

CHANGES IN PLANT COMMUNITY ATTRIBUTES AND CARBON STOCKS IN ALTIMONTANE FOREST ISLANDS IN THE ATLANTIC FOREST-CERRADO TRANSITION UNDER DIFFERENT CONSERVATION CONDITIONS

RICARDO DA SILVA CARVALHO¹, JORGE CORTÉS-FLORES^{2*},
 GUSTAVO HENRIQUE DE OLIVEIRA MOURÃO¹, ANNE PRISCILA DIAS GONZAGA¹,
 EVANDRO LUIZ MENDONÇA MACHADO¹, MÁRCIO LELES ROMARCO DE OLIVEIRA¹,
 JOSÉ ROBERTO RODRIGUES PINTO³ AND ANDRÉ RODRIGO RECH¹

¹ Department of Forest Sciences, Universidade Federal dos Vales do Jequitinhonha e Mucuri-Campus JK, Diamantina, Minas Gerais, Brazil.

² Jardín Botánico, Instituto de Biología, Sede Tlaxcala, Universidad Nacional Autónoma de México, Santa Cruz Tlaxcala, Tlaxcala, Mexico.

³ Universidade de Brasília, Department of Forestry Engineering and Reference Center for Nature Conservation and Recovery of Degraded Areas, Darcy Ribeiro University Campus, Brasília, DF, Brazil.

*Corresponding author: jorge.cortes@ib.unam.mx

Abstract

Background: Ecotonal regions in tropical mountains, such as the Altimontane Forest Islands, are home to unique, highly biodiverse, and vulnerable plant communities. Human activities alter the functionality, structure, diversity, and provision of ecosystem services in these ecosystems. Uncertainties persist regarding their resilience to human impacts and the most effective ways to conserve them.

Questions: How do the species composition, vegetation structure, and diversity differ between protected and unprotected forest islands subject to anthropogenic disturbances? Are there differences in the carbon stocks of these forest islands?

Studied species: Vascular plants of the Cerrado-Atlantic Forest.

Study site: Forest Islands in Minas Gerais, Brazil.

Methods: We calculated alpha and beta diversity and estimated aboveground biomass and aboveground carbon stocks from tree samples (diameter at breast height ≥ 5 cm) collected in Forest Islands.

Results: We found that protected and unprotected areas had similar alpha diversity but differed in floristic composition. We observed high beta dissimilarity between protected and unprotected Altimontane Tropical Forest Islands ($\beta_{sor} = 0.93$ and $\beta_{bray} = 0.94$). Unprotected islands show greater species substitution (90 %), unimodal vertical structure, greater susceptibility to colonization by new generalist species, and lower carbon stock ($80.70 \text{ Mg C ha}^{-1}$).

Conclusions: Changes in species composition, vegetation structure, and carbon storage were observed on unprotected islands, demonstrating the need to protect these unique ecosystems.

Keywords: alpha diversity, beta diversity, carbon sequestration, community composition, and structure.

Resumen

Antecedentes: Las regiones de ecotono en montañas tropicales, como las Islas de Bosque Altimontano, albergan comunidades vegetales únicas, altamente biodiversas y vulnerables. Las actividades humanas alteran la funcionalidad, la estructura, la diversidad y la provisión de servicios ecosistémicos en estos ecosistemas. Persisten incertidumbres sobre su resiliencia a los impactos humanos y las formas más efectivas de conservarlos.

Preguntas: ¿Cómo difieren la composición de especies, la estructura de la vegetación y la diversidad entre islas forestales protegida y no protegida sometidas a perturbaciones antropogénicas? ¿Existen diferencias en las reservas de carbono de estas islas forestales?

Especies de estudio: Plantas vasculares del Cerrado-Bosque Atlántico.

Sitio de estudio: Islas de Bosque en Minas Gerais, Brasil.

Métodos: A partir del muestreo de individuos arbóreos ($\text{DAP} \geq 5$ cm) en las Islas de Bosque, se calculó la diversidad alfa y beta, y se estimó la biomasa aérea y el almacén de carbono aéreo.

Resultados: Se encontró que las áreas protegidas y no protegidas presentaban una diversidad alfa similar, pero una composición diferente. Se observó alta disimilitud de especies entre ambos tipos de área ($\beta_{sor} = 0.93$ y $\beta_{bray} = 0.94$). La isla no protegida mostró mayor recambio de especies (90 %), estructura vertical unimodal, mayor susceptibilidad a la colonización por nuevas especies generalistas y menores reservas de carbono $80.70 \text{ Mg C ha}^{-1}$.

Conclusiones: Los cambios en la composición de especies, la estructura de la vegetación y el almacenamiento de carbono en la isla no protegida refuerzan la necesidad de proteger estos ecosistemas únicos.

Palabras clave: composición y estructura de la comunidad, diversidad alfa, diversidad beta, almacén de carbono.

This is an open access article distributed under the terms of the Creative Commons Attribution License CCBY-NC (4.0) international.

<https://creativecommons.org/licenses/by-nc/4.0/>



Tropical forests are essential ecosystems for maintaining biodiversity and regulating the global climate (Bañares-De-Dios *et al.* 2024). However, tropical forests face major challenges from socio-economic development and growing environmental degradation (Cowie 2022). A large portion of primary natural habitats in tropical and subtropical regions has already been altered, leading to declines in biodiversity and ecosystem services essential to life on Earth and human well-being (Fernandes *et al.* 2020, Cunha-Blum *et al.* 2025).

Despite covering only 25 % of the Earth's surface, mountains play a strategic role in species conservation, harboring around 87 % of the global biodiversity, with high levels of endemism due to their altitudinal and climatic variations (Humboldt & Bonpland 1805, Myers *et al.* 2000, Mittermeier *et al.* 2005, Bañares-de-Dios *et al.* 2024). On a global scale, the Espinhaço Range Biosphere Reserve (ERBR) is a hotspot, recognized as a megadiverse region in the Neotropic (Myers *et al.* 2000, Cunha-Blum *et al.* 2025). Despite occupying only 1 % of the Brazilian territory, ERBR is home to approximately 15 % of Brazil's vascular flora, and around 40 % of its species are endemic (Coelho *et al.* 2018a, Silveira *et al.* 2019, Fernandes *et al.* 2020, Lima *et al.* 2020).

Within ERBR, the Altimontane Seasonal Forests of the Atlantic Forest stand out, which are part of the Grassland-Savannah transition of Cerrado (Coelho *et al.* 2018a). Known as “Capões de Mata” or forest islands, these formations are adapted to the high environmental heterogeneity and unique conditions of Brazilian mountains (Costa *et al.* 2023, Ribeiro *et al.* 2018). Forest islands have emerged as endemic centers of animal and plant species in South America, acting as local and regional biodiversity centers (Myers *et al.* 2000, Mittermeier *et al.* 2005, Coelho *et al.* 2016, Neves *et al.* 2018, Costa *et al.* 2021b).

The impacts of human activities have put the resilience of ERBR forest islands to the test (Coelho *et al.* 2018a, Morellato & Silveira 2018). Thus, understanding these forest islands for their flora, their vegetation structure and their key ecosystem services crucial to humanity, like carbon (C) stocks is essential (Costa *et al.* 2021a, Gonçalves *et al.* 2023). After all, these studies help to understand local biodiversity and establish strategies to mitigate the effects of global climate change, especially in the Neotropical region (Cunha-Blum *et al.* 2025, Tassinari *et al.* 2025), making it possible to guarantee its conservation against growing human and environmental pressures.

Changes in floristic composition, vegetation structure and species diversity on forest islands might be a multifactorial process. These changes include the conservation and land use regime, as a consequence of recurrent anthropogenic actions and the effects of climate change (Costa *et al.* 2021b, 2023), which modify soil properties, dynamics, and ecological function of forest-island ecosystems (Coelho *et al.* 2018b). Consequently, such changes influence floristic composition, species diversity and carbon sequestration (Souza *et al.* 2020, Campos *et al.* 2021). In addition to these factors is the fragility of elevational environments, which are characterized by high spatial and temporal variability, mainly due to bioclimatic and geomorphological conditions (MMA 2016, Barral *et al.* 2023, Montes *et al.* 2023).

In the ERBR region, some forest islands are protected by conservation units (Coelho *et al.* 2018b). However, no studies to date have focused on comparing the provision of ecosystem services by vegetation in areas with different land use and conservation regimes in the region. Studies conducted in other phytophysiognomies systems have highlighted the importance of protected areas in preserving biodiversity and increasing carbon stocks, compared with disturbed areas (Françoso *et al.* 2015, 2016, Barral *et al.* 2023, Carvalho *et al.* 2024). Thus, it is essential to investigate the potential effectiveness of forest-island vegetation in providing ecosystem services, with the aim to promoting management and conservation practices that enhance their environmental sustainability in scenarios of climate change and different land uses (Coelho *et al.* 2018a).

In general, preserved forest islands exhibit high beta diversity (Coelho *et al.* 2017, Moura *et al.* 2021) and harbor environmentally sensitive species (*e.g.*, *Richeria grandis* Vahl, *Tapirira guianensis* Aubl.) associated with higher soil moisture and preserved conditions (Coelho *et al.* 2016, 2018b, Pereira *et al.* 2017, Costa *et al.* 2023, Moura *et al.* 2025). On the other hand, forest islands exposed to frequent anthropogenic disturbances, particularly fires and grazing, show an increase in pioneer or disturbance-tolerant species (*e.g.*, *Myrsine umbellata* Mart., *Myrcia splendens* (Sw.) DC), and a reduction in the vertical structure of the forest (Coelho *et al.* 2018a, Costa *et al.* 2022). Therefore, these changes lead to the replacement of plant species composition and a reduction in aboveground biomass and carbon stocks (Chave *et al.* 2014, Scolforo *et al.* 2016, Souza *et al.* 2022, Sullivan *et al.* 2025).

