters on community assembly due to climate-induced (Swenson and Enquist, 2007) and habitat-induced constraints (Hulshof et al., 2013). In our study, we identified elevation as a key driver of tree community assemblies (e.g. Kamimura et al., 2022; Loiola et al., 2023), with distinct species and phylogenetic compositions observed across different forest types. Species distribution clearly distinguishes subplots among vegetation types, indicating that species richness and composition, and phylogenetic diversity are structured by elevational gradients. This underscores the importance of elevation in determining community structure and functioning in tropical forests (Cavender-Bares et al., 2009; Kamimura et al., 2022). However, we found that selective logging had a greater impact in submontane forests, where high diversity and intense interspecific competition can amplify shifts in species composition and phylogenetic structure (Kamimura et al., 2022; Ndiribe et al., 2013). In contrast, montane communities, shaped by stronger abiotic filters such as cooler temperatures (Kamimura et al., 2022; Swenson et al., 2007), but with greater aboveground biomass (Alves et al., 2010), showed greater phylogenetic clustering and smaller responses to disturbance. Despite equivalent recovery times across elevations,

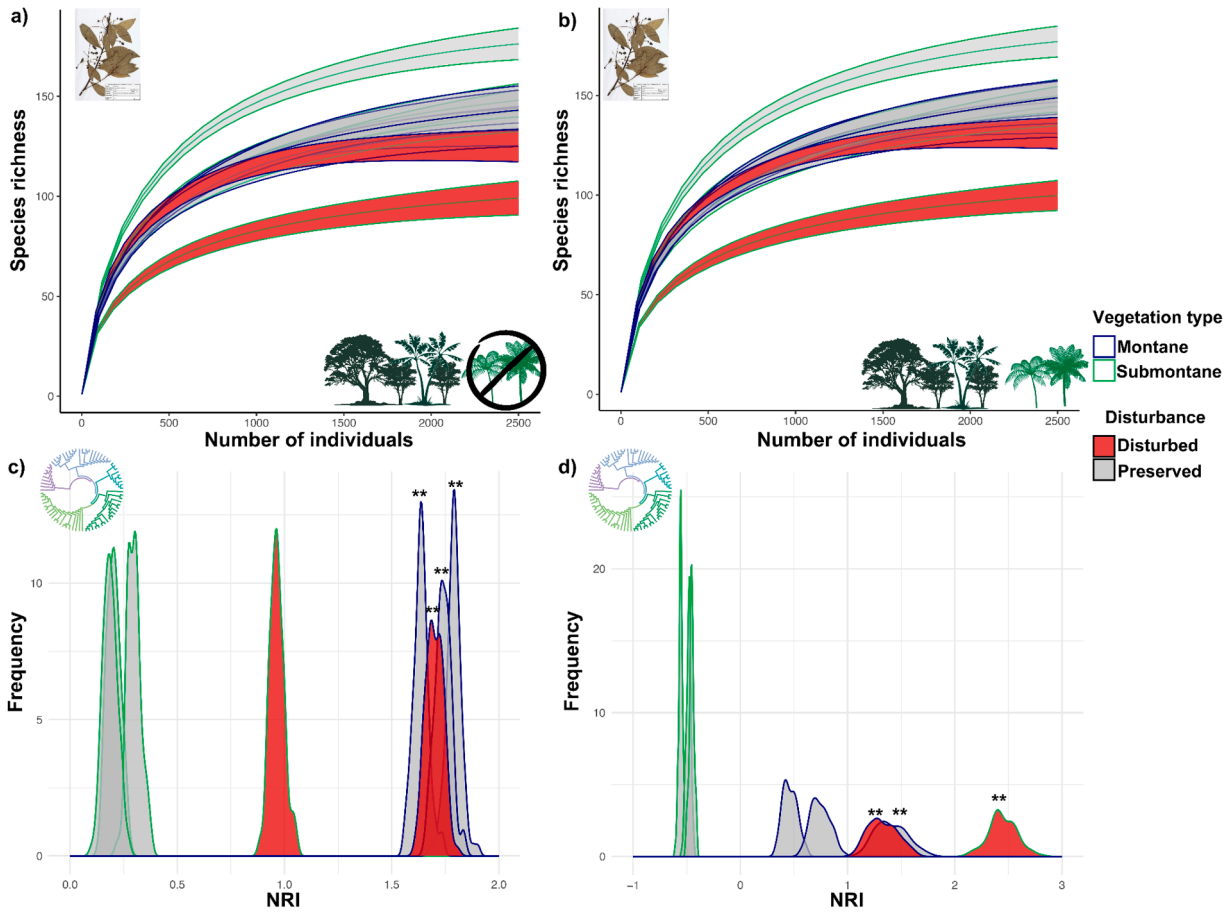

Fig. 3. Individual-based rarefactions of Hill numbers (a and b) and probability distributions of phylogenetic structures (c and d) for eight tree communities in submontane and montane forests of the Atlantic Forest, Southeastern Brazil. One community in each forest type was affected by selective logging. The shaded regions on the rarefaction curves represent the 95 % confidence intervals determined using bootstrap methods. **: $p < 0.05$.

divergences in effects of selective logging across elevation may lead to distinct phylogenetic and functional trajectories under climate change, potentially undermining ecological processes, and ecosystem resilience in different ways (Bergamin et al., 2024; Kamimura et al., 2023).

The elevation filters might select species from more closely related clades, with functional traits that allow their survival in such conditions (Culmsee and Leuschner, 2013; Emerson and Gillespie, 2008). In general, we found a phylogenetic clustered pattern for communities at higher elevations, and an overdispersion pattern for communities at lower elevations. However, anthropogenic disturbance conducted changes in phylogenetic structure at submontane forest, driving it toward a clustering pattern, but did not affect the results of montane community. This aligns with our hypothesis that lower elevation communities, which typically exhibit higher species richness due to favorable climatic conditions and resource availability, are