The Atlantic Forest of South America: spatiotemporal dynamics of the vegetation and implications for conservation

Maurício Humberto Vancine[a,*], Renata L. Muylaert[b], Bernardo Brandão Niebuhr[c], Júlia Emi de Faria Oshima[d], Vinicius Tonetti[a], Rodrigo Bernardo[a], Carlos De Angelo[e], Marcos Reis Rosa[f], Carlos Henrique Grohmann[g], Milton Cezar Ribeiro[a,h,*]

[a] Universidade Estadual Paulista (Unesp), Instituto de Biociências, Departamento de Biodiversidade, Laboratório de Ecologia Espacial e Conservação, Rio Claro, SP, Brazil.
[b] Molecular Epidemiology and Public Health Laboratory, Hopkirk Research Institute, Massey University, Palmerston North, New Zealand.
[c] Norwegian Institute for Nature Research (NINA), Oslo, Norway.
[d] Universidade de São Paulo (USP), Institute of Biosciences, Movement Ecology Laboratory, Ecology Department, Rua do Matão, 321, 05508-090, São Paulo, SP, Brazil.
[e] Instituto de Ciencias de la Tierra, Biodiversidad y Ambiente, Río Cuarto, Córdoba, Argentina.
[f] Universidade de São Paulo, Department of Geography, São Paulo, Brazil.
[g] Universidade de São Paulo, Institute of Energy and Environment, Spatial Analysis and Modelling Lab (SPAMLab), Prof. Luciano Gualberto Avenue, 1289, São Paulo, 05508-010, Brazil.
[h] Universidade Estadual Paulista (Unesp), Environmental Studies Center (CEA), Laboratório de Ecologia Espacial e Conservação, Rio Claro, SP, Brazil.

*** Correspondence**

Maurício Humberto Vancine and Milton Cezar Ribeiro, Universidade Estadual Paulista (Unesp), Institute of Biosciences, Department of Biodiversity, Rio Claro, SP, Brazil. Emails: mauricio.vancine@gmail.com (MHV); milton.c.ribeiro@unesp.br (MCR).

Highlights

- There is 23% forest and 36% natural vegetation cover in the Atlantic Forest.
- Between 1986 and 2020, native forest cover decreased by 2.4% and natural vegetation by 3.6%.
- Since 2005, there has been a 1 Mha increase in forest area by small fragments (1 ha).
- Roads and railways subdivide the largest vegetation fragments (>500,000 ha), reducing their size by 56%–94%.
- Alarmingly, 97% of fragments are small (<50 ha) and 50–60% of the vegetation is <90 m from its edges.

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

Abstract

The Atlantic Forest in South America (AF) is one of the world's most diverse and threatened biodiversity hotspots. We present a comprehensive spatiotemporal analysis of 34 years of AF landscape change between 1986 and 2020. We analyzed landscape metrics of forest vegetation only (FV), forest plus other natural vegetation (NV), and the sensitivity of metrics to linear infrastructure. Currently, the AF remnants comprise 22.9% of FV and 36.3% of NV, an extent that has decreased by 2.4% and 3.6% since 1986, respectively. Linear infrastructure affected mainly the largest fragments (>500,000 ha), reducing their size by 56%–94%. The period before 2005 was characterized by loss of FV and NV (3% and 3.43%) and decrease in the number of FV and NV fragments (8.6% and 8.1%). In contrast, after 2005 the vegetation stabilized, with a recovery of 1 Mha of FV (0.6%) and an increase in the number of fragments, due in part to environmental policies. However, the AF is still a highly fragmented domain: 97% of the vegetation fragments are small (<50 ha), with an average fragment size between 16.3 and 25.5 ha; 50–60% of the vegetation is <90 m from its edges, and the isolation between fragments is high (250–830 m). Protected areas and indigenous territories cover only 10% of the AF vegetation, and most vegetation lies are >10 km in these areas. Our work highlights the importance of legislation and analysis of landscape dynamics to help future conservation and restoration programs for biodiversity in the Atlantic Forest.

Keywords: Landscape structure; Habitat loss; Habitat fragmentation; Edge effect; Isolation; Connectivity.

1 Introduction

Habitat loss, fragmentation, and degradation caused by human-induced changes are identified as the main drivers of biodiversity loss worldwide (Chase et al., 2020). The accelerated land use conversion resulting from these changes has affected especially forest ecosystems, causing a decrease in fragment size and an increase in edge effects (Fischer et al., 2021; Hansen et al., 2020). In recent decades, tropical and subtropical regions have lost >100 million hectares (Mha) of natural forests due to anthropogenic activities (Zalles et al., 2021). Despite the large impacts, few studies presented a spatiotemporal panorama long enough to describe and analyze changes in the landscape structure dynamics, especially in the Americas, where one of the most diverse and threatened biodiversity hotspot in the world is located: the Atlantic Forest in South America (AF) (Sloan et al., 2014).

The AF covers almost all the coast of Brazil and portions of Paraguay and Argentina, the three countries with the largest deforestation areas in the world between 1982 and 2016 (Song et al., 2018). Before European colonization, its vegetation covered over 1.6 million km^2 (Marques et al., 2021). Due to its high environmental heterogeneity, topographic variability, and pre-historic process of formation, the AF has high species diversity and endemism (Peres et al., 2020). With >18,000 species of plants (Flora e Funga do Brasil,

2023) and 3,500 species of vertebrates (Figueiredo et al., 2021; Reis et al., 2016), >65% of all (and 82% of the endemic) tree species are classified as threatened (de Lima et al., 2024). Additionally, the AF provides ecosystem services for >150 million people, such as water provisioning, hydroelectric energy generation, food production, pollination, soil protection, climate regulation, carbon storage, air quality, and cultural services (Joly et al., 2014).

An intensified degradation of the AF arises with the Portuguese colonization and the establishment of agricultural processes such as large plantation systems (sugarcane and coffee), extensive cattle production, energy demand (charcoal), fires, mining, and urban and industrial growth (Solórzano et al., 2021). These landscape modifications have affected the biodiversity in the AF for different taxonomic groups (Püttker et al., 2020) and ecological processes, such as seed dispersal (Marjakangas et al., 2020), carbon storage (de Lima et al., 2020), pollination (Varassin et al., 2021), and top-down regulation through top predators (Paviolo et al., 2016). Furthermore, other processes pose risks to the landscapes within the AF, such as defaunation (Galetti et al., 2021) and climate change (Vale et al., 2021). More recently, however, conservation actions have reduced deforestation rates and increased natural regeneration, especially the Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest Law No. 11,428/2006) (Piffer et al., 2022b).

Despite the recent changes on the AF, few studies have analyzed the landscape structure in a space-time context on large time scales. In the most comprehensive study to our knowledge, Ribeiro et al. (2009) showed that only 11–16% of the forest cover remained in 2005, 83% of which was concentrated on isolated fragments smaller than 50 ha, and half of all forests were <100 m from their edges. Additionally, Tabarelli et al. (2010) and Ribeiro et al. (2011) showed a large proportion of forests remained in high elevations (>1600 m). Based on finer scale satellite data (5 m-spatial resolution), Rezende et al. (2018) estimated 28% of AF vegetation. In more recent studies, using data from MapBiomas (Souza et al., 2020), Bicudo da Silva et al. (2020) showed that landscape composition did not change substantially between 1985 and 2018, and that the loss in areas of montane vegetation was smaller than at lower elevations. In addition, Rosa et al. (2021) showed that the relative temporal stability of AF native forest cover (28 Mha) in recent years, was in fact due to the replacement of old-growth native forests in flatter terrains by young forests in marginal agricultural areas, resulting in increased isolation between forest fragments.

Even with these studies, there is a demand for a refined understanding of how landscape structure varied over time in the AF. Currently, Brazilian initiatives such as MapBiomas have been mapping land use and land cover change with wide thematic coverage, high spatiotemporal resolution, and standardized classification (Souza et al., 2020). This allows for the calculation and comparison of landscape metrics for large territorial extensions and time periods to understand the landscape dynamics of entire domains (Bicudo da Silva et al., 2020; Rosa et al., 2021). Moreover, the AF has a high density of linear infrastructure (e.g. roads, railways, power transmission lines and oil and gas pipelines) because of its high (and increasing) human population and industrial development, and the main large-scale effect on landscape configuration is related to roads and railways. These linear infrastructures severely impact natural vegetation connectivity and biodiversity (e.g. through deforestation, noise disturbance, pollution, and animal roadkill) (Cassimiro et al., 2023; Martinez Pardo et al., 2023), but have never been analyzed in the context of the landscape structure.