We evaluated the floristic composition, vegetation structure, species diversity and carbon stock in two communities in the Espinhaço Range Biosphere Reserve, Brazil, subject to different land use regimes, one inside a Conservation Unit and the other in an unprotected area. Our objective, within a case study framework, was to address the following questions: (i) How do the species composition, vegetation structure, and diversity differ between protected and unprotected forest islands subject to anthropogenic disturbances? And are there differences in the carbon stocks of these forest islands? We hypothesized that the floristic composition would differ between the two areas. On the protected forest island (PAI), species with greater moisture and soil conservation requirements are expected to be present, while in the unprotected area (UPA), with disturbances such as grazing and fire, pioneer and disturbance-tolerant species will be more frequent. In terms of species diversity and vegetation structure, we believe that the PAI will have a higher tree density and more diverse biomass, contributing to higher carbon stocks, while in the UPA, we expect homogenization of the vegetation, a reduction in biomass, and lower carbon stocks.

Materials and methods

Study areas. We conducted this study in two forest-island areas with different use and conservation regimes, each approximately 1,200 m² (0.12 ha), located in the Espinhaço Range Biosphere Reserve (ERBR) in Minas Gerais, Brazil ([Figure 1](#)). The PAI is within the Rio Preto State Park (RPSP) (18° 14' 13" S, 43° 19' 37" W), where no significant disturbances have been recorded in the past 50 years. The UPA is located within the RPSP buffer zone (18° 14' 29" S, 43° 18' 37" W) and is subject to frequent disturbances, including cattle presence and forest fires (Coelho *et al.* 2018b, Ferreira *et al.* 2022, Mucida *et al.* 2022). Both areas are located at an average of 1,600 m asl.

The vegetation of these forest islands is classified as Altimontane Seasonal Semideciduous Forest, and, phyto-geographically, they are part of an enclave of Atlantic Forest disjunctions within the Cerrado biome (Ab'Saber 1967, Coelho *et al.* 2016, Gonçalves *et al.* 2020). The region's climate is subtropical Altimontane (Cwb) (Köppen), with rainy summers and dry winters, with average temperatures ranging from 10 to 19 °C and annual rainfall from 850 to 1,500 mm (INMET 2023, Pinto *et al.* 2023, Barral *et al.* 2023). The region is geologically characterized by quartzite rocks and shallow soils (Bispo *et al.* 2015, Coelho *et al.* 2016). The forest islands occur predominantly on organic Histosols and hydromorphic soils in areas associated with the fragility of the quartzite and are always near water springs (Coelho *et al.* 2018a). In the two areas studied, the soils are classified as Histosols according to the USDA Soil Taxonomy (Soil Survey Staff 2010), specifically as the Typic Haplosaprists (Bispo *et al.* 2015), while in the World Reference Base for Soil Resources (WRB) they correspond to Ombric Sapric Histosols (IUSS Working Group WRB 2022).

Vegetation sampling. In both, the PAI by RPSP, and the adjacent UPA, ten 10 × 10 m plots (100 m² each) were installed sequentially one after the other, totaling a sampled area of 0.1 ha per island, following the guidelines of the Cerrado Permanent Plots Manual (Felfili & Rezende 2005). In the plots, all living trees with a diameter at breast height (DBH) ≥ 5 cm were measured. Trees with subdivided stems were included in the survey when the total basal area of one of the stems reached DBH ≥ 5 cm. The total height of the trees was estimated using a graduated botanical collecting pole (Felfili & Rezende 2005).

When possible, botanical identification was done *in situ*. Otherwise, botanical material was collected for later identification by comparison in herbaria, consultation with specialists and specialized literature. The botanical samples were deposited in the Jeanini Felfili Dendrological Herbarium (HDJF) at Universidade Federal dos Vales do Jequitinhonha e Mucuri (UFVJM), Minas Gerais, Brazil.

We classified the species according to the *Angiosperm Phylogeny Group* (APG 2016) and updated taxonomic names in accordance to Flora e Funga do Brasil - Reflora (Flora e Funga do Brasil 2024). We consulted the National Center for the Conservation of Flora - CNCFlora (CNCFlora 2024) to assess the species' threat categories. In this study, we adopted the threat categories defined by the World Conservation Union (IUCN 2024).

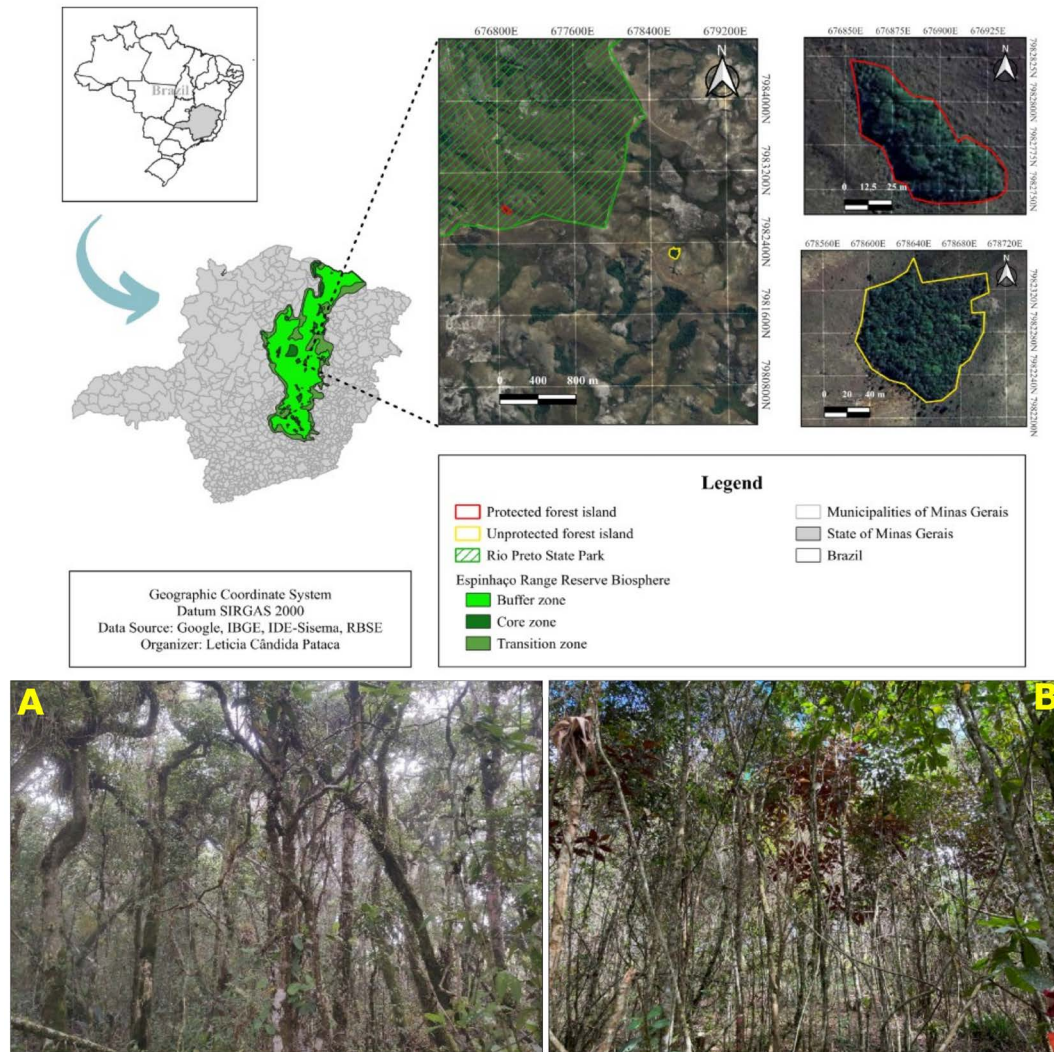


Figure 1. Geographical location of the forest islands (Capões de Matas) in the Rio Preto State Park-RPSP. (A) protected area and (B) adjacent unprotected area in the Espinhaço Range Biosphere Reserve-ERBR, Minas Gerais, Brazil.

Species diversity and vegetation structure. Taxonomic alpha diversity (α) was calculated by the effective number of species (Jost 2006). Three orders of taxonomic diversity were calculated: 0q , which equals to species richness; 1q , which weighs the number of species by their abundance in the community, and 2q , which gives greater weight to the abundance of the dominant species in the community. Alpha diversity (α) was calculated using the “hillR” package (Li 2018) in the R software (R Core Team 2024, version 4.3.3).

Beta diversity (β) was analyzed by calculating the Sørensen and Bray-Curtis dissimilarity indices (Magurran 2004). In addition, we examined the relationship between dissimilarity and species turnover in the plots, and how the latter relates to the shared richness of species and sites (nestedness; Baselga *et al.* 2012a, 2016). To analyze β diversity, the “betapart” package (Baselga *et al.* 2012b, Baselga 2016) was used in R. Vegetation structure was assessed using phytosociological parameters (Mueller-Dombois & Ellenberg 1976) and based on the distribution of trees in diameter and height classes. We adopted a fixed amplitude of 5 cm between diameter classes and of 3 cm for height classes.

