



Research Letters

Topographic drivers of anthropization in the Brazilian Atlantic Forest

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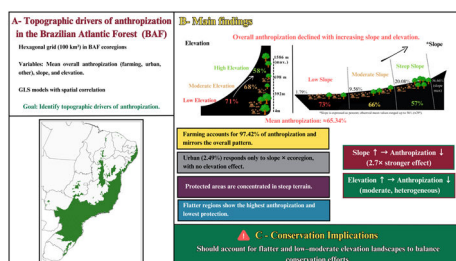
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HIGHLIGHTS

- Overall anthropization decreases with increasing slope and elevation.
- Anthropization is strongly constrained by slope; elevation effects are moderate and variable.
- Farming drives most anthropization and follows overall constraints.
- Urbanization responds to slope and ecoregions but not to elevation.
- Protected areas are concentrated in steeper terrain.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropization is a major driver of environmental change in tropical forests and is influenced by non-random factors, including topographic constraints. The Brazilian Atlantic Forest (BAF) is a highly fragmented biodiversity hotspot facing intense anthropogenic pressure. Here, we evaluated how elevation and slope mediate anthropization patterns across the BAF ecoregions. We quantified overall anthropized land (mostly farming and, secondarily, urban), slope, and elevation within a 100-km² hexagonal grid. A generalized least squares (GLS) model indicated that overall anthropization was driven by slope and elevation, without interaction with ecoregions. Anthropization (65% of the BAF) decreased with increasing slope and elevation, with slope having a 2.7-times stronger and less variable effect than elevation. Farming, responsible for 97% of all anthropized areas, followed the overall pattern. Urban land-use was driven by a slope × ecoregion interaction, with no detectable effect of elevation. Protected areas were disproportionately concentrated in steeper terrain, which also favors natural regeneration. In contrast, anthropization is most intense in flatter, low- and moderate-elevation regions, driven primarily by farming expansion. This mismatch reveals a persistent topographic bias: protected areas tend to safeguard lands of low farming suitability, while leaving the most pressured landscapes underrepresented and with ecosystem services most threatened. Addressing this imbalance is essential for promoting more effective and equitable conservation strategies in the BAF.

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Introduction

Tropical forests are among the most critical biodiversity refuges globally (Barlow et al., 2018; Pillay et al., 2022). However, they are also undergoing extensive deforestation because of expanding anthropization through different human activities such as urban development and farming (Global Forest Watch, 2024; Hansen et al., 2013). Deforestation in tropical forests is typically non-random and is influenced by economic interests, accessibility, topography, and road infrastructure (Geist and Lambin, 2002). Understanding the spatial drivers of deforestation is critical for conservation and restoration efforts.

The Atlantic Forest (AF) is one of the most biodiverse tropical forests in the world, harboring about 8% of the planet's biodiversity (Silva and Casteleti, 2003; Myers et al., 2000). However, it is also one of the most impacted by human occupation (Joly et al., 2014; Ribeiro et al., 2011). Originally, the AF extended across eastern Brazil, northern Argentina, and southeastern Paraguay (Muylaert et al., 2018), with at least eight biogeographic sub-regions identified (Silva and Casteleti, 2003; Olson et al., 2001; Tabarelli et al., 2010). However, human occupation over the past 12,000 years, along with Portuguese colonization, industrialization, and urbanization, has significantly altered the AF's natural habitats (Dean, 2003; Joly et al., 2014; Solórzano et al., 2021). Currently, estimates indicate that about 28–36.3% of the original AF natural vegetation cover remains (Rezende et al., 2018; Vancine et al., 2024), as a mosaic of highly fragmented remnants separated by a matrix of degraded areas (Joly et al., 2014).

Given its high levels of diversity, endemism, and habitat loss, the AF is recognized as a global biodiversity hotspot (Myers et al., 2000; Rezende et al., 2018; Ribeiro et al., 2011). This combination provides a strong rationale for investigating the factors driving anthropization (i.e., human-induced land-use change) in AF, as anthropization is driven by non-random factors (Busch and Ferretti-Gallon, 2017; Tabarelli et al., 2010). Due to the AF's topographic complexity (Peres et al., 2020) and the historical exploitation of natural resources, biophysical factors, especially elevation and slope, have influenced deforestation patterns (Tabarelli et al., 2010). Although some studies have documented associations between anthropization and topographic variables, particularly the tendency of higher altitudes and steeper slopes to retain more forest cover (e.g., Precinoto et al., 2022; Santos et al., 2024; Teixeira et al., 2009), these patterns were reported only in local scales. To date, no study has yet directly quantified the potential associations between anthropization and elevation or slope across AF ecoregions.

Here, we identified the main topographic drivers of anthropization in the AF ecoregions, by analyzing the relationships between anthropization, elevation, and slope. We hypothesized that anthropization would decrease with increasing slope and elevation. In addition, we expected that ecoregions with greater topographic complexity would exhibit more heterogeneous patterns. Our goal was to characterize anthropogenic land-use patterns, and the distribution of protected areas across AF ecoregions, and to assess their relationships with topographic factors to inform conservation planning in this complex tropical forest.

Methods

The AF originally covered approximately 1.62 million km² within its integrative boundaries (Muylaert et al., 2018). The AF's elevation ranges from sea level to 2,891 m, encompassing a wide variety of topographic features (Silva and Casteleti, 2003). Analysis were conducted within the biogeographic ecoregions of the AF (Olson et al., 2001) using the integrative boundaries (Muylaert et al., 2018). We excluded portions of Argentina and Paraguay and created a hexagonal grid (100 km² per hexagon) for the Brazilian Atlantic Forest (BAF). We removed hexagons that were (i) not entirely within the BAF (<100 km²), (ii) overlapped more than one ecoregion, or (iii) fell within the Cerrado biome. We also restricted the analyses to ecoregions with ≥ 100 valid hexagons. The final study grid comprised 8683 valid hexagons across

eight BAF ecoregions (Fig. 1).