Here, we analyzed the spatiotemporal dynamics of the landscape structure of vegetation in the Atlantic Forest every five years from 1986 to 2020. To accomplish this large-scale evaluation, we used a wide delimitation of the Atlantic Forest, including Brazil, Argentina, and Paraguay. We accounted for forest vegetation types only (FV) and forest plus other natural vegetation types (NV) and quantified, in addition, the effect of linear infrastructure on the AF landscape metrics. To understand the spatiotemporal landscape structure vegetation dynamics, we calculated the following landscape metrics for all FV and NV fragments in the AF domain: habitat amount, fragment size, number of fragments, fragment temporal dynamic, edge area, functional connectivity, isolation between fragments and distance from protected areas (PA) and indigenous territories (IT). These metrics were generated through an approach that allows for ecological interpretation of the influence of the landscape structure on organisms by accounting for species mobility, gap-crossing abilities, and sensitivity to edge effects (Riva and Nielsen, 2020).

2 Methods

2.1 Study region

AF extends from 3ºS to 33ºS, and from 35ºW to 58ºW with about 163 Mha, covering large coastal and inland portions of Brazil, Argentina, and Paraguay (Marques et al., 2021) (Fig. S1a). Due to its wide extent, the AF boundaries create important ecotones with other vegetation domains such as Cerrado, Caatinga, Chaco and Pampa (Marques et al., 2021). The vegetation from AF is a complex mosaic, mainly composed of five forest vegetation types—Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal, and Deciduous Seasonal (Joly et al., 2014). Additionally, the AF also includes mangroves and coastal scrub vegetation (Marques et al., 2021). There are also many marginal habitats such as altitude grasslands (*campos rupestres* and *campos de altitude*), oceanic islands, beaches, rocky shores, dunes, marshes, inland swamps, and mountain forest (*brejos de altitude*) in the Northeast region (Scarano, 2002). To provide a broad

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

picture in ecological and evolutionary terms, we used an integrative delimitation adapted from Muylaert et al. (2018), which encompasses the main proposed delimitations across several associated ecosystems. This delimitation was produced by overlapping available AF delimitations (Fig. S1[b-e] and Table S1) and adjusting the delimitation in the Eastern coastal areas using the Brazilian territorial delimitation from IBGE (https://www.ibge.gov.br) for 2021 (IBGE, 2021). This step ensures that areas of coastal vegetation such as mangroves, dunes, and wooded sandbank/sandy coastal plain vegetation (hereafter *restinga*) (Scarano, 2002) are better represented. The final delimitation has a total area of 162,742,129 ha, distributed within 3653 municipalities from 18 Brazilian states (93.1%), 70 municipalities of one province in Argentina (1.6%), and 127 municipalities from 11 departments in Paraguay (5.3%) (Fig. S1a, Fig. 3).

2.2 Mapping

We compiled land use and land cover maps for Brazil, Argentina, and Paraguay from MapBiomas Brazil collection 7 (https://mapbiomas.org) and MapBiomas Bosque Atlántico collection 2 (https://bosqueatlantico.mapbiomas.org) (Souza et al., 2020). These datasets reconstruct annual land use and land cover information at 30-m spatial resolution from 1985 to 2021, based on a pixel-based random forest classifier of Landsat satellite images using Google Earth Engine, with AF general accuracy of 89.8% (Souza et al., 2020). We used data for every fifth year between 1986 and 2020. We excluded the years 1985 and 2021 because there was no validation for the previous and subsequent year, respectively. We defined two groups of vegetation classes to convert the maps into non-vegetation/vegetation (0/1) binary rasters for landscape analyses. The first comprises only forest vegetation types ("Forest Vegetation", FV), which included the classes Forest Formation, Mangrove and Wooded Sandbank Vegetation (*restinga*). The second group of vegetation classes considered both forests and other natural vegetation types ("Natural Vegetation", NV), including Forest Formation, Mangrove, Wooded Sandbank Vegetation (*restinga*), Savanna Formation, Wetland, Grassland, Salt Flat, Herbaceous Sandbank Vegetation and Other Non-Forest Formations (Fig. S2a-h and Table S2).

We used roads and railways (for the year 2021 in Brazil and Argentina, and for 2012 in Paraguay) to trim their overlapping FV and NV fragments (henceforth called "trimmed" and "not trimmed" scenarios) (Fig. S11). This procedure enabled us to avoid overestimating the size of large fragments of vegetation and check the metrics' sensitivity to linear infrastructure (following Antongiovanni et al., 2018), since these structures might subdivide entire fragments, decrease landscape connectivity, and threaten multiple taxonomic groups (Cassimiro et al., 2023). Therefore, we analyzed four vegetation maps: "FV not trimmed", "FV trimmed", "NV not trimmed", and "NV trimmed". Further, we analyzed the overlap between FV and NV fragments with Protected Areas (PA; for the year 2022) and Indigenous Territories (IT; for the year 2021) (Fig. S12). Details of road, railway, PA, and IT maps are presented in the Data section in the Supplementary Material (Fig. S11 and Fig. S12). All geospatial datasets were rasterized and warped to 30 m-spatial resolution (112663 × 83307 ≈ 9.4 billion cells and ca. 1.8 billion cells with values) using the Albers Conical Equal Area Brazil (SIRGAS 2000) projection (https://spatialreference.org/ref/sr-org/albers-conical-equal-area-brazil-sirgas-2000). International map displays were generated using Natural Earth (1:10,000,000) data and QGIS 3.22 LTR (QGIS Development Team, 2023).

2.3 Landscape metrics

All landscape metrics were processed in GRASS GIS 8.2.1 (Neteler et al., 2012) through the R 4.3.0 (R Core Team, 2023), using the *rgrass* package (Bivand, 2022), implemented on the LSMetrics package (Niebuhr et al. *in prep.*). We calculated six landscape metrics: number of fragments, fragment size, edge area, isolation, functional connectivity, and distance from PA and IT (Figure S13 and Table S3). The number of fragments and fragment size allowed us to account for the number and area of vegetation fragments for different size classes (Table S3). Fragments were defined using the eight-neighbor rule (Queen's case), which defines areas connected to pixels in eight directions (Turner and Gardner, 2015). We also examined the area and number of fragments that appeared and disappeared throughout time, and the areas of increase, reduction, and stability of fragments that remained in the landscape (Table S3) (Rosa et al., 2021). Edge area was calculated for different edge depths (distance from the edge of the fragment) (Table S3), allowing us to assess the amount and percentage of forest area subjected to edge effects (Harper and Macdonald, 2011).

Two metrics of functional connectivity were computed for different gap-crossing distances (species' capacities to cross non-habitat) (Table S3). First, we calculated the sum of the areas of all fragments closer than the gap-crossing distance, which can be interpreted as the functional available area of each clump of fragments (Awade and Metzger, 2008) or the amount of functional (i.e. suitable and well-connected) habitat (van Moorter et al., 2023). Second, we computed the expected cluster size as the mean fragment clump size, and then compared it with the highest cluster size in the entire study region. Isolation was calculated using an index adapted from the ‘‘*Empty Space Function*" (Dale and Fortin, 2014), similar to Ribeiro et al. (2009): we computed a Euclidean distance map from all the fragments, extracted its values and calculated the mean. We repeated this process by removing different-sized fragments in several steps (see Table S3 for classes of distance), and then

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

created new Euclidean distance maps to recompute the mean distance values. These values represented the isolation of fragments while also providing insights about the importance of the smaller fragments (*stepping stones*) (Diniz et al., 2021). We calculated the amount of FV, NV, and vegetation classes (see Table S2) covered by PA and IT, and the shortest Euclidean distance from each FV and NV pixel to these areas (see Table S3 for classes of distance).