Estimation of Above Ground Biomass (AGB) and Above Ground Carbon (AGC). To calculate AGB, we used the Pantropical allometric equation proposed by Chave *et al.* (2014): $AGB_{est} = 0.0673 \times (\rho D^2 H)^{0.976}$, $est = \rho(\sigma = 0.357, AIC = 3130, df = 4002)$, where: ρ = wood density of each species (g/cm^3), D = diameter at breast height (cm) and H = height (m). The wood density data for the species were obtained according to Oliveira Filho & Scolforo (2008) and ranged from 0.409 to 0.82 g/cm^3 . To obtain the AGC stored in the two communities (in hectares), the AGC values for each tree were calculated and then extrapolated to the entire community in $Mg\ C\ ha^{-1}$ and multiplied by 0.47 (47 %) (CETEC 1995, IPCC 2014, Liu *et al.* 2023).

Data analysis. To compare patterns of species diversity between the two forest islands under contrasting conservation regimes, we applied generalized linear models (GLM) (Da Silva *et al.* 2022). We modeled abundance, α diversity (0q , 1q and 2q), Sørensen turnover, dissimilarity, and nesting as response variables and the effect of areas as the explanatory variable. Abundance and richness (0q) were modeled with Poisson, quasi-Poisson, or negative binomial distributions, depending on model fit. For diversity indices 1q and 2q , we tested Gaussian and Gamma distributions with a log link and used beta regression models for dissimilarity (turnover and nestedness) and β diversity (Sørensen and Bray-Curtis), using the ‘betareg’ package (Cribari-Neto & Zeileis 2010). In all analyses, the residuals were evaluated to determine the best distribution using the “performance” package (Lüdecke *et al.* 2021) in R.

We checked the distribution of vegetation structure (diameter and height classes) using the Shapiro-Wilk (W) and Kolmogorov-Smirnov (D) tests. To test differences in floristic composition between the areas, we applied a Permutational Multivariate Analysis of Variance (PERMANOVA) with Bray-Curtis dissimilarity and 1,000 permutations (Clarke 1993, Anderson 2001, 2006).

Results

Floristic composition and species diversity. We recorded 102 species belonging to 38 families and 36 genera, of which 47 species (20 families) occurred in the PAI and 55 species (18 families) in the UPA. The families with the highest richness and density in the PAI were Myrtaceae (10 species and 95 trees), Phyllanthaceae (1 and 31), Lauraceae (6 and 30) and Araliaceae (2 and 23). In total, these families accounted for 40.43 % of the species and 59.45 % of the trees recorded (Table S1). In the UPA, the most representative botanical families were Primulaceae (1 species and 60 trees), Myrtaceae (10 and 46), Melastomataceae (11 and 36), Lauraceae (10 and 35). Together, they accounted for 74.54 % of the trees and 58.18 % of the species in this area (Table S2).

In the evaluation of α diversity, no significant differences were observed between the areas for species richness, (0q) ($\chi^2 = 0.034$, d.f. = 19, $P = 0.855$), nor alpha diversity: 1q ($F = 0.522$, d.f. = 19, $P = 0.479$) and 2q ($F = 0.79$, d.f. = 19, $P = 0.385$) (Figure 2).

However, species composition differed between the compared areas ($F = 7.251$, $R^2 = 0.287$, $P < 0.001$), and 28.7 % of this variation may be attributable to the use and conservation regimes of the forest islands. These data are corroborated by the high dissimilarity between both type of areas, as indicated by the Sørensen and Bray-Curtis indices (92.6 and 93.6 %, respectively), with turnover values exceeding 90 % and nestedness at just 1.0 % for both indices. We found significant difference in Sørensen’s dissimilarity between the areas ($z = 2.47$, $P = 0.013$) and the Bray-Curtis β diversity value ($z = 2.08$, $P = 0.037$), with higher values in the UPA (Figure S1).

Ten species were shared between the PAI and UPA: *T. guianensis* Aubl., *Rhodostemonodaphne anomala* (Mez) Rohwer, *Ocotea pulchella* (Nees & Mart.) Mez, *Miconia flammea* Casar, *M. trianae* Cogn., *M. umbellata* Mart., *Myrcia venulosa* DC., *Styrax ferrugineus* Nees & Mart., *Cabralea canjerana* (Vell.) Mart., and *Guapira opposita* (Vell.) Reitz. Species abundance was directly affected by the conservation status of the area ($\chi^2 = 21.10$; d.f. = 19; $P = 0.014$), being higher in the PAI, suggesting that it accumulates a greater number of species. In contrast, the UPA showed lower abundance and less variability in the community (Figure S2).

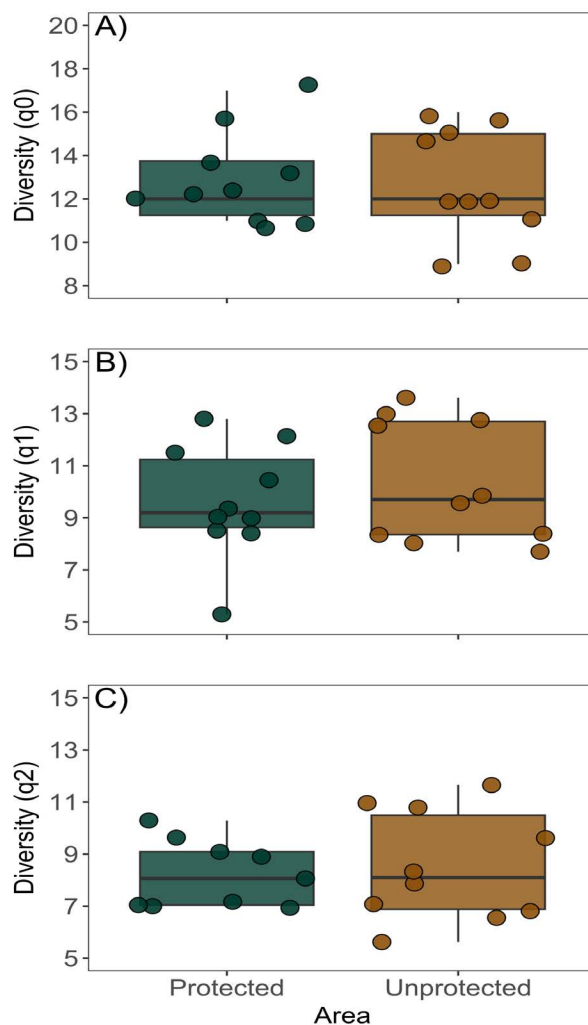


Figure 2. Alpha diversity values for tree vegetation (DBH ≥ 5 cm) sampled on protected and unprotected forest islands in the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil. A) q^0 = richness, B) q^1 = all species are weighted proportionally by their abundance in the community and C) q^2 = abundance of the dominant species.

Vegetation structure. We sampled a total of 545 trees, of which 301 (55.23 %) and 244 (44.77 %) were recorded in PAI and UPA, respectively. Regarding the total basal area of $93.4 \text{ m}^2 \text{ ha}^{-1}$, there was a significant difference between the areas ($D = 0.342$, $P < 0.001$). The highest values were observed in the PAI, with an average basal area per tree of $0.022 \pm 0.003 \text{ m}^2$, representing 70.3 % of the total value ($65.7 \pm 1.6 \text{ m}^2 \text{ ha}^{-1}$). In contrast, the UPA had a total basal area of $27.7 \pm 1.8 \text{ m}^2 \text{ ha}^{-1}$ (29.64 %), equivalent to an average basal area per tree of $0.011 \pm 0.001 \text{ m}^2$. In the PAI, the species that contributed the most biomass were *R. grandis*, accounting for 28.3 % of the community's basal area ($18.6 \text{ m}^2 \text{ ha}^{-1}$), Myrtaceae sp., with 14.8 % ($9.74 \text{ m}^2 \text{ ha}^{-1}$), and an undetermined species, with 7.1 % ($4.68 \text{ m}^2 \text{ ha}^{-1}$) (Table S1). In the UPA, the species *M. umbellata* contributed 20.03 % ($5.55 \text{ m}^2 \text{ ha}^{-1}$) of the total average basal area of the community, followed by *C. canjerana* with 7.87 % ($2.18 \text{ m}^2 \text{ ha}^{-1}$) and *Cryptocarya aschersoniana* Mez with 6.82 % ($1.89 \text{ m}^2 \text{ ha}^{-1}$) (Table S2).

We found statistical differences in the distributions of height classes between both compared areas ($D = 0.141$ and $P = 0.0089$). In the PAI, the tree stratum ranged in height from 2 to 18 m, and in the UPA from 3 m to 27 m (Figure 3A, B). However, in both areas we found that trees were concentrated in the 6-12 meter classes (6-9 m and 9-12 m), which represents 64.2 and 79.5 % trees in the PAI and UPA, respectively. In the last type of protected

area, only 5.3 % of the trees reached heights of more than 15 m. We detected a similar pattern in the diameter distributions, which differed between the PAI and UPA ($D = 0.28$ and $P < 0.001$). In the former, most trees concentrate between 5 and 20 cm (Figure 3C), whereas in the latter, 68.8 % of the trees had DBHs between 5 and 10 cm (Figure 3D).

Above-ground biomass (AGB) and above-ground carbon (AGC). The AGB and AGC values estimated for both areas combined were 471.85 Mg ha⁻¹ and 221.77 Mg C ha⁻¹, respectively. In all metrics, the PAI had higher average values (AGB = 300.14 ± 25.3 Mg ha⁻¹ and AGC = 141.06 ± 11.9 Mg C ha⁻¹ (63.6 %) than the UPA (AGB = 171.70 ± 31.7 Mg ha⁻¹ and AGC = 80.70 ± 14.9 Mg C ha⁻¹ (36.4 %). We found significant differences between the areas for both AGB ($W = 16$, $P = 0.011$) and AGC ($W = 84$, $P = 0.0089$). The carbon stock in the PA was 60.4 Mg C ha⁻¹ higher than in the UPA (Figure 4). The species that contributed the most AGB and AGC were Myrtaceae sp. and *R. grandis* in the PAI, and *M. umbellata*, *Byrsonima japurensis* A.Juss., and *B. chrysophylla* Kunth., in the UPA (Table 1).