Land-use, elevation, and slope rasters at 1 arc-second (~30 m) resolution were obtained for Brazil (MapBiomass Collection, 2025; Topodata, 2024). The mean values of anthropized area, elevation, and slope were calculated for each hexagon. Slope is expressed as percentage: $100 \times (\text{rise}/\text{run})$, where rise is the vertical elevation difference between adjacent pixels and run is the horizontal distance (Valeriano, 2008; Valeriano and Albuquerque, 2010). This percentage can be converted to degrees using $\arctan(\text{rise}/\text{run})$. In our dataset, the maximum mean slope among hexagons was 56%, which corresponds to $\sim 29^\circ$. No anomalous values were detected.

For the land-use map, we reclassified the original 38 categories into four classes: (1) non-anthropized areas (forests, other natural vegetation categories, lakes, beaches), (2) farming areas (all agricultural and pasture categories combined), (3) urban areas, and (4) other anthropized areas (mining, aquaculture, and photovoltaic plants). Overall anthropization was defined as the sum of the three anthropized classes (farming + urban + other). Agriculture and pasture were aggregated as farming because they were indistinguishable in many pixels. Thus, mean overall anthropization in hexagons ranged from 0 to 1, with continuous values, where 0 indicated no anthropization and 1 indicated full anthropization (Fig. 1B). We focused on overall anthropization as the dependent variable rather than native vegetation cover, because it reflects human-induced land-use changes more comprehensively, whereas native vegetation does not account for non-native, non-anthropized areas (e.g., lakes).

For descriptive summaries and maps, hexagon values for each predictor (slope and elevation) were ordered from minimum to maximum and partitioned into three quantile-based categories, each containing $\sim 1/3$ of all hexagons ($n \approx 2894$ per class). This approach avoids uneven sample sizes and arbitrary class boundaries. For slope, the resulting categories were Low Slope (1.79–9.56%), Moderate Slope (9.57–20.07%), and Steep Slope (20.08–56.66%) (Fig. 1C). For elevation, the resulting categories were Low Elevation (3.66–392.32 m), Moderate Elevation (392.44–697.82 m), and High Elevation (698.06–1585.86 m) (Fig. 1D).

We first built a set of Generalized Least Squares (GLS) models to test for the best structure to account for spatial autocorrelation in overall anthropization (first GLS round). Overall anthropization was treated as a continuous dependent variable. Elevation and slope were included as continuous independent variables, because they were only weakly correlated (Pearson's $r = 0.21$); their interaction with ecoregion was also considered, resulting in a full "interaction" model. Several spatial correlation structures were tested for this model, including exponential, linear, Gaussian, spherical, and ratio. A null model without spatial structure was also included. AICc comparisons identified the exponential correlation structure as the best-performing option, and the resulting model presented normally distributed residuals (Table A1). Subsequently, we fixed the exponential structure and tested a second suite of GLS ecological models, containing all combinations of elevation, slope, ecoregions, and their interactions (second GLS round). Ten candidate models plus a null model were evaluated in this second step. The geographic coordinates (latitude and longitude) of each hexagon's centroid were used in the spatial autocorrelation analyses.

We repeated the same analyses for farming and urban separately, treating each as continuous dependent variable. Farming was strongly correlated with overall anthropization ($r = 0.96$), whereas urban showed a weak correlation ($r = 0.12$). The exponential structure was again the best-fitting spatial model for both farming and urban (Tables A2, A4). The "other" category was not analyzed with GLS models because it occupies a negligible portion of the biome (0.06% of all pixels; Table A6), resulting in extremely sparse and zero-inflated distributions unsuitable for model fitting.

After selecting the best ecological model for each response variable (overall anthropization, farming, and urban), we quantified standardized effect sizes to compare the relative importance of elevation and