3 Results

3.1 Forest and natural vegetation cover

The proportion of the Atlantic Forest domain covered by forests and natural vegetation decreased in the past 34 years, from 25.26% (41.1 Mha) to 22.86% (37.2 Mha) for FV and from 39.86% (64.8 Mha) to 36.27% (59 Mha) for NV (Fig. 1 and Table S4). For the entire period, in Brazil the percentages decreased from 22.85% (34.6 Mha) to 22.27% (33.7 Mha) for FV and from 37.34% (56.5 Mha) to 35.25% (53.4 Mha) for NV, with an increase in the proportion since 2005 (Fig. S3). NV was mainly composed of savannas, grasslands, and wetlands, besides the forest formations. In Argentina, the loss of vegetation cover was proportionately larger, from 67.36% (1.8 Mha) to 56.89% (1.52 Mha) for FV, and 67.96% (1.81 Mha) to 57.33% (1.53 Mha) for NV, showing an increase in the rate of deforestation in the last five years (Fig. S3). In Paraguay, the loss of vegetation cover was higher than in the other countries, dropping from 54.57% (4.7 Mha) to 22.85% (2 Mha) for FV, and 75.26% (6.5 Mha) to 47.74% (4.1 Mha) for NV (Fig. S3), but it has remained relatively stable since 2005.

Beyond presenting the percentages for the integrative delimitation (Fig. S1a), we also present results for five other delimitations (Table S5). The results for 2020 (Fig. S1[b-f]) varied for FV from 23.15% (31.6 Mha) for the delimitation of Da Silva and Casteleti (2003) to 26.47% (29.3 Mha) for the delimitation of IBGE (2019), all trimmed by roads and railways. For NV, the results ranging from 31.45% (34.8 Mha) for the IBGE (2019) trimmed to 37.04% (40.9 Mha) for the delimitation of the Dinerstein et al. (2017) not trimmed (Table S5).

3.2 Number of fragments and fragment size distribution

Roads and railways greatly impacted the large-sized fragments, depending on the year and the scenario considered. These effects were mainly reflected in vegetation fragments larger than 500,000 ha, which reduced the maximum fragment size by 56%–94% (Fig. 2, Fig. S4, and Table S4). By accounting for linear infrastructure, the fragment size

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

classes >500,000 ha ceased to exist for FV for all years and were heavily reduced for NV, and the total area and number of fragments increased for fragments of all size classes <500,000 ha for FV and NV (Fig. 2, Fig. 3, and Fig. S4). Despite this effect for large fragments, our results showed no difference between the scenarios “trimmed” and “not trimmed” for other landscape metrics. Therefore, we henceforth chose to demonstrate the results with the linear infrastructure effect (trimmed scenario) in the main text and present the additional results in the Supplementary Material.

For the trimmed scenario, about 97% of the fragments have an area of <50 ha, with 0.4% of variation over the years. However, between 1986 and 2020 the total area covered by these small fragments increased from 18.8% to 22.2% for FV and from 11.7% to 13.5% for NV (Fig. 2 and Fig. S4). For fragments between 50 ha and 25,000 ha, the proportion of the total number of fragments is low (2.5%), varying non-linearly for FV from 2.44% in 1986 to 2.61% in 2020; and for NV with 2.34% in 1986 to 2.61% in 2020. However, total area covered by fragments of this size class increased from 1986 to 2020, going from 40% to 46.1% for FV, and from 29.8% to 35.1% for NV (Fig. 2 and Fig. S4). For the last set of categories of fragment area, above 25,000 ha, we found a very small proportion of number of fragments (0.001%), with values falling from 0.0082% to 0.0061% for FV, and from 0.0127% to 0.0118% for NV, between 1986 and 2020. Total area values for FV fragments in these categories fell from 41.1% to 31.9% and for NV from 58.6% to 51.3%, between 1986 and 2020 (Fig. 2 and Fig. S4).

In 1986, the largest FV fragments were located in the coast of Bahia (*South of Bahia —cabruca region*), São Paulo, Paraná, and Santa Catarina (*Serra do Mar region*), and inland areas of Paraná, Santa Catarina and Rio Grande do Sul in Brazil. For the same period, there were large FV fragments in Misiones in Argentina and the eastern portion of Paraguay (Fig. 3a). We observed the same for NV, with additions of huge fragments in portions of Bahia, Minas Gerais, and Piauí in Brazil, mainly in the regions named *São Francisco* and *Brejos Nordestinos* (see these region concepts in Ribeiro et al., 2009) (Fig. 3c). In 2020, these same regions concentrated the largest fragments of FV and NV, but with a decrease in their area (Fig. 3[b-d]). The exception was Paraguay, where there was a vast deforestation process, mainly for FV (Fig. 3[c-d]). Our results also show a large effect of roads and railways on maximum fragment size, for the same regions (compare Fig. 3[a-d] with Fig. S5[a-d]).

The spatial-temporal analysis revealed a turning point for the AF landscape structure in 2005. For the first period (1986–2005), the number of fragments decreased by 8.6% for FV and 8.1% for NV; for the second one (2005–2020), it increased to 12.2% for FV and 9.3% for NV (Fig. 4a). From 2010 onwards, the number of FV and NV fragments tended to become more like each other (Fig. 4a). The average fragment size in the first period for FV

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

dropped by 3.6% (18.4 to 17.8 ha) and remained stable for NV, dropping 0.5% (28.2 to 28 ha). In the second period, the FV had a larger drop of 8.5% for FV (17.8 to 16.3 ha) and 8.9% for NV (28 to 25.5 ha) (Fig. 4b).

The temporal dynamics of the landscape from 1986 to 2005 revealed a reduction in the total area of 4.87 Mha of FV (3%) and 5.56 Mha of NV (3.4%) (Table S6). However, between 2005 and 2020, there was an increase of 990,000 ha of FV (0.6%) and a small decrease of 240,000 ha of NV (0.15%). Considering the balance of fragments gained and lost, in the first period there was a sharp drop in the number of fragments for FV (242,000) and NV (227,000), but in the second period there was an increase for FV (385,000) and NV (314,000). Between 1986 and 2005, the average size of lost FV and NV fragments (1.2 to 1.35 ha) was greater than the size of restored fragments (1.08 to 1.14 ha); between 2005 and 2020, this pattern reversed, with the average size of fragments lost being smaller (0.94 to 0.97 ha) than that of fragments gained (1.03 to 1.08 ha).

3.3 Core and edge area

The percentage of FV and NV located <90 m from the edge increased over time, going from 51.9% to 58.8% for FV and 42.2% to 48.3% for NV, as well as the percentage <240 m, from 76% to 81.7% for FV and 66.2% to 72.2% for NV (Fig. 5[a-b]). Conversely, the amount of FV and NV located >500 m from any edge ("core areas") decreased, from 12.4% to 8.9% and from 19.5% to 15%, respectively. The maximum distances from fragment edges for FV and NV were substantially different— around 11 km for FV and 32 km for NV— showing that NV fragments have larger core areas (Fig. 5[a-b]). From 90 m onwards, there is an inversion in the edge percentage over time: between 1986 and 2020, there is a gradual increase in the percentage of vegetation <90 m; and a decrease in the percentage of vegetation >90 m from edges, showing a threshold for central areas of fragments into edge areas (Fig. 5[c-d]).

3.4 Functional connectivity

The average functionally connected vegetation area—i.e. the vegetation area available and reachable for species—decreased for species with low-mobility in non-vegetation matrices (up to 60 m of gap-crossing) for both types of vegetation (decreasing 9.4% for FV and 6.5% for NV between 1986 and 2020, Fig. 6[a-b]). However, for species with high-mobility (gap-crossing above 120 m), the functional connectivity decreased until 2005 and then increased afterwards. The functional connectivity of the NV was always higher in numerical terms for the same years, but they followed the same patterns of annual trends and gap-crossing as the FV.

When we analyzed the largest functionally connected vegetation cluster, we noticed that species restricted to vegetation areas (gap-crossing = 0) have relatively small vegetation area available (the largest fragments correspond to 1% of FV and 4% of NV cover, for all years, Fig. 6[c-d]). However, the area of the largest functionally connected cluster increases rapidly as species become more mobile, with the rate of increase varying largely between years and for species with different mobility. For high-mobility species (gap-crossing >600 m) the curve presenting the largest functionally connected cluster reaches an asymptote (representing 85% for FV and 72% for NV), and there is no increase in the largest functional patches even if species can move further into non-vegetation matrices. These patterns are similar for FV and NV.