more susceptible to anthropogenic disturbances, as observed in other studies as well (Beche et al., 2022; Pauchard et al., 2009). Moreover, selective logging may be more pronounced at lower altitudes, where the proximity to roads may facilitate tree extraction and transport of wood (Hall and Rodgers, 1986; Lovett et al., 2006), which emphasizes the need for conservation measures considering these aspects in areas that are not protected.

The removal of economically valuable tree species can have varying effects on tree community assembly across different elevations. Selective logging typically targets species with high wood density and height, which often play critical roles in forest structure and carbon storage (Dean, 1996; Imai et al., 2012; Lacerda et al., 2023). These high wood density species are particularly vulnerable to logging, and their removal can lead to decreased forest resilience and altered ecological dynamics. This impact extends beyond the targeted species, affecting those that depend on them for habitat and other ecological functions (Fredericksen and Mostacedo, 2000;). At lower elevations, where biodiversity is typically higher and environmental conditions favor faster-growing species, the removal of these key species can significantly shift community structure, reducing species richness and altering species composition (Hall et al., 2003). In contrast, at higher elevations, where environmental conditions are more challenging, the impact of selective logging may be less pronounced but still significant. These differences highlight the importance of developing habitat-specific management and conservation strategies to mitigate the impacts of selective logging on tropical forest ecosystems (Klenner et al., 2000).

In tropical forests, environmental filters and disturbance affect the phylogenetic diversity of plant communities, mostly tree communities, however the studies that evaluated it have generally excluded an important group in their analysis, as the tree ferns species (Duarte et al., 2014; Feng et al., 2014; Qian et al., 2014). Here, we show that this practice might impact the conclusions of the studies, as they change the outcomes of the analysis. The inclusion of tree ferns revealed a significant clustering effect on the phylogenetic structure of disturbed submontane forests, as previously observed in other studies conducted in the Andean region (Worthy et al., 2019) and in southern Brazil (Duarte et al., 2012). This finding underscores the importance of specific clades in influencing community resilience to anthropogenic disturbances (Cadotte et al., 2012; Chen et al., 2024). Furthermore, the differential responses of tree species clades to environmental filters and selective logging underscore the need for clade-specific conservation strategies.