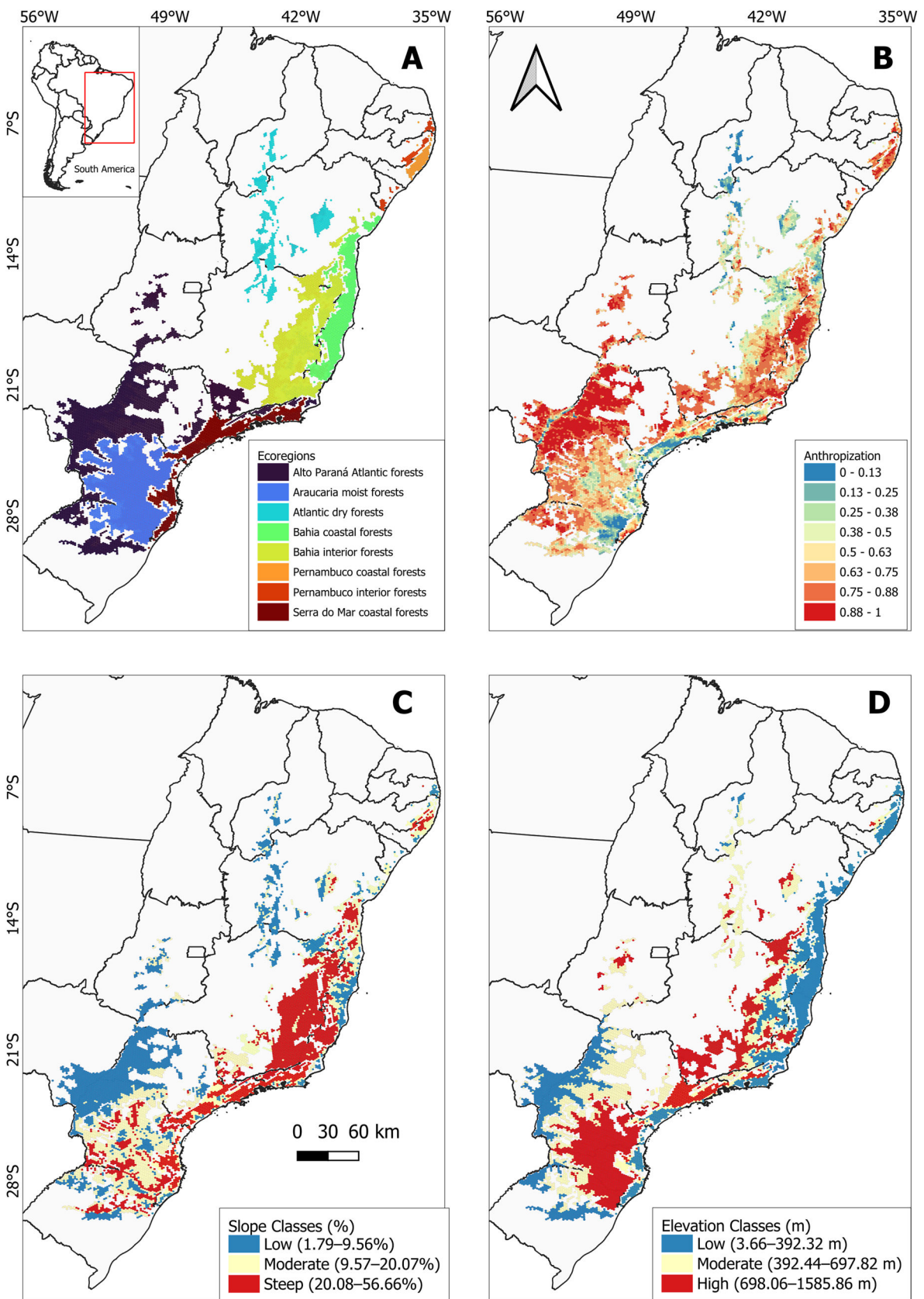


Fig. 1. Spatial distribution of land-use and topographic variables across the Brazilian Atlantic Forest: (A) ecoregions, (B) overall anthropization (%), (C) slope classes (%), and (D) elevation classes (m).

slope. Standardized coefficients were computed by multiplying each raw coefficient by the ratio of the predictor’s standard deviation to the standard deviation of model-predicted values. Standardized coefficients thus express how much anthropized or farming or urban area changes (in SD units) in response to a one-standard-deviation increase in each predictor.

Although the best-fit ecological model for overall anthropization did not include interactions with ecoregions, we used the full interaction model (including both predictors and their interactions with ecoregion) for visualization purposes (see second-ranked model in Table 1). This interaction model allowed us to illustrate how slope and elevation effects vary for each dependent variable across ecoregions. Ecoregion-specific effects were summarized using a forest plot of standardized coefficients from the interaction model. We then generated partial-effect plots for slope and elevation by predicting overall anthropization while holding the non-focal predictor (either slope or elevation) at its median. Partial residuals (predicted + residual) were added to illustrate within-ecoregion variation. We repeated this approach using the interaction model for farming and urban areas (Tables A3 and A5).

Additionally, we identified hexagons that were entirely or partially within Brazilian protected areas (MapBiomias, 2024) to investigate potential topographic biases in protection. For each slope and elevation quantile class, we quantified the proportion of protected hexagons and calculated cross-class means (i.e., mean slope within elevation classes and mean elevation within slope classes). These summaries allowed us to assess whether protection was disproportionately concentrated in steep or high-elevation terrain. We also calculated the total area of protected areas within the integrated BAF boundaries. All spatial data and analyses were projected using the Albers Equal Area Conic Brazil (ESRI:102033) coordinate system and the QGIS 3.40.1 software. All analyses were performed in R 4.5.0 using the nlme, MuMIn, and ggplot2 packages. Data and reproducible scripts are available in an online repository (see Data Availability Statement; <https://github.com/guilhermrs/BAF-Anthropization>).

Results

Overall anthropization

The model containing elevation + slope, without interactions, had the lowest AICc and was selected as the best-fit ecological model for explaining overall anthropization in the BAF (Table 1). Standardized coefficients showed that slope had the strongest negative effect on anthropization (-0.88 ± 0.02), whereas elevation also contributed substantially but with a more moderate and variable effect (-0.32 ± 0.04). A one-standard deviation increase in slope ($\approx 10.16\%$) reduced anthropization by 0.11 (≈ 11 percentage points), whereas a one-standard deviation increase in elevation (≈ 290 m) reduced anthropization by 0.04 (≈ 4 percentage points). Thus, slope exerted an effect approximately 2.7 times stronger than elevation across the BAF.

Table 1

Results of the model selection based on Akaike Information, used to evaluate the factors influencing overall anthropization in the Brazilian Atlantic Forest. The models are ranked from best to worst based on Δ AICc values. The columns represent the model structure, degrees of freedom (df), log-likelihood (logLik), corrected AIC (AICc), difference in AICc relative to the top model (Δ AICc), and model weight.

Model combination	df	logLik	AICc	Δ AICc	Weight
Elevation + Slope	5	7941.788	-15873.6	0	1
Elevation + Slope + Ecoregion: Elevation + Ecoregion:Slope	19	7947.508	-15856.9	16.64	0
Elevation + Slope + Ecoregion	12	7940.035	-15856	17.53	0
Slope	4	7909.67	-15811.3	62.23	0
Slope + Ecoregion	11	7910.358	-15798.7	74.88	0
Slope: Ecoregion	18	7903.584	-15771.1	102.48	0
Elevation:Ecoregion	18	7416.131	-14796.2	1077.39	0
Elevation	4	7332.27	-14656.5	1217.03	0
Elevation + Ecoregion	11	7332.064	-14642.1	1231.47	0
None	3	7200.799	-14395.6	1477.97	0
Ecoregion	10	7201.185	-14382.3	1491.22	0

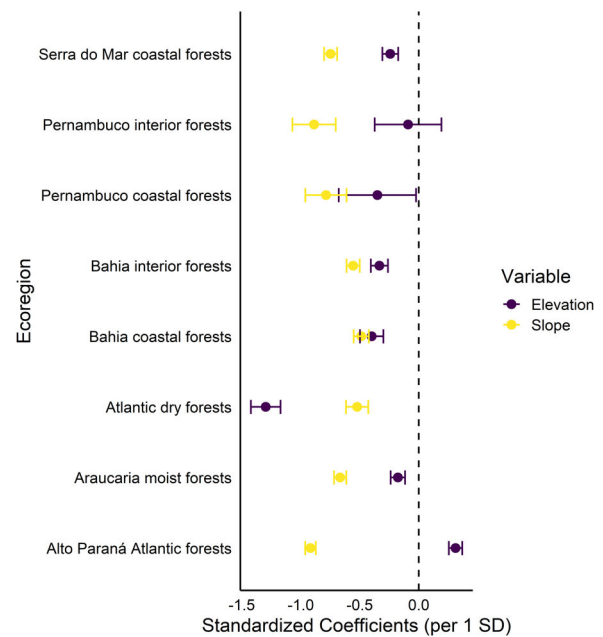


Fig. 2. Standardized effects of elevation and slope on overall anthropization across the Brazilian Atlantic Forest ecoregions. Standardized coefficients were extracted from the second-ranked GLS full interaction model (see Table 1). Each point represents a standardized coefficient, with bars indicating 95% confidence intervals. Coefficients represent the expected change in overall anthropization (in standard deviation units) for a one standard deviation increase in either elevation or slope. Negative coefficients indicate a decrease in anthropization with increasing elevation or slope values.