3.5 Mean isolation

Small fragments were key to reducing isolation between fragments in all analyzed scenarios. For example, when we disregard fragments <50 ha, the mean isolation increases by 370–495% for FV and 351–444% NV (Fig. 7[a-b]). As we increase the size of fragments removed, there is a gradual increase in isolation, varying to 4-22 km for FV and 1-12 km for NV. Importantly, the mean isolation was reduced by 65–70% when considering that NV also connects forests and other NV fragments (Fig. 7[a-b], Fig. S8[a-b]). Considering the temporal trends, in 1986, the mean isolation for the entire AF region was 773 m for FV and 273 m for NV. The isolation reached its maximum values in 1995, after which, it slowly decreased until 2015, and more recently it fell to 832 m for FV and 253 m for NV in 2020 (Fig. 7[a-b]).

3.6 Protected areas and indigenous territories

Protected areas (PA) covered 4.6 Mha (2.84%) and indigenous territories (IT) covered 1.3 Mha (0.81%) of the AF limit. These values represent 12.4% and 7.8% of the total FV and NV area for PA, and 3.6% and 2.2% of the total FV and NV area for IT in 2020. However, only 3.1 Mha (8.4%) of FV and 4.1 Mha (7%) of NV cover overlaps with PA (Fig. 8[a-b]), and only 560,000 ha (1.5%) of FV and 760,000 ha (1.3%) of NV overlaps with IT (Fig. 8[c-d]), since other types of land cover occur within PA and IT. Only 2.7% of FV and 2.2% of NV are within 1 km of PA and 0.8% of FV and 0.7% of NV to IT. For vegetation within 10 km, there are 23.4% of FV and 19.2% of NV of PA, and 9.5% of FV and 8.7% of NV of IT (Fig. 8). On the other hand, 68.2% of the FV and 73.9% of NV are over 10 km away from PA, and 89% of the FV and 90.2% of NV are over 10 km away from IT, demonstrating the lack of protection for these fragments of vegetation (Fig. 8).

The vegetation class with the largest area overlap is the Forest formation, with 3 Mha (8.2%) for PA and 536,000 ha (1.5%) for IT (Fig. S10). The classes with the largest proportional cover under protection are *restinga* with 133,000 ha (21.6%), Mangrove with 23,000 ha (11.9%), and Herbaceous sandbank vegetation with 31,000 ha (9.6%) (Fig. S10b). For IT, the class with the most cover proportion is the Other non-forest formations 1,400 ha (8.6%), followed by *restinga* with 22,000 ha (3.6%), and Mangrove with 4,600 ha (2.4%) (Fig. S10d). The Savanna formation class is the smallest cover protection with only 507,000 ha (3.8%) in PA (Fig. S10b) and 120,000 ha (0.9%) in IT (Fig. S10d), whose total area is second in terms of total area, 13 Mha (22.5%).

4 Discussion

4.1 Main results

We present here a new panorama on the Atlantic Forest vegetation dynamics, by providing a comprehensive spatial and temporal analysis, integrating different types of vegetation, and considering for the first time the whole distribution of the AF, including Brazil, Argentina, and Paraguay. In the 34-year period analyzed, there was a substantial decrease in the vegetation cover in the AF, especially in Paraguay and Argentina and in Brazil until 2005. Within Brazil, and to a lesser extent in Argentina and Paraguay, we found a turning point for the Atlantic Forest around 2005. The period before 2005 was characterized by deforestation and decrease in the number of forest fragments; the period after 2005 was instead characterized by a larger stability in vegetation cover and an increase in the number of fragments. This result is linked, at least in part, to the environmental legislation in these countries (see Fig. 4 and next section for legislation details). Yet, there were marked changes in the spatiotemporal dynamics of the landscape structure for the entire AF, with an overall replacement of larger forest and vegetation areas by smaller fragments and vegetation areas increasingly subject to edge effects. Even with local and temporal changes, and although legislation, natural regeneration and small restoration actions appear to have positively affected them, the overall picture is still of a highly fragmented domain: a few vegetation fragments are very large, but >97% of the fragments are smaller than 50 ha, the mean fragment size decreased for both FV and NV, and more than half of the vegetation is closer than 90 m to edges with other land cover types.

Even though forest fragment sizes have decreased, we showed that the small fragments might still be very important for decreasing the isolation between forests and increasing the functional connectivity for medium- to high-mobile organisms. In this regard, we showed that non-forest natural vegetation is very important to increase connectivity between forests and between other non-forest natural vegetation fragments for organisms that can use them as suitable habitat or to move and reach suitable habitats. In contrast, species with low-mobility which are limited to forest fragments have seen a decrease in the available habitat area over time. We also showed that linear infrastructure such as roads and railways have a critical effect in fragmenting forests and natural vegetation, especially in the larger fragments. Importantly, there is only a small amount of forest and natural vegetation within the protected areas and indigenous territories, and most of the vegetation (70% for FV and 90% for NV) lies beyond 10 km from these areas. Below, we revisit these results to put them into context, and we explore key implications of our findings.

4.2 Forest and natural vegetation cover

Determining how much of the AF vegetation cover is left has always been a complex task. While we found 22.86% for FV and 36.27% for NV using an integrative AF delimitation in 2020, for the same year, the vegetation cover values varied from 23.15% to 37.04% for different delimitations and vegetation types. These values are smaller than the vegetation cover estimated in the Caatinga (50% in 2009; Antongiovanni et al., 2018), the Cerrado (54% in 2019; Pompeu et al., 2024) and the Brazilian Amazon (80% in 2021; Guedes Pinto et al., 2023). However, over the years, several studies have shown values ranging from 8% to 28% for different years for the AF (e.g. Bicudo da Silva et al., 2020; Da Silva and Casteleti, 2003; Rezende et al., 2018; Ribeiro et al., 2009). These estimates vary according to mapping resolution, size of vegetation fragments, types of vegetation (forest or non-forest), vegetation quality (primary or secondary forest), and AF delimitation (Ribeiro et al., 2009). We highlight that the use of MapBiomas mapping version 7, with image standards and classification methods, made the comparison of annual maps possible due to the decrease in random error between them (Souza et al., 2020). However, there are limitations associated with the methods used for mapping that are intrinsic from the database that we used. As an example, despite having a precise scale, MapBiomas does not clearly define vegetation successional stages and the quality of the forest remnants.

The vegetation cover showed a considerable decrease over time for Paraguay and Argentina, and a less pronounced decrease for Brazil, between 1986 and 2005. After 2005, the percentage of vegetation stabilized or increased, mainly in Brazil and for FV. These effects can at least partially be related to nature conservation laws (see Fig. 4 for some examples), which were initiated almost in the same period in Brazil (Atlantic Forest Law in 2006, and Native Vegetation Protection Law in 2012), Argentina (Forest Law in 2007), and

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

Paraguay (The Zero Deforestation Law in 2004) (Silva et al., 2017; Dam et al., 2019). In Brazil, the AF Law has a clear effect on forest regeneration, as it reduces deforestation in advanced successional stages and requires that, when it occurs, it must be compensated, causing forests to emerge in secondary stages of regeneration (Piffer et al., 2022b). Besides, in Brazil, other specific conservation laws were established from 1998 on (Fauna Protection in 1988, and National System of Conservation Units in 2000), and more recently, the 2012 legislation Natural Vegetation Protection National Law (Law 12.651/2012 – known as Forest Code – FC) created the Rural Environmental Registry [Cadastro Ambiental Rural (CAR)], which requires environmental information from private rural properties. CAR can be a fundamental tool to stimulate and regulate natural regeneration and direct vegetation restoration efforts through legal reserves (LR; in the Atlantic Forest it represents 20% of private land) and permanent preservation areas (PPA; riparian vegetation along stream and springs) (Brock et al., 2021; da Silva et al., 2023). Furthermore, since 2009, the Pact for the Restoration of the Atlantic Forest (AFPR; https://pactomataatlantica.org.br) has been encouraging restoration with the goal to restore 15 Mha by 2050 (Melo et al., 2013), with about 700,000 ha forest restored between 2011 and 2015 (Crouzeilles et al., 2019). Yet, Bicudo da Silva et al. (2023) showed that between 2001 and 2015 there was a process of forest transition in the AF, from forest cover loss to forest recovery (Rudel et al., 2005), due to the stagnation of agricultural activities and subsequent migration of small farmers to urban areas, the emergence of non-agricultural rural activities and the decrease in precipitation, which, together, led to the abandonment of land and favored natural regeneration.