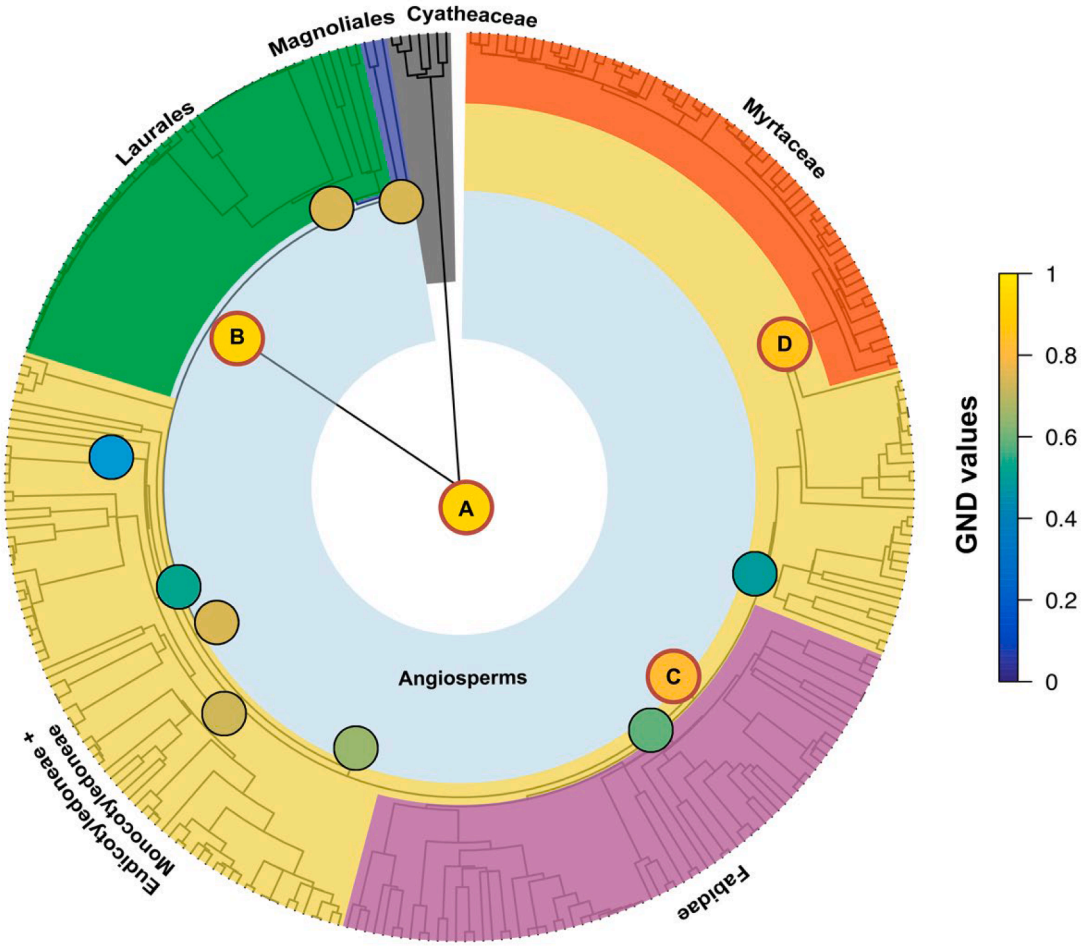

Fig. 4. Geographical node divergence (GND) values for tree species are shown in a circular phylogenetic tree. Nodes with the highest degrees of allopatry (GND values > 0.8) are highlighted with red circles (A, B, C and D), while others (black circles) with GND values ranging from 0.4 to 0.8 are also depicted. Key clades, such as Cyatheaceae (A - gray), Laurales (B - Green), Fabidae (C - pink) and Myrtaceae (D - orange) separated by the nodes with the highest GND values, are labeled around the phylogenetic tree. Species were sampled in eight tree communities distributed across two elevation ranges (submontane and montane forests) in the Atlantic Forest, southeastern Brazil. In each forest type, one community was affected by the disturbance of selective logging management.