Observed patterns across slope and elevation classes (Tables A6 and A7) reinforced the outcomes of the GLS models. Mean anthropization was 65.34% across the BAF, declining from 73.03% to 57.47% along the low-to-steep slope gradient, and from 70.74% to 57.53% along the low-to-high elevational gradient. Farming was the predominant activity within anthropized land (97.42% of all anthropization; 63.65% of total land cover) and also declined consistently with increasing slope and elevation (Table A8). Natural vegetation (34.66% on average) increased correspondingly. Urban areas (1.63%) and other uses (0.06%) remained minor in area, though both increased slightly at higher elevations.

To visualize variation in slope and elevation effects across ecoregions, we used the second-ranked (full interaction) model (Table 1). Overall, slope showed stronger and more consistent negative effects on anthropization across ecoregions (Figs. 2 and 3), whereas elevation effects were weaker and more heterogeneous, including a weak positive effect in Alto Paraná (Figs. 2 and 4).

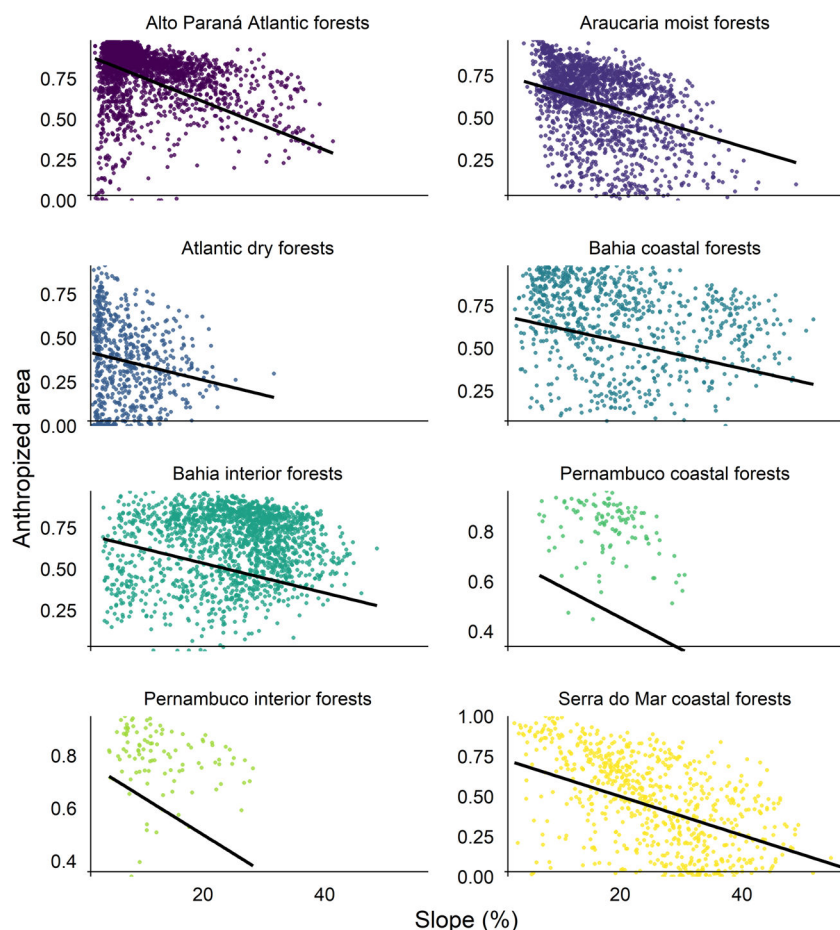


Fig. 3. Relationship between slope and overall anthropization across the Brazilian Atlantic Forest ecoregions. Lines represent the predicted values of the second-ranked GLS model (see Table 1), holding elevation at its median. Points are partials (predicted values plus residuals).

Farming and urban classes

Farming responded similarly to overall anthropization, with the same additive model (elevation + slope) identified as the most plausible (Table A3). Standardized coefficients were -0.86 ± 0.03 for slope and -0.36 ± 0.04 for elevation. A one-SD increase in slope reduced farming by ~ 9 percentage points, while a one-SD increase in elevation reduced farming by ~ 3.8 points. In the full interaction model used for visualization, slope responses remained relatively consistent across ecoregions, whereas elevation responses showed stronger variation. Even so, farming declined with increasing slope and elevation in nearly all regions (Figs. A1–A3).

For the urban class, the model containing only a slope \times ecoregion interaction was the most plausible, indicating that elevation had no detectable effect (Table A5). Standardized slope coefficients varied widely (-0.07 to -2.53 ; mean = -0.95 ± 0.29), indicating strong regional dependence: declines were strongest in Serra do Mar, Pernambuco interior, and Alto Paraná, and minimal in Atlantic Dry Forests. A one-SD increase in slope ($\approx 10.16\%$) reduced urban cover by 0.14–4.69 percentage points (Table A9). Visualization panels (Figs. A4–A6) corroborated these results: elevation was consistently unrelated to urbanization, whereas slope showed negative but heterogeneous effects.

Protected areas biases

The integrated BAF boundary contained 263,419 km² of protected areas (16.26% of the total area). Across the study domain, 21.19% of all hexagons partially or fully overlapped with protected areas. Protection

patterns were unevenly distributed across topographic gradients (Tables A10–A11). Along the slope gradient, Steep hexagons held the largest fraction of protected hexagons (29.88%), followed by Moderate (18.11%) and Low slopes (15.58%). Mean elevation varied across these slope classes (Low = 328 m, Moderate = 470 m, Steep = 660 m), but the values remained near the biome's intermediate elevational range (~ 521 m), indicating that protection patterns were primarily associated with slope.