In Argentina, the percentage of forest has been reduced linearly since the 1990s, with the combined effect of the advance of small-scale agriculture associated with population growth and road construction in some areas, and the increase of monospecific forest plantations incentivized by government subsidies and the participation of large timber companies (Izquierdo et al., 2008). The forest loss rate was lower during 20052–015, potentially because of the effect of the certified wood market in this region and the approval of the National Forest Law and the implementation of the National Fund for the Enrichment and Conservation of Native Forests (Fundación Vida Silvestre Argentina & WWF, 2017). However, forest loss increased in the last period (2015–2020) most likely due to higher levels of economic growth and the impact of long-term policies on the expansion of agriculture and cattle raising in Misiones (Mohebalian et al., 2022). Paraguay showed the highest rates of deforestation of the entire Atlantic Forest between 1986 and 2005 due to the massive expansion of agriculture. However, since the creation of the Zero Deforestation Law and the implementation of associated mechanisms, there has been a relative stabilization of vegetation loss (Da Ponte et al., 2017; Fundación Vida Silvestre Argentina & WWF, 2017).

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

While legislation and conservation instruments to protect forests and natural vegetation are essential to reduce habitat destruction, stimulate restoration and natural regeneration, they come with heavy social consequences, entering in conflicts with the rural life and work of peasants and traditional and indigenous groups that depend directly on the forests (Sparovek et al., 2012; Gerhardt, 2016). Furthermore, a large part of the land in the AF is currently private or public land already subject to protection, which poses yet another challenge for future protection (Sparovek et al., 2019). Future research should investigate how spatiotemporal changes in landscape structure are linked to land tenure distribution, population migration to cities, and the social and cultural consequences of these processes. Melo et al. (2023) showed that restoration opportunities in the Caatinga should account for land concentration and socioeconomic contexts if one wants to avoid reproducing inequalities, what is also critical in the AF and should be a priority for future research and policies.

4.3 Number of fragments and fragment size distribution

Our analyses demonstrated that between 2005 and 2020 there was an increase in the amount, number of fragments, and higher mean fragment gain for forest vegetation, with new fragments appearing in previously deforested areas. This change illustrates in time a large-scale process which includes both natural forest regeneration (Crouzeilles et al., 2020) and forest transitions (Bicudo da Silva et al., 2023) related to other processes, and confirms the results found by Rosa et al. (2021), Piffer et al. (2022b) and Dias et al. (2023), who highlighted the replacement of older vegetation by younger vegetation in the AF. This replacement can lead to the loss of habitat quality in vegetation fragments, altering landscape features and affecting vital ecological processes and ecosystem functioning, such as carbon cycling (Piffer et al., 2022a) and vegetation structure (Faria et al., 2023).

We also found a large effect of roads and railways on fragment size, more pronounced in FV than in NV due to greater density of these linear infrastructures in large forest fragments located in Serra do Mar and southern Bahia in Brazil, and in the region of Misiones in Argentina. Roads and railways have a large impact on biodiversity, for example by modifying animal movement patterns, reducing connectivity between populations, and causing roadkills, which might lead to population declines and local extinctions (Cassimiro et al., 2023; Martinez Pardo et al., 2023). For example, almost 38 thousand mammal roadkills were estimated in 10 years in the state of São Paulo (which is covered almost entirely by Atlantic Forest vegetation), and an extrapolation of the analysis predicted 40 thousand roadkills per year only in the state of São Paulo (Abra et al., 2021).

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

When analyzing the distribution of fragment sizes, we noticed a reduction in the number and area of the fragments >500,000 ha of FV and NV between 1986 and 2020 and a clear increase in small fragments <50 ha. These results show a worrying pattern, much worse than Ribeiro et al. (2009), and can be explained by the increase in mapping quality, with MapBiomas standardized approaches for mapping in detail vegetation fragments (including fragments <3 ha) that are considered secondary vegetation (Rosa et al., 2021). The increase in the proportion of smaller fragments has a direct impact on the maintenance of species diversity and population size of multiple taxonomic groups. Several studies have estimated fragment size and habitat amount thresholds for assemblage diversity in the AF, such as terrestrial mammals (Magioli et al., 2015), bats (Muylaert et al., 2016), birds (Barbosa et al., 2017), and multiple other groups (Banks-Leite et al., 2014).

However, since 97% of the fragments are <50 ha in the AF, the overall scenario is already well under the thresholds that are known to affect biodiversity persistence and composition (Banks-Leite et al., 2014; Magioli et al., 2015). In this context, approaches for conservation could be focused on single large *and* several small (SLASS) fragments (Szangolies et al., 2022). The SLASS approach can be more beneficial for conserving the AF biodiversity than choosing a unique type of conservation approach (SLOSS debate - single large or several small, see Fahrig et al. 2022). The current scenario is composed by a continuum of forest fragments within protected areas in the mountain range (Serra do Mar and Serra da Mantiqueira regions) and small remnants in the countryside mostly composed by riparian forest and legal reserves protected by law, added to hundreds of Private Reserves of Natural Heritage (RPPNs) to locally protecting endangered species (Rambaldi et al., 2005). Drastically changes in the vegetation configuration of the AF nowadays are highly unlikely since agricultural land, pasture and urban areas are already established in flatter terrains (Rosa et al., 2021). Therefore, the SLASS strategy could help to ensure that the vegetation in steeper terrain remains protected and increase the protection of riparian forests in flatter terrain.

4.4 Core and edge area

Our results showed that around 50% of the vegetation is up to 90 m, 75% of the vegetation is up to 240 m, and almost 90% of the vegetation is up to 500 m from the nearest edge (similar to Haddad et al. 2015), and may therefore be subjected to edge effects (de la Sancha et al., 2023; Parra-Sanchez and Banks-Leite, 2020; but see Harper et al., 2023). Over time, there was an increase in vegetation located closer than 90 m from the edges, revealing a possible edge effect threshold in the AF. Below this value, there is an intensification of edge effects, and above it, there is a decrease in the amount of vegetation core. This threshold is probably associated with the massive number and small average size of fragments we detected. Importantly, small fragments are more subject to edge effects due to their size and shape (Fahrig, 2003). The edge effect changes the AF landscape features such as microclimate and carbon cycle (Magnago et al., 2015, 2017) depending on the fragment shape (Banks-Leite et al., 2013) and the matrix effect (Adorno et al., 2021). In that regard, numerous studies have demonstrated the negative effects of edge changes for epiphyte plants, small mammalian, and birds in the AF (de la Sancha et al., 2023; Morante-Filho et al., 2018; Parra-Sanchez and Banks-Leite, 2020). Despite this, Harper et al. (2023) showed that the edge effect for plant species did not exceed 20 m but recognizes its importance for conservation planning. Added to that, Pivello et al. (2021) and dos Santos et al. (2019) identified that AF is highly fire-sensitive, which changes the conditions of the edges and hinder natural regeneration. Some measures such as forested or agroforestry matrices and strips of trees being planted, forming a buffer around the existing fragments, can reduce the edge effect (Gama-Rodrigues et al., 2021; Tavares et al., 2019).

4.5 Functional connectivity and mean isolation

Functional connectivity and isolation had co-varying response patterns over time, with the lowest functional connectivity and highest isolation among fragments between 1990 and 2000, and from 2005 onwards there were clear signs of improvement, with increase of functional and decrease of isolation between vegetation fragments. The vegetation amount has not changed noticeably since 2005, and this improvement was due to the appearance of new fragments that increased the connectivity of the landscape, serving as stepping stones for mobile species. In this way, small fragments (<50 ha, which represents 97% of AF remnants) play a fundamental role in keeping large fragments connected, mainly for species that can cross non-vegetation matrices (Hatfield et al., 2018b; Diniz et al., 2021). Additionally, we have shown here that non-forest natural vegetation plays a key role in decreasing the isolation between forest fragments. Although there may be fewer forest-specialist species that use other types of vegetation, other natural vegetation types can be critical to maintaining AF connectivity for multiple species groups and ecological processes (Lyra-Jorge et al., 2010).

Our approach to evaluate connectivity and isolation focus on landscape structure, and when applied should be complemented by assessments of the permeability of the matrix between vegetation fragments (Hatfield et al., 2018a). Practices such as agroecology and forestry can increase the connectivity by increasing the permeability of the matrix for some groups of organisms (Tubenchlak et al., 2021). Furthermore, the AFPR and the CAR might be a great opportunity for land use planning to create and improve ecological corridors (da

Silva et al., 2023; Melo et al., 2013; Pinto et al., 2014). Finally, although connectivity and isolation were not sensitive to roads and railways, this lack of sensitivity appear due to short-distance divisions into FV or NV fragments, and to the fact that the additional cost that these linear infrastructures pose to animal movement and survival (Martinez Pardo et al., 2023) was not considered. Thus, management measures such as fauna passages might be fundamental for improving landscape permeability to maintain wildlife gene flow and reduce roadkill in landscapes highly fragmented by linear infrastructure such as the AF (Cassimiro et al., 2023; Teixeira et al., 2017, 2022).