For instance, the exclusion of tree ferns from the analyses resulted in a shift towards a more random phylogenetic structure in disturbed areas, suggesting that certain clades are more sensitive to logging activities. This variability in clade sensitivity necessitates tailored conservation approaches that consider the unique ecological and evolutionary characteristics of each clade (Caldwell et al., 2024). Thus, our results emphasize the intricate relationship between elevation, selective logging, and phylogenetic structure, demonstrating that conservation strategies must account for both abiotic gradients and the selective pressures exerted by human activities.

4.2. Spatial phylogenetic patterns under elevation and disturbance pressures

The spatial distribution of specific over-representation scores (SOS) for Cyatheaceae, Magnoliids, Fabidae, and Myrtaceae illustrates how elevation and selective logging interact to shape spatial phylogenetic patterns. Cyatheaceae and Magnoliids were predominantly over-represented in montane forests, while Fabidae and Myrtaceae showed higher representation in submontane forests. In addition, selective logging altered these patterns, particularly for Fabidae in submontane communities, where disturbed areas exhibited an under-representation of this clade. While previous studies have explored the impact of including lineages from non-flowering plant clades, such as tree ferns, in tree community studies (e.g., Feng et al., 2014; Worthy et al., 2019), our research demonstrates how a phylogenetic regionalization tool can elucidate the responses of specific clades to the complex interplay of environmental filters and anthropogenic disturbances on community assembly. The varying sensitivity of clades to anthropogenic disturbances, particularly basal lineages such as tree ferns and Magnoliids, underscores the value of incorporating node-based analyses in ecological research (Borregaard et al., 2014; Ndiribe et al., 2013) and conservation planning (Winter et al., 2013). Variation in under- and over-representation of key clades in disturbed areas further indicates potential long-term losses in functional diversity (Kamimura et al., 2023) and shifts in ecosystem structure (Bergamin et al., 2024; Winter et al., 2013).

In Tropical Forest, floristic composition tends to recover to a pre-logging state after 25 years (Gaui et al., 2019). However, we found that selective logging significantly alters spatial phylogenetic patterns, highlighting the intense impact of selective logging on phylogenetic structure and the potential for long-term ecological consequences. The under-representation of Magnoliids in both submontane and montane disturbed communities further highlights the sensitivity of this clade to anthropogenic disturbances. Similarly, Myrtaceae species showed a marked under-representation in disturbed montane forests, indicating that human activities can significantly disrupt the spatial phylogenetic structure of particular clades in these communities (Cisneros et al., 2014; Daru et al., 2019). These findings point out the importance of incorporating spatial phylogenetic patterns into conservation planning.