Along the elevational gradient, Low-elevation hexagons contained the highest proportion of protected areas (24.78%), closely followed by High-elevation hexagons (23.56%), whereas Moderate elevations had the lowest protection (15.24%). Within all elevation classes, protected hexagons tended to occur in steeper terrain, with slope values near or above the biome-wide average ($\sim 17\%$): Low = 19.32%, Moderate = 26.74%, and High = 27.55%. This indicates that protection is concentrated in steeper areas across the elevational gradient.

Discussion

Our results show that overall anthropization within the BAF ecoregions is strongly structured by topography, with markedly lower levels in steeper and higher-elevation areas. Because farming is by far the dominant land-use type within the BAF (63.65% of the study area) and accounts for nearly all anthropized land (97.42%), the spatial pattern of overall anthropization largely reflects the distribution of farming intensity. Accordingly, natural vegetation increased systematically along both slope and elevation gradients. On average, natural areas covered 34.66% of the study area, closely matching the $\sim 36.3\%$ of remaining natural vegetation in the AF reported by Vancine et al. (2024). These

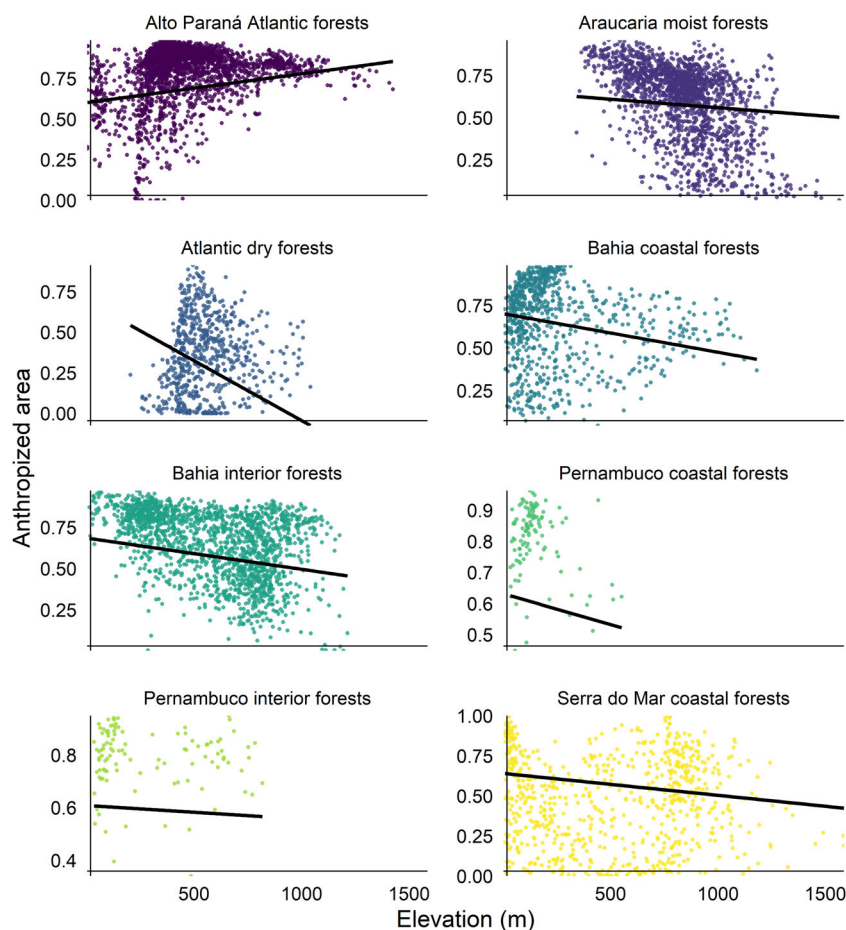


Fig. 4. Relationship between elevation and overall anthropization across the Brazilian Atlantic Forest ecoregions, based on the second-ranked GLS model (see Table 1). Lines show the predicted partial effects of elevation, holding slope at its median. Points represent partial residuals (predicted values plus their residuals).

broad spatial patterns are consistent with the historical occupation of the BAF, which was initially concentrated in coastal flat lowlands and later intensified across low- to moderate-elevation areas with gentle slopes through colonial and post-colonial land conversion (Solórzano et al., 2021; Tabarelli et al., 2010), as detailed below.

Human societies have occupied the BAF for at least 12,000 years, progressively converting original vegetation into secondary forests. Early settlements were mostly concentrated on flat, low-elevation coastal plains, as documented for Sambaqui populations (Dean, 2003). By ~5000 years ago, slash-and-burn agriculture by Tupi groups had expanded into lowland and upland forests, reinforcing the preferential use of accessible terrain (Dean, 2003; Solórzano et al., 2021). Portuguese colonization from the 16th century onward further intensified deforestation in these lowlands through brazilwood extraction and sugarcane plantations, a crop strongly associated with lower elevations (Ross, 2006).

In the 18th and 19th centuries, coffee cultivation advanced into submontane regions, whereas higher elevations remained comparatively less affected (Solórzano et al., 2021). Subsequent urbanization and industrialization increased energy demand and added pressure on forests via charcoal production, particularly on accessible slopes and foothills near urban centers (Rodrigues et al., 2019; Solórzano et al., 2021). These historical trajectories match our findings: anthropization remains highest in flat and low-elevation areas, where land-use profitability has long been concentrated, and declines with increasing slope and elevation. This pattern is also consistent with global evidence that deforestation tends to decrease at steeper slopes and higher elevations (Busch and Ferretti-Gallon, 2017).

Across the BAF, slope emerged as the dominant topographic

constraint on overall anthropization and farming, a pattern clearly supported by the best-fit GLS model. Standardized coefficients showed that slope had a negative effect 2.7 and 2.4 times stronger than elevation, for overall anthropization and farming, respectively. Observed patterns across slope classes mirrored these effects, with overall anthropization decreasing by 16% and farming by 14% from low to steep slopes. In addition, the exploratory full interaction model used to visualize differences among ecoregions showed little variation in slope effects at the ecoregion level, reinforcing the biome-wide consistency of slope as a constraint on land conversion. This consistency aligns with previous studies in the BAF that have shown that vegetation loss predominantly occurs in areas with gentle slopes (Espírito-Santo et al., 2020; Precinoto et al., 2022; Rodrigues et al., 2019; Santos et al., 2024; Teixeira et al., 2009).