4.6 Protected areas and indigenous territories

Alarmingly, we show that the proportion of total vegetation area formally protected by PAs (9.9% for FV and 8.3% for NV) is far below the targets of the post-2020 Global Biodiversity Framework (30% land surface by 2030, Jung et al., 2021). We highlight that indigenous territories, despite not being PA, have proven to be fundamental for forest restoration in the AF (Benzeev et al., 2023), but they only comprise 1.5% of FV and 1.3% of NV total area. Moreover, we found that most of the vegetation is located >10 km distant from PA and IT (70% for FV and 90% for NV). Our findings are consistent but more alarming than those found by Ribeiro et al. (2009) and Rezende et al. (2018). The Forest Formation class has the greatest overlap with PAs (8.2%) and IT (1.5%), given that forests are the main target for the creation of PAs and IT, and is the main class in the composition of the AF (62.1%). In addition, *restinga* and mangroves had a high overlap with PA and TI (40%), due to the high density of these protective measures on the Brazilian coast, especially in Serra do Mar. However, despite this high proportion of protection, these ecosystems have faced many threats in recent decades, which can affect several functions of ecosystems and local populations (Diniz et al., 2019). Savanna formation was critical to ensuring overall connectivity in the AF, but this class has the lowest proportion in PA and TI (4.7%) despite representing 23% of the amount of vegetation, possibly because this vegetation formation is not formally protected by specific AF protection laws. Since deforestation outside PA and IT has been lower than in private rural areas (da Silva et al., 2023), these areas are essential to ensure and promote biodiversity conservation (Avigliano et al., 2019; Benzeev et al., 2023). Therefore, it is necessary to create new protection instruments that focus on multiple types of natural vegetation, as well as strengthen the connection network between existing ones, and that account for the surroundings of forested areas to promote the regeneration and restoration of vegetation.

4.7 Conservation implications and applications

The Atlantic Forest presented a panorama of greater effect of vegetation loss and fragmentation than other biomes such as the Caatinga (Antongiovanni et al., 2018), the Cerrado (Pompeu et al., 2024) and the Amazon (Lapola et al., 2023). Despite this, due to their long history of occupation and degradation, valuable conservation lessons can be applied to these biomes, mainly in relation to the abundance of restoration studies carried out in the Atlantic Forest (Guerra et al., 2020). Guedes Pinto et al. (2023) highlight governance lessons from the Atlantic Forest that can be applied in the Brazilian Amazon: (i) to create large protected areas for conserved areas in public lands, (ii) to create protected areas in the hotspots of deforestation in private lands [Reserves of Natural Heritage (RPPN)], (iii) to create a specific legislation for the biome (such as AF Law) in addition to the FC, (iv) forest restoration of LR and PPA in accordance with the FC, and (v) ensure natural regeneration and stimulate it through mechanisms such as payment for ecosystem services. The authors also point out that the main lesson is regarding the urgency of these measures, given the context of climate crisis and ecosystem services, the formulation and implementation of these measures must be adopted urgently in the Amazon, unlike the Atlantic Forest. Similar measures can be adapted and applied to other biomes, such as Cerrado and Caatinga, which despite having less vegetation remnants than Amazon, can benefit from conservation lessons learned and implemented in the Atlantic Forest.

Complementary studies to this one should focus on prioritizing the restoration of the Atlantic Forest, such as that developed by Tambosi et al. (2014) in the Atlantic Forest and by Antongiovanni et al. (2022) in the Caatinga, for long-term planning of restoration and regeneration programs, while also accounting for land and social inequality (Melo et al. 2023). Additionally, studies must still focus on how compliance with the FC (restoration of RL and APP in private lands) can be beneficial for the structure of the landscape, such as that carried out by De Marco et al. (2023) in the Cerrado. Finally, there is an urgent need for studies to evaluate the quality of fragments in terms of successional stages, such as that carried out by Dias et al. (2023). Piffer et al. (2022b) point out that fragments regenerated <10 years ago are in the initial stages of regeneration and have limited protection from the AF Law and are mostly deforested, preventing the regeneration process and its benefits for biodiversity. Thus, Guedes Pinto et al. (2023) propose a review of the Atlantic Forest Law to become a Zero deforestation to prevent loss of forest in initial successional stages. Moreover, expansion of payment programs for ecosystem services (e.g. Conexão Mata Atlântica; https://conexaomataatlantica.mctic.gov.br/cma/portal), can be favorable for forest recovery (Ruggiero et al., 2019).

5 Conclusion

To our knowledge, this is the first study that analyzed the spatiotemporal dynamics of the entire Atlantic Forest landscape structure through multiple landscape metrics, considering a broad tri-national delimitation, not only for forest vegetation but also for other natural vegetation types, and including the effect of linear structure. This study adds to other work carried out in the Caatinga (Antongiovanni et al., 2018), the Cerrado (Pompeu et al., 2024) and the Brazilian Amazon (Guedes Pinto et al., 2023) to understand the dynamics of the landscape structure of these biomes through landscape metrics and propose governance lessons for conservation. Our findings allow a detailed understanding of the habitat fragmentation process in the AF in the last three and a half decades. The number of forest fragments has increased, which comes accompanied by a modest but essential increment of vegetation, mainly from natural regeneration. Besides that, natural vegetation fragments—fundamental to promoting connectivity—are far from being under sufficient protection. Overall, the fragmentation scenarios in Argentina, Brazil, and Paraguay are equally worrying (97% of fragments are very small and highly isolated, and more than half may be under edge effect). We highlight the substantial effect of roads and railways on breaking large FV fragments apart, likely disrupting the functional connectivity of several ecological processes. These findings reinforce the need for conservation and restoration actions considering linear infrastructure, and investing in implementing conservation plans for large fragments. Beyond that, promoting the connectivity of small fragments, managing the matrix to minimize edge effects and improve connectivity, and leading restoration actions in key areas, such as large and isolated fragments, are all measures of great importance. Added to potential coordinated actions, we highlight the importance of planning and building fauna passages to improve landscape connectivity and reduce wildlife roadkill. Finally, the recent increase in vegetation observed in the Atlantic Forest after 2005 appears to be related to two concomitant processes: mostly due to natural regeneration linked to the 2005 protection legislation (AF Law) and a long process of forest transition (abandonment of agricultural land), and to a lesser extent due to restoration associated with local initiatives such as the Pact for the Restoration of the Atlantic Forest started in 2009 and the implementation of the CAR began in 2012 by the FC. The continuity and expansion of these measures are essential to guarantee the continuity of this vegetation increase process in the future, given the intensified effects of climate change taking place and the further expansion of urban and agricultural areas.

Vancine, Maurício Humberto; Muylaert, Renata L.; Niebuhr, Bernardo Brandão; Oshima, Júlia Emi Faria; Tonetti, Vinicius; Bernardo, Rodrigo; de Angelo, Carlos; Rosa, Marcos Reis; Grohmann, Carlos Henrique; Ribeiro, Milton Cezar. The Atlantic Forest of South America: Spatiotemporal dynamics of the vegetation and implications for conservation. Biological Conservation 2024 ;Volum 291 10.1016/j.biocon.2024.110499

Funding

MHV was supported by grants #2013/02883-7, #2017/09676-8, and #2022/01899-6, São Paulo Research Foundation (FAPESP), and CAPES (grants 88887.513979/2020-00 and 1588183). RLM was supported by Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. BBN was supported by the NINA basic funding (Research Council of Norway, grant 160022/F40). CHG is a research fellow of the National Council for Scientific and Technological Development - CNPq (grant 311209/2021-1). JEFO was supported by grants #2014/23132-2, and #2021/02132-8, São Paulo Research Foundation (FAPESP). MCR was supported by grants #2013/50421-2, #2020/01779-5, #2021/08322-3, #2021/08534-0, #2021/10195-0, #2021/10639-5, #2022/10760-1, São Paulo Research Foundation (FAPESP) and CNPq (grants #442147/2020-1, #440145/2022-8, #402765/2021-4, #313016/2021-6, and #440145/2022-8), and São Paulo State University - UNESP for their financial support. This study was financed in part by CAPES Brazil – Finance Code 001. This study is also part of the *Center for Research on Biodiversity Dynamics and Climate Change*, grant #2021/10639-5, São Paulo Research Foundation (FAPESP).