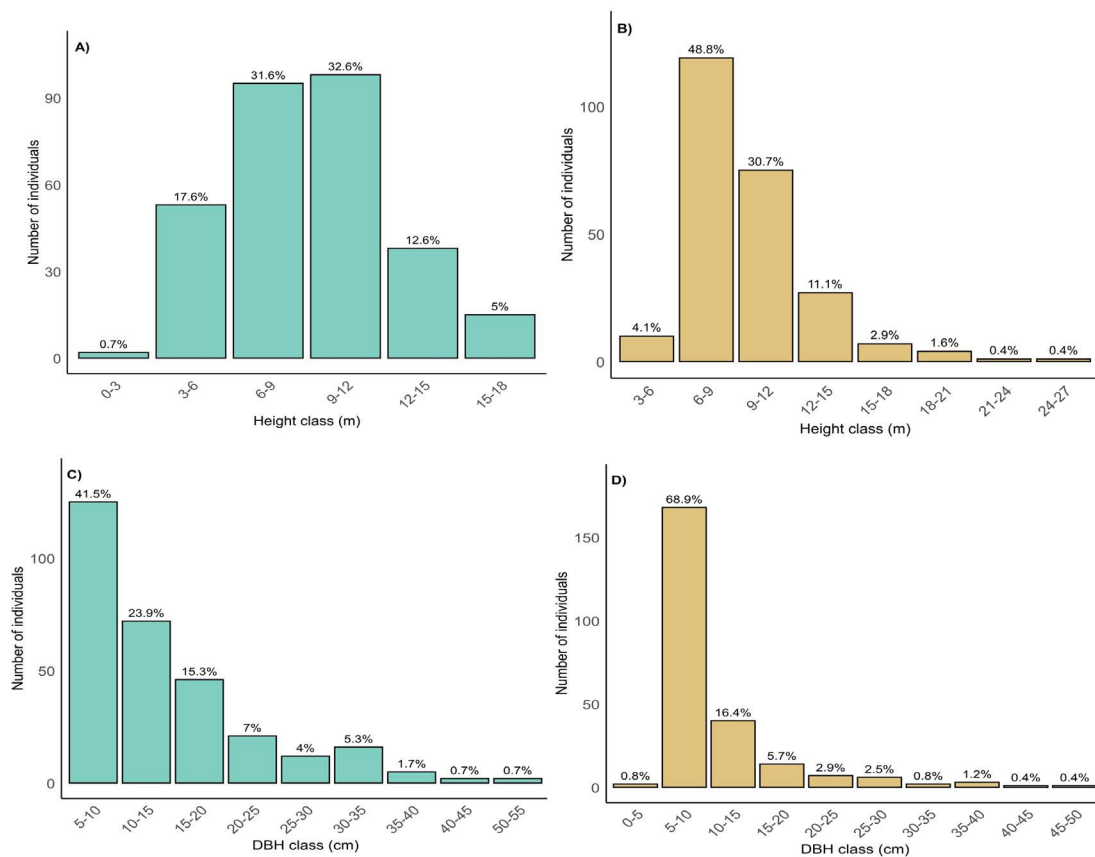


Figure 3. Distribution of trees (DBH ≥ 5 cm) in height and diameter classes between the protected (A and C) and unprotected (B and D) forest islands in the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil 2024. The values above the bars represent the percentage of each class.

Discussion

Floristic composition, α and β diversity, and vegetation structure. Our findings describe the complexity and uniqueness of the Altimontane Tropical Forest Islands, located in the Atlantic Forest-Cerrado transition, showing clear patterns of variation in floristic and structural characteristics, as well as in the provision of ecosystem services (carbon

stock), which differ in the conservation context. Based on the floristic composition, the altitudinal forest islands are essential elements of the Atlantic Forest-Cerrado biogeographic transition zone in the ERBR region. This is due to the high representation of families typical of elevational formations and forests of the Atlantic Forest biome (such as Myrtaceae, Lauraceae, and Primulaceae; see [Tables S1](#) and [S2](#); Magalhães *et al.* 2018, Costa *et al.* 2021a, 2023). This, in turn, suggests that elevation gradient and the associated abiotic conditions shape distinct communities (*e.g.*, *M. umbellata*, *C. canjerana*), which, in addition to sharing affinities with other biomes and/or specific environments, also harbor endemic plant species (Coelho *et al.* 2016, 2018b). These results reinforce the role of Brazilian Protected Areas in maintaining biodiverse communities (Françoso *et al.* 2015, Souza *et al.* 2020, Barral *et al.* 2023).

Environmental conditions imposed by high elevation, such as higher humidity, hydromorphic and dystrophic soils (Myers *et al.* 2000, Coelho *et al.* 2016, Costa *et al.* 2021a, Moura *et al.* 2021, Costa *et al.* 2022), may also explain the dominance of species such as *R. grandis*, Myrtaceae sp., and *T. guianensis* in the protected area. The increased presence of species such as *M. umbellata*, *C. aschersoniana*, and *Myrcia splendens* in the UPA seem to be linked to the ecological characteristics that enable them to colonize areas with more stressful environmental conditions. Species in Primulaceae, such as *M. umbellata* and *M. guianensis*, have been reported to show a range of adaptations to grazing and fire. Although described as fire-sensitive, these plants are resilient and are often abundant in fire-disturbed areas (Rios *et al.* 2018, Antunes *et al.* 2025). These adaptations include tolerance to soil compaction, chemical changes linked to ammonification from deposition of cattle manure and urine, tolerance to variations in soil moisture, and resistance to fire (Bauer *et al.* 2012, Amorim *et al.* 2019, Salomão *et al.* 2023).

Our results also indicate that, although the areas are subject to distinct levels of conservation, they exhibit a relatively similar pattern across the three orders of taxonomic diversity assessed. This is because a balanced abundance distribution, with few significant variations among species, yields low diversity. This, in turn, reduces the sensitivity of the diversity metrics (1q - proportionally weighted by their abundance in the community, and 2q - abundance of the dominant species in the community) to differences in abundance, bringing these indices closer to species richness

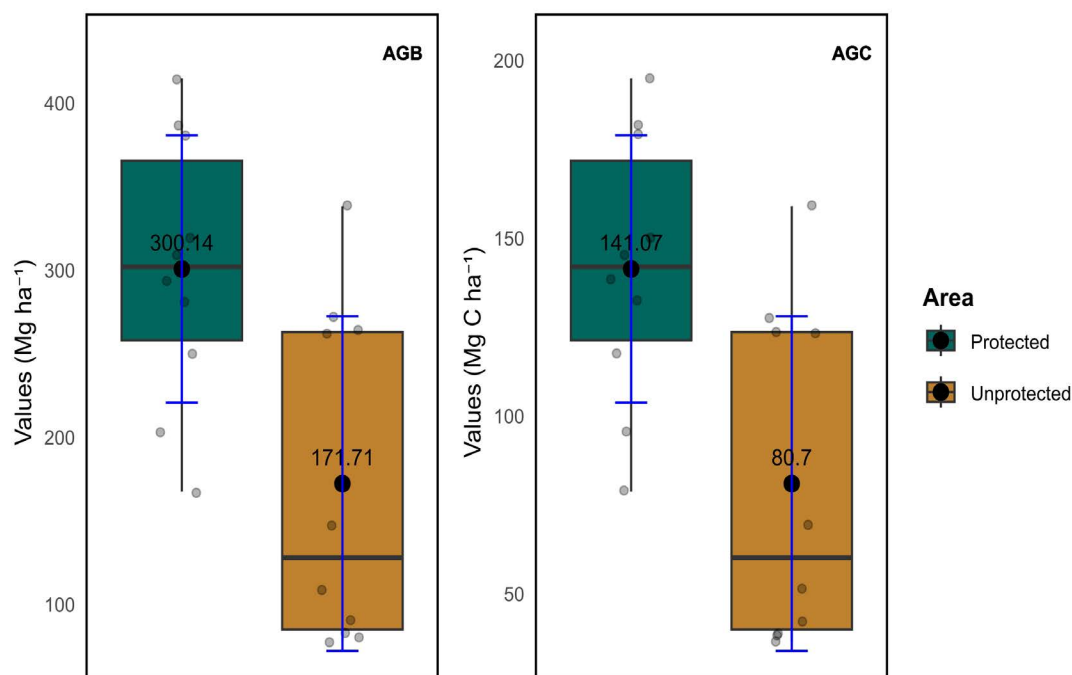


Figure 4. Aboveground biomass (AGB), aboveground carbon stock (AGC) and carbon dioxide equivalent (CO₂-eq) in unprotected and protected forest islands sampled in the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil.

(⁰g). The richness of species and genera, combined with the balanced distribution of abundances, contributes to the homogeneity of the diversity indices, reflecting similar taxonomic patterns between the analyzed areas. The high level of species turnover recorded in the areas was considerably higher on the UPA (90 %) than on the PAI (78 %). This suggests that species composition is strongly influenced by the intensity of anthropogenic changes to abiotic conditions in the UPA. These altered conditions have, in turn, facilitated the colonization by generalist species adapted to disturbed environments (Donoghue 2008, Chao *et al.* 2014, Coelho *et al.* 2016, 2018b).