Our results also reveal a consistent decline in overall anthropization and farming with increasing elevation across most of the BAF, as indicated by both GLS predictions and quantile-based summaries. From low to high elevation classes, overall anthropization decreased by 13.2 percentage points, with an almost identical reduction in farming. This pattern is consistent with previous studies reporting that the highest elevations, although spatially restricted, retain disproportionately large forest remnants in the BAF (Da Silva et al., 2020; Precinoto et al., 2022; Ribeiro et al., 2011; Tabarelli et al., 2010). Despite this general tendency, elevation had weaker and more variable effects than slope (SE: elevation = 0.04; slope = 0.02), indicating that elevational responses are more heterogeneous across ecoregions. Exploratory coefficients from the second-ranked (full interaction) model reinforce this interpretation, showing substantially larger variation among regions. The Alto Paraná ecoregion illustrates this clearly: it is the only ecoregion

where anthropization increases from low to higher elevations. This pattern, also shown in quantile-observed anthropization values, reflects the exceptionally fertile soils and extensive flat plateaus of this ecoregion, which enable highly mechanized agriculture (Graeff, 2015). In this setting, slope becomes the dominant physical constraint, a trend also noted by Mohebalian et al. (2022).

Urbanization exhibited a markedly different pattern compared to overall anthropization and farming. Elevation had no detectable influence on urbanization, whereas slopes had heterogeneous effects that varied across ecoregions. This indicates that elevation per se is a poor predictor of urban land-use in the BAF. Although early occupation was concentrated in coastal lowlands, where most coastal state capitals are located, subsequent economic expansion into the interior resulted in major urban centers at mid to high elevations (Dean, 2003). Major metropolitan capitals, such as São Paulo (~800 m; Serra do Mar ecoregion) and Curitiba (~900 m; Araucaria ecoregion), illustrate this pattern: they occur at high elevations, but in relatively flat terrains. Against this historical background, slope emerges as the key topographic constraint on urbanization, rather than elevation. Ecoregions with historically intense urban development, such as Serra do Mar, showed the strongest slope effects on urbanization: each one-SD increase in slope reduced urban cover by ~5%. In contrast, Atlantic Dry Forests showed weak slope effects simply because urban land-use was minimal (<0.31%).

The divergent responses of farming and urban land-use to topography indicate that distinct anthropization processes operate under different physical and economic constraints. For farming, steep slopes reduce mechanization efficiency, lower soil fertility, and increase erosion risk (Jasinski et al., 2005; Trigueiro et al., 2020; Weintraub et al., 2015), while legal restrictions further limit deforestation on steep terrain (Brancalion et al., 2016). In contrast, urbanization imposes mixed but structurally different influences. Although urban areas occupy a relatively small fraction of the landscape, their demographic and economic growth can indirectly increase farming demand and drive land conversion elsewhere (Seto et al., 2012). At the same time, urban centers tend to concentrate governance, environmental education, and enforcement capacity, which can enhance compliance with environmental legislation and promote ecosystem restoration (Brancalion et al., 2016). In this sense, our results likely capture this duality: urban expansion can act as a distal driver of anthropization while simultaneously creating institutional and social conditions that favor conservation-oriented initiatives.

Implications for conservation

Our findings reveal clear topographic biases in conservation patterns across the BAF. Protected areas (PAs) were still disproportionately concentrated in steep terrain: nearly 30% of steep-slope hexagons overlapped with PAs, compared to only 18% in moderate-slope and 16% in low-slope areas. Mean elevation within slope classes varied but remained near the biome's intermediate elevational range. This indicates that protection patterns did not reflect an independent elevational bias, but rather the strong association between protection and slope. A similar, though weaker, bias emerged along the elevational gradient: low- and high-elevation classes had nearly identical PA coverage (24.78% and 23.56%, respectively), whereas the moderate-elevation band showed the lowest protection (15.24%). This pattern reflects a non-monotonic relationship, meaning that protection does not follow a simple increasing trend with elevation. Importantly, even within each elevational class, protected hexagons tend to occur in steeper terrain, indicating that the non-monotonic elevational pattern is secondary and masks an underlying topographic bias driven by slope. These patterns reinforce the tendency for protected areas to be more frequent in steeper areas, where land is less profitable for farming (Joppa and Pfaff, 2009; Precinoto et al., 2022; Vieira et al., 2019). Because flatter lowlands and submontane areas concentrate both

agricultural pressure and biodiversity loss, these biases leave these most threatened landscapes systematically underprotected.

In addition, natural ecosystem recovery also exhibits a strong topographic signature. Global syntheses and regional studies in the BAF show that natural regeneration and forest persistence occur disproportionately in marginal terrain, steeper, rougher, or less accessible areas where farming profitability is limited (Espírito-Santo et al., 2020; Li and Li, 2017; Piffer et al., 2022; Wagner et al., 2020). While these areas function as important refuges for biodiversity, relying on passive regeneration alone reinforces the same topographic biases observed in the PAs network. Simply allowing forests to regenerate in naturally unprofitable lands does little to improve protection in flat and productive lowlands, where anthropization is most intense and ecosystem services are most threatened.

Therefore, effective conservation planning must explicitly counteract these biases. Restoration and protection efforts should prioritize flatter, low-elevation and submontane landscapes, precisely where human pressure is greatest and where natural regeneration is least likely to occur without intervention. Policy mechanisms such as carbon markets, environmental reserve quotas, and incentives for assisted natural regeneration (Bicudo Da Silva et al., 2025; Crouzeilles et al., 2020; Young and de Castro, 2021) offer promising avenues to redirect conservation toward these high-priority areas. A more spatially balanced conservation network, integrating active restoration into accessible flatlands with the protection of naturally regenerating highland refuges, is essential to ensure long-term biodiversity persistence and ecosystem resilience in the BAF.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Chat GPT and Perplexity to revise and improve text grammar. After using these tools, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

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Data availability statement

The data and scripts used for the analysis are openly available in the following GitHub repository: <https://github.com/guilhermrs/BAF-Anthropization>. This repository includes the hexagons dataset and R script for reproducing the analyses presented in this study.