CRediT authorship contribution statement

Maurício Humberto Vancine: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing, Funding acquisition, Project administration, Validation. **Renata L. Muylaert**: Conceptualization, Writing – review & editing, Supervision. **Bernardo Brandão Niebuhr**: Conceptualization, Methodology, Software, Supervision, Validation, Writing—review and editing. **Júlia Emi de Faria Oshima**: Conceptualization, Writing – review & editing. **Vinicius Tonetti**: Conceptualization, Writing – review & editing. **Rodrigo Bernardo**: Writing – review & editing. **Carlos De Angelo**: Writing – review & editing. Marcos Reis Rosa: Writing – review & editing. **Carlos Henrique Grohmann**: Methodology, Software, Writing – review & editing. **Milton Cezar Ribeiro**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Writing – review & editing, Validation.

Acknowledgements

We thank Luis Fernando Guedes Pinto from SOS Mata Atlântica for the assistance with MapBiomas data and Atlantic Forest delimitation, Alexandre Uezu for valuable contributions to the manuscript, Alejandro R. Vargas for the discussion about vegetation cover in Argentina and Paraguay, Maurício E. Graipel by for fruitful comments on the role of legislation in large-scale vegetation dynamics, and Daniela Sant'Ana for helping to understand the social and anthropological vision of Atlantic Forest conservation. Likewise, we thank all members from the Spatial Ecology and Conservation Lab (LEEC) for their help with fruitful discussions about the Atlantic Forest and its fragmentation process, especially Rafael Souza. MHV thanks Lauren Ono, João Giovanelli, Rodrigo Nobre, Rafael Fávero, Thiago Gonçalves-Souza, and Mathias Mistretta Pires for their suggestions on data analysis and discussion of results. We thank the Editor and two anonymous Reviewers for helping us to greatly improve this manuscript.

Data availability

Code for reproducing the analysis is provided in GitHub (https://github.com/LEEClab/ms-atlantic-forest-spatiotemporal-dynamics). Input data and code are provided in Open Science Files (OSF) (https://doi.org/10.17605/OSF.IO/RFWBZ). A comprehensive set of maps presenting the detailed methods and maps for the landscape metrics presented here is found in Vancine et al. (2023) and in Open Science Files (OSF) (https://doi.org/10.17605/OSF.IO/AJUMC).

References

Abra, F.D., Huijser, M.P., Magioli, M., Bovo, A.A.A., Ferraz, K.M.P.M. de B., 2021. An estimate of wild mammal roadkill in São Paulo state, Brazil. Heliyon 7, e06015.

Adorno, B.F.C.B., Barros, F.M., Cezar Ribeiro, M., da Silva, V.X., Hasui, É., 2021. Landscape heterogeneity shapes bird phylogenetic responses at forest–matrix interfaces in Atlantic Forest, Brazil. Biotropica 53, 409–421.

Antongiovanni, M., Venticinque, E.M., Fonseca, C.R., 2018. Fragmentation patterns of the Caatinga drylands. Landscape Ecology 33, 1353–1367.

Antongiovanni, M., Venticinque, E.M., Tambosi, L.R., Matsumoto, M., Metzger, J.P., Fonseca, C.R., 2022. Restoration priorities for Caatinga dry forests: Landscape resilience, connectivity and biodiversity value. Journal of Applied Ecology 59, 2287–2298.

Avigliano, E., Rosso, J.J., Lijtmaer, D., Ondarza, P., Piacentini, L., Izquierdo, M., Cirigliano, A., Romano, G., Nuñez Bustos, E., Porta, A., Mabragaña, E., Grassi, E., Palermo, J., Bukowski, B., Tubaro, P., Schenone, N., 2019. Biodiversity and threats in non-protected areas: A multidisciplinary and multi-taxa approach focused on the Atlantic Forest. Heliyon 5, e02292.

Awade, M., Metzger, J.P., 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecology 33, 863–871.

Banks-Leite, C., Ewers, R.M., Metzger, J.P., 2013. The confounded effects of habitat disturbance at the local, patch and landscape scale on understorey birds of the Atlantic Forest: Implications for the development of landscape-based indicators. Ecological Indicators 31, 82–88.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., Metzger, J.P., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345, 1041–1045.

Barbosa, K.V. de C., Knogge, C., Develey, P.F., Jenkins, C.N., Uezu, A., 2017. Use of small Atlantic Forest fragments by birds in Southeast Brazil. Natureza & Conservação 15, 42–46.

Benzeev, R., Zhang, S., Rauber, M.A., Vance, E.A., Newton, P., 2023. Formalizing tenure of Indigenous lands improved forest outcomes in the Atlantic Forest of Brazil. PNAS Nexus 2, pgac287.

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. Landscape and Urban Planning 204, 103948.

Bicudo da Silva, R.F., Moran, E., Viña, A., Millington, J.D.A., Dou, Y., Vieira, S.A., Lopez, M.C., Liu, J., 2023. Toward a forest transition across the Brazilian Atlantic Forest biome. Frontiers in Forests and Global Change 6, 1071495.

Bivand R., 2022. rgrass: Interface Between ‘GRASS’ Geographical Information System and ‘R’. R package version 0.3-6.

Brock, R.C., Arnell, A., Simonson, W., Soterroni, A.C., Mosnier, A., Ramos, F., Ywata de Carvalho, A.X., Camara, G., Pirker, J., Obersteiner, M., Kapos, V., 2021. Implementing Brazil’s Forest Code: a vital contribution to securing forests and conserving biodiversity. Biodiversity Conservation 30, 1621–1635.

Cassimiro, I.M.F., Ribeiro, M.C., Assis, J.C., 2023. How did the animal come to cross the road? Drawing insights on animal movement from existing roadkill data and expert knowledge. Landscape Ecology 38, 2035–2051.

Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., May, F., 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584, 238–243.

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. Conservation Letters 13, e12709.

Crouzeilles, R., Santiami, E., Rosa, M., Pugliese, L., Brancalion, P.H.S., Rodrigues, R.R., Metzger, J.P., Calmon, M., Scaramuzza, C.A. de M., Matsumoto, M.H., Padovezi, A., Benini, R. de M., Chaves, R.B., Metzker, T., Fernandes, R.B., Scarano, F.R., Schmitt, J., Lui, G., Christ, P., Vieira, R.M., Senta, M.M.D., Malaguti, G.A., Strassburg, B.B.N., Pinto, S., 2019. There is hope for achieving ambitious Atlantic Forest restoration commitments. Perspectives in Ecology and Conservation 17, 80–83.

Da Ponte, E., Mack, B., Wohlfart, C., Rodas, O., Fleckenstein, M., Oppelt, N., Dech, S., Kuenzer, C., 2017. Assessing Forest Cover Dynamics and Forest Perception in the Atlantic Forest of Paraguay, Combining Remote Sensing and Household Level Data. Forests 8, 389.

Da Silva, J.M., Casteleti, C.H.M., 2003. Status of the Biodiversity of the Atlantic Forest of Brazil, in: Galindo-Leal, C., Câmara, I. (Eds.), Washington (DC): C. Galind-Leal, IG Câmara. The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook. Conservation International. Pp. 3–11.

da Silva, R.F.B., de Castro Victoria, D., Nossack, F.Á., Viña, A., Millington, J.D.A., Vieira, S.A., Batistella, M., Moran, E., Liu, J., 2023. Slow-down of deforestation following a Brazilian forest policy was less effective on private lands than in all conservation areas. Communication Earth & Environment 4, 1–12.

Dale, M.R.T., Fortin, M.-J., 2014. Spatial analysis: a guide for ecologists, Second Edition. Ed. Cambridge University Press, Cambridge; New York.