The environmental degradation observed on the unprotected island would also be the primary factor responsible for the high dissimilarity values (Sørensen: 0.92 and Bray-Curtis: 0.93) recorded in the areas. This is because such conditions influence the composition between areas, which was mainly attributed to species substitution, as observed by Fernandes *et al.* (2020). This shows that each area supports different floristic assemblages, depending on its state of land conservation and use (Baselga *et al.* 2012b, Bispo *et al.* 2016, Alvarado *et al.* 2017, Coelho *et al.* 2018a, Souza *et al.* 2020, Moura *et al.* 2021, Barral *et al.* 2023, Guerrini *et al.* 2024).

Thus, the influence of conservation status on the beta diversity of each forest island reinforces the idea that unprotected areas are subject to greater selective pressure (Coelho *et al.* 2018b, Costa *et al.* 2022, Bañares-de-Dios *et al.* 2024). This would explain, for example, the presence of pioneer species like *Eremanthus erythropappus* (DC.) MacLeish on the unprotected island. This species is widely distributed in Campos Rupestres (rupestrian grasslands), which feature shallow, quartzite soils with low water retention and fertility (Coelho *et al.* 2016, Pereira *et al.* 2017).

The observed species substitution pattern is consistent with environmental filtering (MacArthur & Wilson 1963, Rosindell *et al.* 2011). The abiotic conditions, such as reduced soil humidity, increased compaction, and greater luminosity, resulting from the presence of cattle and fire, led to a unique floristic composition, featuring species from the forest environment as well as plants from other environments, according to the microclimate variations existing on the UPA. In contrast, PAI maintain more stable environmental conditions, allowing species distributed in the area not to be replaced too intensively, as their environments are more similar (Coelho *et al.* 2016, 2018a, Pereira *et al.* 2017, Gonçalves *et al.* 2023).

This same aspect supports the low contribution of nestedness among the islands, suggesting that the communities are not subsets of each other, but are structured independently under different abiotic conditions, formed by species adapted to the environmental conditions present on each forest island. After all, there is a strong connection between the abundance of species and acidic, aluminum-rich, and less fertile soils on forest islands (Coelho *et al.* 2016, 2018b). Thus, we believe that these characteristics influence the floristic composition and structure of the vegetation, resulting in a low basal area and monodominance of some species, such as those found in the UPA: *M. umbellata*, *C. aschersoniana*, *M. splendens*, and *Miconia* sp.

Biomass and carbon stock. The above-ground biomass (AGB) and above-ground carbon (AGC) values obtained are higher than those reported by Carvalho *et al.* (2024), who recorded 10.47 Mg ha⁻¹ of AGB and 5.23 Mg C ha⁻¹ of AGC for another forest also located in a Conservation Unit. The higher AGB values in the PAI are attributed to the presence of trees with larger basal area, average total height, canopy density, and higher wood density (Coelho *et*

Table 1. Species with the highest contributions to AGB and AGC in protected and unprotected forest islands sampled in the Espinhaço Range Biosphere Reserve, Minas Gerais, Brazil.

Area	Species	Total AGB (Mg ha ⁻¹)	Total AGC (Mg C ha ⁻¹)
Protected	<i>Myrtaceae</i> sp.	59.69	28.04
Protected	<i>Richeria grandis</i>	55.35	26.57
Unprotected	<i>Myrsine umbellata</i>	43.07	20.24
Unprotected	<i>Byrsonima japurensis</i>	19.50	7.16
Unprotected	<i>Byrsonima chrysophylla</i>	15.17	7.03

al. 2018a, Lutz *et al.* 2018, Ali *et al.* 2020, Vargas-Larreta *et al.* 2021, Abbasi *et al.* 2022). These factors are directly linked to greater capacity to store biomass and carbon (Coelho *et al.* 2017, Lutz *et al.* 2018, Ali *et al.* 2020). This result highlights the importance of conserving forest islands, such as the one in the RPSP, not only for flora and biodiversity, but also for maintaining ecosystem services. However, further studies including a larger set of forest islands are needed to confirm these patterns.

In contrast, in the UPA, changes in floristic composition, species diversity, and vegetation structure, resulting from anthropogenic disturbances, reduce its carbon stock. Our results also indicate that anthropogenic disturbances, such as cattle presence and fire, on forest islands lead to homogenization of vegetation structure, resulting in smaller DBHs and greater dominance by some species. As a result, there is a reduction in biodiversity, tree biomass and carbon stocks (Souza *et al.* 2022, Barral *et al.* 2023, Kurtz *et al.* 2024, Antunes *et al.* 2025).

Recent research indicates that AGC accumulation is strongly influenced by species richness and composition (Bryant *et al.* 2024). These findings highlight the importance of species diversity in maximizing carbon stocks (Morandi *et al.* 2020, Pichler *et al.* 2022, Carvalho *et al.* 2024), as corroborated by our results. In our results, we found some carbon-hyperdominant species in both areas (*e.g.*, Myrtaceae sp., *R. grandis*, *M. umbellata*, *B. japurensis*, and *B. chrysophylla*, among others) (Table 1). Other studies in Atlantic montane forests have also found species of Lauraceae, Melastomataceae, Myrtaceae and, Primulaceae to be carbon hyperdominant (Antunes *et al.* 2025, Souza *et al.* 2023). In other words, biodiverse ecosystems, such as the PAI, have a greater capacity to sequester carbon than ecosystems with ecologically dominant species that are shorter, have smaller diameters, and have lower wood densities, as was recorded on the UPA.

The AGC values recorded for the PAI are within the documented range for intermediate-elevation Atlantic mountain formations (1,600-1,700 m), such as 120.36 and 170.4 Mg C ha⁻¹ (Souza *et al.* 2023), and also those reported by Antunes *et al.* (2025) of 54-199 Mg C ha⁻¹, and Altomare *et al.* (2025) with a maximum value of 165.48 Mg C ha⁻¹. In contrast, the lowest stock observed in the UPA is close to the lowest values recorded in these studies, which are generally associated to low elevations, environments subject to anthropogenic disturbances, and soils with low phosphorus concentrations. Although we did not include the effects of other environmental variables, other studies have reported a direct relationship between elevation and soil fertility, as well as an inverse relationship between fire occurrence and AGC stocks (Antonelli *et al.* 2018, Souza *et al.* 2021, 2022, Griffiths *et al.* 2021, Antunes *et al.* 2025). These results reinforce the importance of Conservation Units (CUs) for protecting high-elevation forest islands, which are unique and fundamental environments for maintaining ecosystem services. Furthermore, they confirm our hypothesis that disturbed forests have a reduced capacity to sequester carbon, in agreement with previous studies (Gallo *et al.* 2009, Avigliano *et al.* 2019, Bryant *et al.* 2024).

This is the first study to describe the floristic composition and quantify vegetation structure, species diversity, above-ground biomass, and above-ground carbon in Altimontane forest islands of the Espinhaço Range in Brazil. This makes it clear that ERBR forest islands are a priority for future sustainability and conservation efforts (Barros *et al.* 2023). Finally, Protected Areas are especially important for the conservation and protection of tropical Altimontane environments, which remain largely neglected. These include forest islands, which are essential for providing ecosystem services, mitigating the global effects of climate change, and ensuring the quality of life and well-being of the human population. As this study was based on two forest islands, our results should be interpreted within the scope of a case study. Nevertheless, they provide valuable baseline information on the floristic composition, diversity, vegetation structure, and carbon stocks of Altimontane Forest Islands in the Espinhaço Range. These findings highlight the importance of expanding future research to include a larger number of forest islands across different conservation contexts and environmental gradients, to test the generality of the patterns observed here. Although we did not find differences in species diversity, our study demonstrated that the degradation of these ecosystems promotes the replacement of many native species of Altimontane Forest Islands. This result, therefore, highlights the need to protect these areas to conserve biodiversity and maintain the integrity of this unique and fragile ecosystem.

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3818>

Acknowledgements

The authors thank the entire team of researchers from PELDturf (Long-Term Ecological Research Program), GEEBE (Espinhaço Ecology and Biogeography Study Group-Peatlands of the Southern Espinhaço Mountains), PHYVE (Phytogeography Vegetation and Ecology), and CAFESIN (Center for Advanced Studies in Ecological Systems and Interactions). We also thank the team at the Jeanine Felfili Dendrological Herbarium of UFVJM and all other specialists for their support in identifying the species. Finally, we are deeply grateful to the three anonymous reviewers and the editor section, Dr. Guillermo Ibarra Manríquez, whose comments enabled us to improve the manuscript.