CRedit authorship contribution statement

Guilherme Machado: Conceptualization, Data curation, Methodology, Validation, Project administration, Formal analysis, Investigation, Writing - original draft. **Caryne Braga:** Conceptualization, Validation, Writing - review & editing. **Marcos de Souza Lima Figueiredo:** Methodology, Writing - review & editing. **Maria Lúcia Lorini:** Methodology, Writing - review & editing. **Jayme Augusto Prevedello:** Conceptualization, Formal analysis, Investigation, Methodology, Validation, Supervision, Writing - review & editing.

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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Appendix A. Supplementary data

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References

- Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L., Economo, E.P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A.C., Parr, C.L., Wilson, S.K., Young, P.J., Graham, N.A.J., 2018. The future of hyperdiverse tropical ecosystems. *Nature* 559, 517–526. <https://doi.org/10.1038/s41586-018-0301-1>.
- Brancalion, P.H.S., Garcia, L.C., Loyola, R., Rodrigues, R.R., Pillar, V.D., Lewinsohn, T. M., 2016. A critical analysis of the native vegetation protection law of Brazil (2012): updates and ongoing initiatives. *Nat. Conserv.* 14, 1–15. <https://doi.org/10.1016/j.ncon.2016.03.003>.
- Busch, J., Ferretti-Gallon, K., 2017. What drives deforestation and what stops it? A meta-analysis. *Rev. Environ. Econ. Policy* 11, 3–23. <https://doi.org/10.1093/reep/rew013>.
- Crouzeilles, R., Beyer, H.L., Monteiro, L.M., Feltran-Barbieri, R., Pessôa, A.C.M., Barros, F.S.M., Lindenmayer, D.B., Lino, E.D.S.M., Grelle, C.E.V., Chazdon, R.L., Matsumoto, M., Rosa, M., Latawiec, A.E., Strassburg, B.B.N., 2020. Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conserv. Lett.* 13, e12709. <https://doi.org/10.1111/conl.12709>.
- Bicudo Da Silva, R.F., Millington, J.D.A., Moran, E.F., Batistella, M., Liu, J., 2020. Three decades of land-use and land-cover change in mountain regions of the Brazilian Atlantic Forest. *Landsc. Urban Plann.* 204, 103948. <https://doi.org/10.1016/j.landurbplan.2020.103948>.
- Bicudo Da Silva, R.F., Altivo, F., Millington, J.D.A., Dou, Y., Viña, A., Ribeiro, M.C., Vieira, S.A., Liu, J., 2025. Positive effects of an Atlantic Forest program of payment for ecosystem services on native vegetation and pasture quality. *Perspect. Ecol. Conserv.* 23, 191–199. <https://doi.org/10.1016/j.pecon.2025.06.005>.
- Dean, W., 2003. *With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest*, 1. Paperback pr., [Nachdr.], ed. A Centennial Book. Univ. of California Press, Berkeley, Calif.
- Espírito-Santo, M.M.D., Rocha, A.M., Leite, M.E., Silva, J.O., Silva, L.A.P., Sanchez-Azofeifa, G.A., 2020. Biophysical and socioeconomic factors associated to deforestation and Forest recovery in Brazilian tropical dry forests. *Front. For. Glob. Change* 3, 569184. <https://doi.org/10.3389/ffgc.2020.569184>.
- Geist, H.J., Lambin, E.F., 2002. Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52, 143. [https://doi.org/10.1641/0006-3568\(2002\)052\[0143:PCAUDF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2).
- Global Forest Watch [WWW Document], 2024 (Accessed 24 March 2025). URL <https://www.globalforestwatch.org/>.
- Graeff, O., 2015. *Fitogeografia do Brasil - Uma Atualização de Bases e Conceitos*. Editora Nau, Rio de Janeiro.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853. <https://doi.org/10.1126/science.1244693>.
- Jasinski, E., Morton, D., DeFries, R., Shimabukuro, Y., Anderson, L., Hansen, M., 2005. Physical landscape correlates of the expansion of mechanized agriculture in Mato Grosso, Brazil. *Earth Interact.* 9, 1–18. <https://doi.org/10.1175/EI143.1>.
- Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytol.* 204, 459–473.
- Joppa, L.N., Pfaff, A., 2009. High and Far: biases in the location of protected areas. *PLoS One* 4, e8273. <https://doi.org/10.1371/journal.pone.0008273>.
- Li, S., Li, X., 2017. Global understanding of farmland abandonment: a review and prospects. *J. Geogr. Sci.* 27, 1123–1150. <https://doi.org/10.1007/s11442-017-1426-0>.
- MapBiomias, 2024. (Accessed 26 December 2024). URL <https://brasil.mapbiomas.org/tabela-de-camadas/>.
- MapBiomias Collection 10 [WWW Document], 2025. MapBiomias – Coleção 10 da Série Anual de Mapas de Cobertura e Uso da Terra do Brasil. (Accessed 18 August 2025). URL <https://brasil.mapbiomas.org/colecoes-mapbiomas/>.
- Mohebalian, P.M., Lopez, L.N., Tischner, A.B., Aguiar, F.X., 2022. Deforestation in South America's tri-national Paraná Atlantic Forest: trends and associational factors. *For. Policy Econ.* 137, 102697. <https://doi.org/10.1016/j.forpol.2022.102697>.
- Muylaert, R., Vancine, H., Bernardo, R., Emi, J., Oshima, F., Souza, T., Tonetti, V., Niebuhr, B., Ribeiro, M., 2018. Uma nota sobre os limites territoriais da mata atlântica. *Oecol. Aust.* 22, 302–311. <https://doi.org/10.4257/oeco.2018.2203.09>.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. <https://doi.org/10.1038/35002501>.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Rickerts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051%255B0933:TEOTWA%25D2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051%255B0933:TEOTWA%25D2.0.CO;2).
- Peres, E.A., Pinto-da-Rocha, R., Lohmann, L.G., Michelangeli, F.A., Miyaki, C.Y., Carnaval, A.C., 2020. Patterns of species and lineage diversity in the Atlantic rainforest of Brazil. In: Rull, V., Carnaval, A.C. (Eds.), *Neotropical Diversification: Patterns and Processes*. Springer International Publishing, Cham, pp. 415–447.
- Piffer, P.R., Rosa, M.R., Tambosi, L.R., Metzger, J.P., Uriarte, M., 2022. Turnover rates of regenerated forests challenge restoration efforts in the Brazilian Atlantic Forest. *Environ. Res. Lett.* 17, 045009. <https://doi.org/10.1088/1748-9326/ac5ae1>.
- Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Piiego, P., Hansen, A.J., Watson, J. E., Venter, O., 2022. Tropical forests are home to over half of the world's vertebrate species. *Front. Ecol. Environ.* 20, 10–15. <https://doi.org/10.1002/fee.2420>.
- Precinoto, R.S., Prieto, P.V., Figueiredo, M.S.L., Lorini, M.L., 2022. Edges as hotspots and drivers of forest cover change in a tropical landscape. *Perspect. Ecol. Conserv.* 20, 314–321. <https://doi.org/10.1016/j.pecon.2022.07.001>.
- Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hotspot: an opportunity for the Brazilian Atlantic Forest. *Perspect. Ecol. Conserv.* 16, 208–214.
- Ribeiro, M.C., Martensen, A.C., Metzger, J.P., Tabarelli, M., Scarano, F.R., Fortin, M.-J., 2011. The Brazilian Atlantic forest: a shrinking biodiversity hotspot. In: Zachos, F.E., Habel, J.C. (Eds.), *Biodiversity hotspots: distribution and protection of conservation priority areas*. Springer-Verlag, Berlin, Germany, pp. 405–434.
- Rodrigues, A.F., Novotny, E.H., Knicker, H., De Oliveira, R.R., 2019. Humic acid composition and soil fertility of soils near an ancient charcoal kiln: are they similar to Terra Preta de Índios soils? *J. Soils Sediments* 19, 1374–1381. <https://doi.org/10.1007/s11368-018-2162-5>.
- Ross, J.L.S., 2006. *Ecogeografia do Brasil*, 1ª edição. ed. Oficina de Textos, São Paulo.
- Santos, P.M., Bohrer, C.B.D.A., Nascimento, M.T., 2024. Impacts of land use and land cover changes in phytophysiological in the atlantic forest. *Ambient. Soc.* 27. <https://doi.org/10.1590/1809-4422asoc1701vu2711oa>.
- Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U. S. A.* 109, 16083–16088. <https://doi.org/10.1073/pnas.1211658109>.
- Silva, J.M.C., Casteleti, C.H.M., 2003. *Status of the Biodiversity of the Atlantic Forest of Brazil*. Center for Applied Biodiversity Science & Island, Washington, DC, USA, pp. 43–59.
- Solórzano, A., Brasil, L., de Oliveira, R.R., 2021. The Atlantic Forest ecological history: from pre-colonial times to the anthropocene. In: Marques, M.C.M., Grelle, C.E.V. (Eds.), *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-Diverse Forest*. Springer International Publishing, Cham, pp. 25–44. https://doi.org/10.1007/978-3-030-55322-7_2.
- Tabarelli, M., Aguiar, A.V., Ribeiro, M.C., Metzger, J.-P., Peres, C.A., 2010. Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biol. Conserv.* 143, 2328–2340.
- Teixeira, A.M.G., Soares-Filho, B.S., Freitas, S.R., Metzger, J.P., 2009. Modeling landscape dynamics in an Atlantic Rainforest region: implications for conservation. *For. Ecol. Manage.* 257, 1219–1230. <https://doi.org/10.1016/j.foreco.2008.10.011>.
- Topodata [WWW Document], 2024. Banco de Dados Geomorfológicos do Brasil. (Accessed 28 May 2024). URL <http://www.dsr.inpe.br/topodata/acesso.php>.
- Trigueiro, W.R., Nabout, J.C., Tassarolo, G., 2020. Uncovering the spatial variability of recent deforestation drivers in the Brazilian Cerrado. *J. Environ. Manage.* 275, 111243. <https://doi.org/10.1016/j.jenvman.2020.111243>.
- Valeriano, M.M., 2008. *Topodata: guia para utilização de dados geomorfológicos locais*. Instituto Nacional de Pesquisas Espaciais (INPE). São José dos Campos, Brazil. Available at: <http://www.dsr.inpe.br/topodata/documentos.php>.