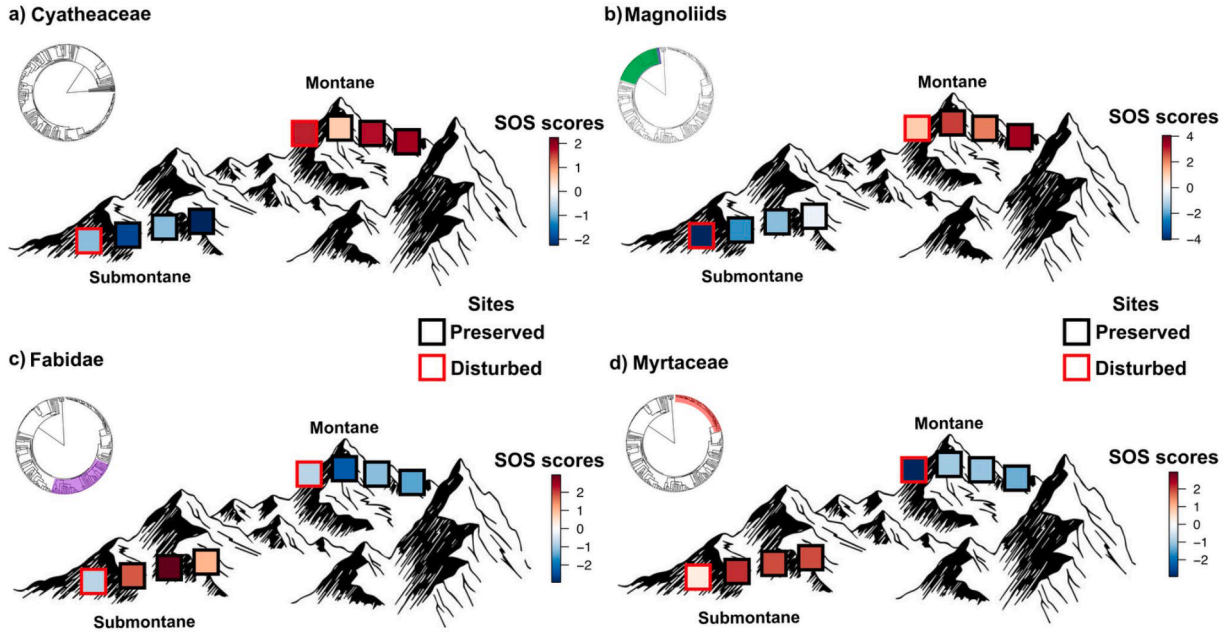

Fig. 5. Spatial distribution of specific over-representation scores (SOS scores) of the four nodes with the highest degrees of node allopatry (GND > 0.8), for eight tree communities in submontane and montane forests of the Atlantic Forest, southeastern Brazil.

By identifying regions and locals where high phylogenetic diversity intersects with areas of anthropogenic disturbance, conservation efforts can be more effectively targeted to preserve both species and their evolutionary heritage (Vane-Wright et al., 1991; Faith, 1992; Winter et al., 2013). The phylogenetic regionalization framework presented in our study offers a valuable tool for prioritizing conservation actions in the Brazilian Atlantic Forest, ensuring that areas with high phylogenetic and species diversity receive the necessary protection to maintain ecological resilience and evolutionary potential (Winter et al., 2013).

In a nutshell, our study highlights the complex interplay between elevation, anthropogenic disturbances, and phylogenetic structure in tropical tree communities. As we expected, the effect of environmental filtering on assembly rules has overshadowed the disturbance effect, which was more pronounced under greater competition of the submontane forests. Our findings reveal that the ecological consequences of anthropogenic disturbance, even when of the same type and history, vary along the elevational gradient, with greater impacts in species and phylogenetic composition in areas of highest diversity and interspecific competition. Importantly, we show the selection of clades to analysis should be made carefully, once the inclusion of basal clades might reveal the effects of disturbances and environmental filters, underscoring the need for clade-specific conservation strategies. These results support our main goal of understanding how elevation and anthropogenic disturbances shape tropical tree communities, providing a framework for targeted conservation efforts. The differential sensitivity of clades to these factors emphasizes the need for targeted conservation strategies that consider both ecological and evolutionary dimensions. By incorporating phylogenetic regionalization tools into conservation planning, we can more effectively address the challenges posed by anthropogenic disturbances at various spatial scales. This approach is particularly crucial for preserving megadiverse regions like the Brazilian Atlantic Forest.

CRediT authorship contribution statement

Vitor de Andrade Kamimura: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Priscilla de Paula Loiola:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Danilo Mesquita Neves:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Gabriel Mendes Marcusso:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Investigation, Data curation. **Gabriel Pavan Sabino:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation. **Marco Antonio Assis:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Carlos Alfredo Joly:** Writing – review & editing, Writing – original draft, Visualization, Validation, Funding acquisition, Data curation. **Fábio Pinheiro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2025.100894.

Data availability

Data is available as Supplementary Material

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