Literature cited

- Abbasi UA, Mattsson E, Nissanka SP, Ali A. 2022. Species α -diversity promotes but β -diversity restricts aboveground biomass in tropical forests, depending on stand structure and environmental factors. *Journal Of Forestry Research* **34**: 889-901. DOI: <http://dx.doi.org/10.1007/s11676-022-01560-8>
- Ab'Saber AN. 1967. Domínios morfoclimáticos e províncias fitogeográficas do Brasil. *Orientação* **3**: 45-48.
- Ali A, Mattsson E, Nissanka SP, Wang Li-Qiu. 2020. Topmost trees and foremost species underlie tropical forest structure, diversity and biomass through opposing mechanisms. *Forest Ecology and Management* **473**: 118299. DOI: <http://dx.doi.org/10.1016/j.foreco.2020.118299>
- Amorim BS, Vasconcelos TNC, Souza G, Alves M, Antonelli A, Lucas E. 2019. Advanced understanding of phylogenetic relationships, morphological evolution and biogeographic history of the mega-diverse plant genus *Myrcia* and its relatives (Myrtaceae: myrteae). *Molecular Phylogenetics and Evolution* **138**: 65-88. DOI: <http://dx.doi.org/10.1016/j.ympev.2019.05.014>
- Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**: 32-46. DOI: <http://dx.doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **62**: 245-253. DOI: <http://dx.doi.org/10.1111/j.1541-0420.2005.00440.x>
- Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A, Muellner-Riehl AN, Kreft H, Linder HP, Badgley C, Fjeldsø J. 2018. Geological and climatic influences on mountain biodiversity. *Nature Geoscience* **11**: 718-725. DOI: <http://dx.doi.org/10.1038/s41561-018-0236-z>
- Antunes K, Villa PM, Caldeira N, Ribeiro JHC, Santana LD, Carvalho FA. 2025. Large-sized trees and altitude drive aboveground carbon stock in Brazilian Atlantic Cloud Forests: An approach based on carbon hyperdominant taxa. *Science of the Total Environment* **962**: 178448. DOI: <https://doi.org/10.1016/j.scitotenv.2025.178448>
- APG [Angiosperm Phylogeny Group]. 2016. An update of the Angiosperm Phylogeny Group Classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean*. DOI: <https://doi.org/10.1111/boj.12385>
- Avigliano E, Rosso JJ, Lijtmaer D, Ondarza P, Piacentini L, Izquierdo M, Cirigliano A, Romano G, Bustos EN, Porta A, Mabragaña E, Grassi E, Palermo J, Bukowski B, Tubaro P, Schenone N. 2019. Biodiversity and threats in unprotected areas: A multidisciplinary and multi-taxa approach focused on the Atlantic Forest. *Heliyon* **5**. DOI: <https://doi.org/10.1016/j.heliyon.2019.e02292>
- Altomare M, Pereira AL, Borges ÉR, Nunes M, Antunes K, Carvalho FA. 2025. From litter to trees: estimating the total carbon stock in a secondary Brazilian Atlantic Forest. *Forests Trees and Livelihoods* **34**: 233-244. DOI: <https://doi.org/10.1080/14728028.2025.2484578>
- Humboldt AV, Bonpland A. 1805. Essai sur la géographie des plantes: accompagné d'un tableau physique des régions

- équinoxiales, fondé sur des mesures exécutées, depuis le dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant les années 1799, 1800, 1801, 1802 et 1803. Paris: Editorial Maxtor. DOI: <https://doi.org/10.5962/bhl.title.9309>
- Alvarado ST, Fornazari T, Cóstola A, Morellato LPC, Silva TSF. 2017. Drivers of fire occurrence in a mountainous Brazilian Cerrado savanna: Tracking long-term fire regimes using remote sensing. *Ecological Indicators* **78**: 270-281. DOI: <https://doi.org/10.1016/j.ecolind.2017.02.037>
- Bañares-De-Dios G, Macía MJ, Arellano G, Lacerda ÍG, Vega-Álvarez J, Arnelas I, Espinosa CI, Salinas N, Cayuela L. 2024. Woody plant taxonomic, functional, and phylogenetic diversity decrease along elevational gradients in Andean tropical montane forests: environmental filtering and arrival of temperate taxa. *Plant Diversity* **46**: 491-501. DOI: <https://doi.org/10.1016/j.pld.2024.03.005>
- Barral UM, Silva AC, Christófaro C, Costa CR, Tassinari D, Penafort Filho A, Macedo GM, Bispo DFA, Gonçalves TS. 2023. Can anthropization govern the water and carbon dynamics? A case study of peatlands in Serra do Espinhaço Meridional, Brazil. *Wetlands Ecology and Management* **31**: 479-497. DOI: <https://doi.org/10.1007/s11273-023-09929-0>
- Barros FDV, Lewis K, Robertson AD, Pennington RT, Hill TC, Matthews C, Lira-Martins D, Mazzochini GG, Oliveira RS, Rowland L. 2023. Cost-effective restoration for carbon sequestration across Brazil's biomes. *Science of the Total Environment* **876**: 162600. DOI: <https://doi.org/10.1016/j.scitotenv.2023.162600>
- Baselga A. 2012a. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**: 1223-1232. DOI: <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga A, Orme C, David L. 2012b. Betapart: an r package for the study of beta diversity. *Methods in Ecology and Evolution* **3**: 808-812. DOI: <https://doi.org/10.1111/j.2041-210x.2012.00224.x>
- Baselga A. 2016. Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* **8**: 799-808. DOI: <https://doi.org/10.1111/2041-210x.12693>
- Bauer D, Goetz MNB, Müller A, Schmitt JL. 2012. Fenologia de três espécies de *Myrsine* l. em floresta secundária semidecídua no Sul do Brasil. *Revista Árvore* **36**: 859-868. DOI: <https://doi.org/10.1590/s0100-67622012000500008>
- Bispo DFA, Silva AC, Christófaro C, Silva MLN, Barbosa MS, Silva BPC, Barral UM, Fabris JD. 2016. Hydrology and carbon dynamics of tropical peatlands from Southeast Brazil. *Catena* **143**: 18-25. DOI: <https://doi.org/10.1016/j.catena.2016.03.040>
- Bispo DFA, Silva AC, Matosinhos CC, Silva MLN, Barbosa MS, Silva BPC, Barral UM. 2015. Characterization of headwaters peats of the Rio Araçuaí, Minas Gerais State, Brazil. *Revista Brasileira de Ciência do Solo* **39**: 475-489. DOI: <https://doi.org/10.1590/01000683rbc20140337>
- Bryant RL, Kothari S, Cavender-Bares J, Curran SJ, Grossman JJ, Hobbie SE, Nash C, Neumiller GC, See CR. 2024. Independent effects of tree diversity on aboveground and soil carbon pools after six years of experimental afforestation. *Ecological Applications* **34**. DOI: <https://doi.org/10.1002/eap.3042>
- Campos PV, Schaefer CEGR, Senra EO, Viana PL, Candido HG, Oliveira FS, Vale Júnior JF, Villa PM. 2021. Disentangling fine-scale effects of soil properties as key driver of plant community diversity on Roraima Table Mountain, Guayana Highlands. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* **156**: 982-993. DOI: <https://doi.org/10.1080/11263504.2021.1985003>
- Carvalho FA, Altomare M, Pereira AL, Gonçalves L, Pacheco F, Jardim TH, Furtado SG, Souza NC, Candido HMN. 2024. Carbon estimates in a neglected non-forest ecosystem: Aboveground biomass in a tropical cloud savanna in Southeastern Brazil. *Ecological Frontiers* **44**: 1090-1095. DOI: <https://doi.org/10.1016/j.eco-fro.2024.01.009>
- CETEC [Centro Tecnológico de Minas Gerais]. 1995. Determinação de equações volumétricas aplicáveis ao manejo sustentado de florestas nativas do estado de Minas Gerais e outras regiões do país Relatório Final. Belo Horizonte: FAPEMIG/CETEC, 295p.

- Coelho OGA, Castro NSTM, Souza AH, van den Berg E. 2017. What can natural edges of gallery forests teach us about woody community performance in sharp ecotones? *Journal of Plant Ecology* **10**: 937-948. DOI: <https://doi.org/10.1093/jpe/rtw083>
- Coelho MS, Fernandes GW, Pacheco P, Diniz V, Meireles A, Santos RM, Carvalho FA, Negreiros D. 2016. Archipelago of montane forests surrounded by rupestrian grasslands: new insights and perspectives. In: Fernandes G. eds. *Ecology and Conservation of Mountaintop grasslands in Brazil*. Cham: Springer, pp. 129-156. DOI: https://doi.org/10.1007/978-3-319-29808-5_7
- Coelho MS, Carlos PP, Pinto VD, Meireles A, Negreiros D, Morellato LPC, Fernandes GW. 2018a. Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands. *Flora* **238**: 51-59. DOI: <https://doi.org/10.1016/j.flora.2017.04.003>
- Coelho MS, Neves FS, Perillo LN, Morellato LPC, Fernandes GW. 2018b. Forest archipelagos: a natural model of metacommunity under the threat of fire. *Flora* **238**: 244-249. DOI: <https://doi.org/10.1016/j.flora.2017.03.013>
- Costa TR, Moura CC, Machado ELM, Gonzaga APD. 2021a. Flora Arbórea de Capões na Reserva da Biosfera da Serra do Espinhaço. *Revista Espinhaço* **1**. DOI: <https://doi.org/10.5281/zenodo.5104405>
- Costa TR, Moura CC, Silva LS, Gonzaga APD, Machado ELM. 2021b. Funcionalidade de ilhas florestais na reserva da biosfera da serra do espinhaço. *Pesquisa e Desenvolvimento de Abordagens Para O Ensino de Ciências Biológicas* **1**: 93-108. DOI: <https://doi.org/10.51859/amplla.pda351.1121-8>
- Costa TR, Silva CC, Henrique C, Bueno ML, Mucida DP, Santos T, Priscila APD. 2022. Vulnerability of the Cerrado–Atlantic Forest ecotone in the Espinhaço Range Biosphere Reserve to climate change. *Theoretical and Applied Climatology* **151**: 1151-1170. DOI: <https://doi.org/10.1007/s00704-022-04321-z>
- Costa TR, Moura CC, Silva LS, Gonzaga APD, Rech AR, Machado ELM. 2023. Environmental factors determining the forest–grassland variation in the Espinhaço Range Biosphere Reserve-Brazil. *Journal of Plant Ecology* **16**. DOI: <https://doi.org/10.1093/jpe/rtac089>
- Cowie RH, Bouchet P, Fontaine B. 2022. The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews* **97**: 640-663. DOI: <https://doi.org/10.1111/brv.12816>
- Cunha-Blum J, Ramos L, Negreiros D, Paiva DC, Gomes VM, Borges LM, Teles AM, Fernandes GW. 2025. Towards the reference ecosystems for quartzitic campo rupestre: Floristic composition and soil relationships. *Ecological Engineering* **211**: 107463-107463. DOI: <https://doi.org/10.1016/j.ecoleng.2024.107463>
- Chao A, Chiu C, Jost L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics* **45**: 297-324. DOI: <https://doi.org/10.1146/annurev-ecolsys-120213-091540>
- Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrizar A, Mugasha AW, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Péliissier R, Ploton R, Ryan CM, Saldarriaga JG, Vieilledent G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* **20**: 3177-3190. DOI: <https://doi.org/10.1111/gcb.12629>
- Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117-143. DOI: <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- CNCFlora. 2024. Lellingeria suspensa in Lista Vermelha da flora brasileira versão 2012.2 Centro Nacional de Conservação da Flora. <https://floradobrasil.jbrj.gov.br/consulta/ficha.html?idDadosListaBrasil=91632> (accessed October 23, 2024).
- Cribari-Neto F, Zeileis A. 2010. Beta Regression in R. *Journal of Statistical Software* **34**: 1-24. DOI: <https://doi.org/10.18637/jss.v034.i02>
- Da Silva FR, Gonçalves-Souza T, Paterno GB, Provete DB, Vancine MH. 2022. Análises ecológicas no R. *Nupee: Recife, PE, Canal 6: São Paulo*. <https://analises-ecologicas.com/>. (accessed October 23, 2024).
- Donoghue MJ. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* **105**: 11549-11555. DOI: <https://doi.org/10.1073/pnas.0801962105>