- Valeriano, M.M., Albuquerque, P.C.G., 2010. TOPODATA: processamento dos dados SRTM. Instituto Nacional de Pesquisas Espaciais (INPE). São José dos Campos, Brazil. Available at: <http://www.dsr.inpe.br/topodata/documentos.php>.
- Vancine, M.H., Muylaert, R.L., Niebuhr, B.B., de Faria Oshima, J.E., Tonetti, V., Bernardo, R., De Angelo, C., Rosa, M.R., Grohmann, C.H., Ribeiro, M.C., 2024. The Atlantic Forest of South America: spatiotemporal dynamics of the vegetation and implications for conservation. *Biol. Conserv.* 291, 110499. <https://doi.org/10.1016/j.biocon.2024.110499>.
- Vieira, R.R.S., Pressey, R.L., Loyola, R., 2019. The residual nature of protected areas in Brazil. *Biol. Conserv.* 233, 152–161. <https://doi.org/10.1016/j.biocon.2019.02.010>.
- Wagner, F.H., Sanchez, A., Aidar, M.P.M., Rochelle, A.L.C., Tarabalka, Y., Fonseca, M.G., Phillips, O.L., Gloor, E., Aragão, L.E.O.C., 2020. Mapping Atlantic rainforest degradation and regeneration history with indicator species using convolutional network. *PLoS One* 15, e0229448. <https://doi.org/10.1371/journal.pone.0229448>.
- Weintraub, S.R., Taylor, P.G., Porder, S., Cleveland, C.C., Asner, G.P., Townsend, A.R., 2015. Topographic controls on soil nitrogen availability in a lowland tropical forest. *Ecology* 96, 1561–1574. <https://doi.org/10.1890/14-0834.1>.
- Young, C.E.F., de Castro, B.S., 2021. Financing conservation in the Brazilian Atlantic Forest. In: Marques, M.C.M., Grelle, C.E.V. (Eds.), *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-Diverse Forest*. Springer International Publishing, Cham, pp. 451–468. https://doi.org/10.1007/978-3-030-55322-7_21.