- Felfili JM, Rezende RP. 2005. *Conceitos e métodos em fitossociologia*. Brasília: UNB, 2003. 68 p. (Comunicações Técnicas Florestais - ISSN, v.5, n.1).
- Fernandes GW, Bahia TO, Almeida HA, Conceição AA, Loureiro CG, Luz GR, Neves ACO, Oki Y, Pereira GCN, Pirani JR. 2020. Floristic and functional identity of rupestrian grasslands as a subsidy for environmental restoration and policy. *Ecological Complexity* **43**: 100833. DOI: <https://doi.org/10.1016/j.ecocom.2020.100833>
- Ferreira MA, França LCJ, Moraes MS, Gontijo BM, Gorgens EB, Mucida DP. 2022. Conflitos do uso da terra em áreas protegidas por lei no Parque Estadual do rio Preto e Zona de amortecimento, Minas Gerais. *Caderno de Geografia* **32**: 377. DOI: <https://doi.org/10.5752/p.2318-2962.2022v32n68p377>
- Françoso RD, Brandão R, Nogueira CC, Salmona YB, Machado RB, Colli GR. 2015. Habitat loss and the effectiveness of protected areas in the Cerrado biodiversity hotspot. *Natureza & Conservação* **13**: 35-40. DOI: <https://doi.org/10.1016/j.ncon.2015.04.001>
- Françoso RD, Haidar RF, Machado RB. 2016. Tree species of South America central savanna: endemism, marginal areas and the relationship with other biomes. *Acta Botanica Brasilica* **30**: 78-86. DOI: <https://doi.org/10.1590/0102-33062015abb0244>
- Flora e Funga do Brasil. 2024. Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/> (accessed December 12, 2024).
- Gallo JA, Pasquini L, Reyers B, Cowling RM. 2009. The role of private conservation areas in biodiversity representation and target achievement within the Little Karoo region, South Africa. *Biological Conservation* **142**: 446-454. DOI: <https://doi.org/10.1016/j.biocon.2008.10.025>
- Gonçalves TS, Mendonça Filho CV, Silva AC. 2023. Deposição de serrapilheira em Capões de Mata associados a turfeiras na Serra do Espinhaço Meridional - Parque Estadual do Rio Preto, MG. *Terr@ Plural* **17**: e2321063. <https://revistas.uepg.br/index.php/tp/article/view/21063>. (accessed October 23, 2024).
- Gonçalves S, Silva C, Filho VM, Costa R, Braga L. 2020. The Capões of seasonal semi-deciduous forest in the Cerrado and rupestrian fields of the Espinhaço chain. *International Journal of Geoscience, Engineering and Technology* **1**: 43-48. DOI: <https://revistas.ufvjm.edu.br/ijget/article/view/366>
- Griffiths AR, Silman MR, Farfan-Rios W, Feeley KJ, Cabrera KG, Meir P, Salinas N, Segó RAS, Dexter OKG. 2021. Evolutionary diversity peaks at mid-elevations along an Amazon-to-Andes elevation gradient. *Frontiers in Ecology and Evolution* **9**: 1-10. DOI: <https://doi.org/10.3389/fevo.2021.680041>
- Guerrini IA, Silva JP, Sivilsaca DCL, Moraes FG, Puglla CAY, Neto CMS, Silva RB, Justino STP, Roder LR, James JN, Capra GF. 2024. Evaluating carbon stocks in soils of fragmented Brazilian Atlantic Forests (BAF) based on soil features and different methodologies. *Scientific Reports* **14**: 10007. DOI: <https://doi.org/10.1038/s41598-024-60629-y>
- INMET [Instituto Nacional de Meteorologia]. 2023. *Ministério da Agricultura Pecuária e Abastecimento*. <https://www.inmet.gov.br> (accessed October 19, 2025).
- IPCC [Intergovernmental Panel on Climate Change]. 2014. Synthesis Report. 2014. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Pachauri RK, Meyer LA. eds. IPCC: Geneva, Switzerland. ISBN (Print 9789291691432).
- IUSS [International Union of Soil Sciences] Working Group WRB. 2022. World Reference Base for Soil Resources: International Soil Classification System for Naming Soils and Creating Legends for Soil Maps, Vienna Austria: IUSS. ISBN 979-8-9862451-1-9
- IUCN [The International Union for Conservation of Nature]. 2024. The IUCN Red List of Threatened Species. Version 2024-21. <https://www.iucnredlist.org> (accessed October 19, 2025).
- Jost L. 2006. Entropy and diversity. *Oikos* **113**: 363-375. DOI: <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kurtz BC, Almeida TMH, Coelho MAN, Deccache LSJ, Tortorelli RM, Gonzaga DR, Madureira LK, Guedes-Oliveira R, Barros CF, Siqueira MF. 2024. Quantifying the Carbon Stocks in Urban Trees: the Rio de Janeiro botanical garden as an important tropical carbon sink. *Journal of Zoological and Botanical Gardens* **5**: 579-589. DOI: <https://doi.org/10.3390/jzbg5040039>

- Li D. 2018. HillR: taxonomic, functional, and phylogenetic diversity and similarity through hill numbers. *Journal of Open Source Software* **3**: 1041. DOI: <https://doi.org/10.21105/joss.01041>
- Liu B, Bu W, Zang R. 2023. Improved allometric models to estimate the aboveground biomass of younger secondary tropical forests. *Global Ecology and Conservation* **41**: 1-11. DOI: <https://doi.org/10.1016/j.gecco.2022.e02359>
- Lima RAF, Oliveira AA, Pitta GR, Gasper AL, Vibrans AC, Chave J, ter Steege H, Prado PI. 2020. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. *Nature Communications* **11**: 6347. DOI: <https://doi.org/10.1038/s41467-020-20217-w>
- Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D. 2021. Performance: an r package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* **6**: 3139. DOI: <https://doi.org/10.21105/joss.03139>
- Lutz JA, Furniss TJ, Johnson DJ, Davies SJ, Allen D, Alonso A, Anderson-Teixeira KJ, Andrade A, Baltzer J, Becker KML *et al.* 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography* **27**: 849-864. DOI: <https://doi.org/10.1111/geb.12747>
- MacArthur RH, Wilson EO. 1963. An equilibrium theory of island biogeography. *Evolution* **17**: 373-387. DOI: <https://doi.org/10.2307/2407089>
- Magalhães JHR, Junior JAP, Vale VS, Schiavini I. 2018. Dinâmica do estrato arbóreo em uma floresta Estacional Semidecidual em Uberlândia, Minas Gerais, Brasil. *Iheringia, Série Botânica* **72**: 394-402. DOI: <https://isb.emnuvens.com.br/iheringia/article/view/655> (accessed January 25, 2025).
- Magurran AE. 2004. *Measuring Biological Diversity*. Oxford: Blackwell Publishing. 256 p. ISBN: 0-632-05633-9
- Mittermeier RA, Gil RP, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Fonseca GAB. 2005. *Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions*. Chicago, Illinois, USA: ISBN: 968-6397-77-9.
- Montes ML, Horák-Terra I, Mercader RC, Silva AC, Errico LA, Taylor MA. 2023. Inventories, profiles, and deposition fluxes of 210Pb in mineral and organic (peatlands) Southern Hemisphere soils. *Journal of South American Earth Sciences* **124**: 104276. DOI: <https://doi.org/10.1016/j.jsames.2023.104276>
- Morandi PS, Marimon BS, Marimon-Junior BH, Ratter JA, Feldpausch TR, Colli GR, Munhoz, CBR, Silva Júnior MC, Lima ES, Haidar RF. 2020. Tree diversity and above-ground biomass in the South America Cerrado biome and their conservation implications. *Biodiversity And Conservation* **29**: 1519-1536. DOI: <https://doi.org/10.1007/s10531-018-1589-8>
- Morellato LPC, Silveira FAO. 2018. Plant life in campo rupestre: new lessons from an ancient biodiversity hotspot. *Flora* **238**: 1-10. DOI: <https://doi.org/10.1016/j.flora.2017.12.001>
- Moura CC, Costa TR, Oliveira PA, Fonseca DC, Machado ELM. 2021. Como é a estrutura e a diversidade alpha e beta de matas de galeria inundáveis? *Diversitas Journal* **6**: 1920-1945. DOI: <https://doi.org/10.17648/diversitas-journal-v6i2-1496>
- Moura CC, Costa TR, da Costa Fonseca D, da Silva LS, Fonseca SN, Oliveira PA, de Moura LC, Gonzaga APD, de Freitas Milani JE, de Castro GC, Machado ELM. 2025. Phenology of *Richeria grandis* Vahl: A dioecious species with wide geographical distribution and unique environmental specificity. *Plant Species Biology* **40**: 452-471. DOI: <https://doi.org/10.1111/1442-1984.70022>
- Mucida DP, Moraes MS, Matosinhos CC, Nunes TKMR, Sperandio HV, Santana RC, Gorgens E. B. 2022. *Zoneamento ambiental e produtivo: bacia hidrográfica do Rio Preto-MG*. Diamantina: Universidade Federal dos Vales do Jequitinhonha e Mucuri (UFVJM), 189 p. ISBN: 978-65-87258-77-5.
- Mueller-Dombois D, Ellenberg H. 1976. Aims and Methods of Vegetation Ecology. *Geographical Review* **66**: 114. DOI: <https://doi.org/10.2307/213332>
- Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858. DOI: <https://doi.org/10.1038/35002501>
- Neves DM, Dexter KG, Pennington RT, Bueno ML, Miranda PLS, Oliveira-Filho AT. 2018. Lack of floristic identity

- in campos rupestres-A hyperdiverse mosaic of rocky montane savannas in South America. *Flora* **238**: 24-31. DOI: <https://doi.org/10.1016/j.flora.2017.03.011>
- Oliveira Filho AT, Scolforo JRS. 2008. Inventário Florestal de Minas Gerais: Espécies Arbóreas da Flora Nativa. Brazil: Lavras: Editora Ufla. ISBN: 8587692607
- Pereira GCN, Coelho MS, Beirão MV, Braga RF, Fernandes GW. 2017. Diversity of fruit-feeding butterflies in a mountaintop archipelago of rainforest. *Plos One* **12**: e0180007. DOI: <https://doi.org/10.1371/journal.pone.0180007>
- Pichler V, Gömöryová E, Merganič J, Fleischer P, Homolák M, Onuchin A, Výboštok J, Prosekin K. 2022. Interrelationships among mountain relief, surface organic layer, soil organic carbon, and its mineral association under subarctic forest tundra. *Scientific Reports* **12**: 17252. DOI: <https://doi.org/10.1038/s41598-022-21521-9>
- Pinto TAA, Tassinari D, Horák-Terra I, Barral UM, Silva AC. 2023. Imputação e análise da série de dados meteorológicos da região da Chapada do Couto, Serra do Espinhaço, Minas Gerais, Brasil. *Revista Espinhaço* **12**: 1-15. DOI: <https://doi.org/10.5281/zenodo.7868629>
- R Core Team. 2024. A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*, Vienna, Austria. Available at: <https://www.R-project.org/>
- Ribeiro JHC, Santana LD, Carvalho FA. 2018. Composition, Structure and biodiversity of Trees in Tropical Montane Cloud Forest Patches in Serra do Papagaio State Park, Southeast Brazil. *Edinburgh Journal of Botany* **75**: 255-284. DOI: <https://doi.org/10.1017/s0960428618000082>
- Rios MNS, Sousa-Silva JC, Malaquias JV. 2018. Mudanças pós-fogo na florística e estrutura da vegetação arbóreo-arbustiva de um cerrado sentido restrito em planaltina, df. *Ciência Florestal* **28**: 469-482. DOI: <https://doi.org/10.5902/1980509832028>
- Rosindell J, Hubbell SP, Etienne RS. 2011. The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology and Evolution* **26**: 340-348. DOI: <https://doi.org/10.1016/j.tree.2011.03.024>
- Salomão NV, Da Silva LS, Costa TR, Blum JC, Mucida DP, Moraes M, Da Silva MD, Fernandes GW, Machado E. 2023. Landscape and Vegetation Changes to Areas of Savanna Submitted to Different Fire Intervals in Parque Nacional dos Sempre Vivas, Brazil. *Preprints*. DOI: <https://doi.org/10.20944/preprints202308.1027.v1>
- Silveira FAO, Barbosa M, Beiroz W, Callisto M, Macedo DR, Patrícia L, Neves FS, Yule RFN, Solar RR, Fernandes GW. 2019. Tropical mountains as natural laboratories to study global changes: A long-term ecological research project in a megadiverse biodiversity hotspot. *Perspectives in Plant Ecology, Evolution and Systematics* **38**: 64-73. DOI: <https://doi.org/10.1016/j.ppees.2019.04.001>
- Soil Survey Staff. 2010. *Soil Taxonomy: Keys to Soil Taxonomy*. Washington: United States Department of Agriculture.
- Souza CR, Paula GGP, Mendes CN, Maia VA, Aguiar-Campos N, Araújo FC, Mariano RF, Oliveira HF, Morel JD, Santos RM. 2020. Local-scale tree community ecotones are distinct vegetation types instead of mixed ones: a case study from the Cerrado: Atlantic forest ecotonal region in Brazil. *Australian Journal of Botany* **68**: 153. DOI: <https://doi.org/10.1071/bt19108>
- Souza CR, Maia VA, Natália de Aguiar-Campos, Alisson BM, Santos AFR, Rodrigues AF, Farrapo CL, Gianasi, FM, Paula GP, Fagundes NCA, Silva WB, Santos RM. 2021. Long-term ecological trends of small secondary forests of the Atlantic forest hotspot: A 30-year study case. *Forest Ecology and Management* **489**: 119043-119043. DOI: <https://doi.org/10.1016/j.foreco.2021.119043>
- Souza CR, Maia VA, Mariano RF, Coelho de Souza F, Araújo FC, Paula GGP, Menino GCO, Coelho PA, Santos PF, Morel JD, Santos RM. 2022. Tropical forests in ecotonal regions as a carbon source linked to anthropogenic fires: A 15-year study case in Atlantic forest – Cerrado transition zone. *Forest Ecology and Management* **519**: 120326. DOI: <https://doi.org/10.1016/j.foreco.2022.120326>
- Souza CR, Mariano RF, Maia VA, Pompeu PV, Santos AM. 2023. Carbon stock and uptake in the high-elevation tropical montane forests of the threatened Atlantic Forest hotspot: Ecosystem function and effects of elevation variation. *The Science of the Total Environment* **882**: 163503-163503. DOI: <https://doi.org/10.1016/j.scitotenv.2023.163503>
- Sullivan MJP, Phillips OL, Galbraith D, Almeida E, de Oliveira EA, Almeida J, Dávila EÁ, Alves LF, Andrade A,

- Aragão L, Araujo-Murakami A, Arets E, Arroyo L, Cruz OAM, Baccaro F, Baker TR, Banki O, Baraloto C, Barlow J, Barroso J. 2025. Variation in wood density across South American tropical forests. *Nature Communications* **16**. DOI: <https://doi.org/10.1038/s41467-025-56175-4>
- Scolforo HF, Roberto J, Marcio J, Rogerio C, Morais VA. 2016. Spatial interpolators for improving the mapping of carbon stock of the arboreal vegetation in Brazilian biomes of Atlantic forest and Savanna. *Forest Ecology and Management* **376**: 24-35. DOI: <https://doi.org/10.1016/j.foreco.2016.05.047>
- Tassinari D, Christofaro C, Barral UM, Costa CR, Pinto AWJ, Silva CÉP, Silva AC. 2025. Multiyear temperature variation in tropical mountain peatlands from the southern Espinhaço Mountain Range in Brazil. *Journal of Mountain Science* **22**: 820-837. DOI: <https://doi.org/10.1007/s11629-024-8973-5>
- Vargas-Larreta B, López-Martínez JO, González EJ, Corral-Rivas JJ, Hernández FJ. 2021. Assessing above-ground biomass-functional diversity relationships in temperate forests in northern Mexico. *Forest Ecosystems* **8**. DOI: <https://doi.org/10.1186/s40663-021-00282-3>

Associate editor: Guillermo Ibarra Manríquez

Author contributions: RSC, research design, database compilation, data analysis, and manuscript writing, review, and editing; JCF, supervision, guidance, critical review and writing of the article; GHOM, article writing and data analysis; ELMM, article writing; ARR, article writing and supervision; MLRMO, support in data analysis, manuscript review and article writing; JRP, review and writing of the article; APDG general supervision, guidance, critical review and writing of the article. All authors contributed to the writing, discussion, review and approval of the final manuscript.

Supporting agencies: This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, RSC doctoral scholarship, and by UFVJM institutional support. We acknowledge that coauthors' research activities were supported by FAPEMIG (projects APQ-01284-22, APQ-02799-21, APQ-02806-22, RED-00039-23, APQ-03364-21, APQ-01151-22, APQ-01822-21, and to the INCT Pollination (CNPq/CAPES/FAPERJ Call 58/2022). The authors JRR Pinto and ARR are grateful to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for the support of productivity scholarships (Grant No. 312571/2021-6 and 311665/2022-5 respectively).

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.