Dam, J. van, Hombergh, H. van den, Hilders, M., 2019. An analysis of existing laws on forest protection in the main soy-producing countries in Latin America.

de la Sancha, N.U., González-Maya, J.F., Boyle, S.A., Pérez-Estigarribia, P.E., Urbina-Cardona, J.N., McIntyre, N.E., 2023. Bioindicators of edge effects within Atlantic Forest remnants: Conservation implications in a threatened biodiversity hotspot. Diversity and Distributions 29, 349–363.

de Lima, R.A.F., Oliveira, A.A., Pitta, G.R., de Gasper, A.L., Vibrans, A.C., Chave, J., ter Steege, H., Prado, P.I., 2020. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nature Communication 11, 6347.

de Lima, R.A.F., Dauby, G., de Gasper, A.L., Fernandez, E.P., Vibrans, A.C., Oliveira, A.A. de, Prado, P.I., Souza, V.C., F. de Siqueira, M., ter Steege, H., 2024. Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383, 219–225.

De Marco, P., De Souza, R.A., F. A. Andrade, A., Villén-Pérez, S., Nóbrega, C.C., Campello, L.M., Caldas, M., 2023. The value of private properties for the conservation of biodiversity in the Brazilian Cerrado. Science 380, 298–301.

Dias, T. da C., Silveira, L.F., Francisco, M.R., 2023. Spatiotemporal dynamics reveals forest rejuvenation, fragmentation, and edge effects in an Atlantic Forest hotspot, the Pernambuco Endemism Center, northeastern Brazil. PLOS ONE 18, e0291234.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience 67, 534–545.

Diniz, C., Cortinhas, L., Nerino, G., Rodrigues, J., Sadeck, L., Adami, M., Souza-Filho, P., 2019. Brazilian Mangrove Status: Three Decades of Satellite Data Analysis. Remote Sensing 11, 808.

Diniz, M.F., Coelho, M.T.P., de Sousa, F.G., Hasui, É., Loyola, R., 2021. The underestimated role of small fragments for carnivore dispersal in the Atlantic Forest. Perspectives in Ecology and Conservation 19, 81–89.

dos Santos, J.F.C., Gleriani, J.M., Velloso, S.G.S., De Souza, G.S.A., Do Amaral, C.H., Torres, F.T.P., Medeiros, N.D.G., Dos Reis, M., 2019. Wildfires as a major challenge for natural regeneration in Atlantic Forest. Science of The Total Environment 650, 809–821.

Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487–515.

Fahrig, L., Watling, J.I., Arnillas, C.A., Arroyo-Rodríguez, V., Jörger-Hickfang, T., Müller, J., Pereira, H.M., Riva, F., Rösch, V., Seibold, S., Tscharntke, T., May, F., 2022. Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. Biological Reviews 97, 99–114.

Faria, D., Morante-Filho, J.C., Baumgarten, J., Bovendorp, R.S., Cazetta, E., Gaiotto, F.A., Mariano-Neto, E., Mielke, M.S., Pessoa, M.S., Rocha-Santos, L., Santos, A.S., Soares, L.A.S.S., Talora, D.C., Vieira, E.M., Benchimol, M., 2023. The breakdown of ecosystem functionality driven by deforestation in a global biodiversity hotspot. Biological Conservation 283, 110126.

Figueiredo, M.S.L., Weber, M.M., Brasileiro, C.A., Cerqueira, R., Grelle, C.E.V., Jenkins, C.N., Solidade, C.V., Thomé, M.T.C., Vale, M.M., Lorini, M.L., 2021. Tetrapod Diversity in the Atlantic Forest: Maps and Gaps, in: Marques, M.C.M., Grelle, C.E.V. (Eds.), The Atlantic Forest. Springer International Publishing, Cham, pp. 185–204.

Fischer, R., Taubert, F., Müller, M.S., Groeneveld, J., Lehmann, S., Wiegand, T., Huth, A., 2021. Accelerated forest fragmentation leads to critical increase in tropical forest edge area. Science Advances 7, eabg7012.

Flora e Funga do Brasil. 2023. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br. Accessed on: 10 Oct 2023.

Fundación Vida Silvestre Argentina & WWF. 2017. State of the Atlantic Forest: Three Countries, 148 Million People, One of the Richest Forests on Earth. Fundación Vida Silvestre Argentina & WWF. Puerto Iguazú, Argentina. Pp 146.

Galetti, M., Gonçalves, F., Villar, N., Zipparro, V.B., Paz, C., Mendes, C., Lautenschlager, L., Souza, Y., Akkawi, P., Pedrosa, F., Bulascoschi, L., Bello, C., Sevá, A.P., Sales, L., Genes, L., Abra, F., Bovendorp, R.S., 2021. Causes and Consequences of Large-Scale Defaunation in the 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. 297–324.

Gama-Rodrigues, A.C., Müller, M.W., Gama-Rodrigues, E.F., Mendes, F.A.T., 2021. Cacao-based agroforestry systems in the Atlantic Forest and Amazon Biomes: An ecoregional analysis of land use. Agricultural Systems 194, 103270.

Gerhardt, C.H., 2016. “Eu seria péssima pra estar na sua banca”: pesquisadores e suas controvérsias sobre áreas protegidas, 1ª ed. Appris Editora.

Guedes Pinto, L.F., Ferreira, J., Berenguer, E., Rosa, M., 2023. Governance lessons from the Atlantic Forest to the conservation of the Amazon. Perspectives in Ecology and Conservation 21, 1–5.

Guerra, A., Reis, L.K., Borges, F.L.G., Ojeda, P.T.A., Pineda, D.A.M., Miranda, C.O., Maidana, D.P.F. de L., Santos, T.M.R. dos, Shibuya, P.S., Marques, M.C.M., Laurance, S.G.W., Garcia, L.C., 2020. Ecological restoration in Brazilian biomes: Identifying advances and gaps. Forest Ecology and Management 458, 117802.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances 1, e1500052.

Hansen, M.C., Wang, L., Song, X.-P., Tyukavina, A., Turubanova, S., Potapov, P.V., Stehman, S.V., 2020. The fate of tropical forest fragments. Science Advances 6, eaax8574.

Harper, K.A., Macdonald, S.E., 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. Ecosphere 2, art94.

Harper, K.A., Yang, J.R., Dazé Querry, N., Dyer, J., Alves, R.S.C., Ribeiro, M.C., 2023. Limited influence from edges and topography on vegetation structure and diversity in Atlantic Forest. Plant Ecology. https://doi.org/10.1007/s11258-023-01353-x.

Hatfield, J.H., Harrison, M.L.K., Banks-Leite, C., 2018a. Functional Diversity Metrics: How They Are Affected by Landscape Change and How They Represent Ecosystem Functioning in the Tropics. Current Landscape Ecology Reports 3, 35–42.

Hatfield, J.H., Orme, C.D.L., Banks-Leite, C., 2018b. Using functional connectivity to predict potential meta-population sizes in the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16, 215–220.

IBGE — Instituto Brasileiro de Geografia e Estatística, 2019. Biomas e Sistema Costeiro-Marinho do Brasil — 1:250000. Available at: https://www.ibge.gov.br/geociencias/cartas-e-mapas/informacoes-ambientais/15842-biomas.html?=&t=acesso-ao-produto.

IBGE — Instituto Brasileiro de Geografia e Estatística, 2021. Bases cartográficas contínuas — 1:250000. Available at: https://www.ibge.gov.br/geociencias/downloads-geociencias.html?caminho=cartas_e_mapas/bases_cartograficas_continuas/bc250/versao2021/.

Izquierdo, A., C. De Angelo & M. Aide. 2008. Thirty years of human demography and land-use change in the Atlantic Forest of Misiones, Argentina: a test of the forest transition model. Ecology and Society 13, 3.

Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist 204, 459–473.

Jung, M., Arnell, A., de Lamo, X., García-Rangel, S., Lewis, M., Mark, J., Merow, C., Miles, L., Ondo, I., Pironon, S., Ravilious, C., Rivers, M., Schepashenko, D., Tallowin, O., van Soesbergen, A., Govaerts, R., Boyle, B.L., Enquist, B.J., Feng, X., Gallagher, R., Maitner, B., Meiri, S., Mulligan, M., Ofer, G., Roll, U., Hanson, J.O., Jetz, W., Di Marco, M., McGowan, J., Rinnan, D.S., Sachs, J.D., Lesiv, M., Adams, V.M., Andrew, S.C., Burger, J.R., Hannah, L., Marquet, P.A., McCarthy, J.K., Morueta-Holme, N., Newman, E.A., Park, D.S., Roehrdanz, P.R., Svenning, J.-C., Violle, C., Wieringa, J.J., Wynne, G., Fritz, S., Strassburg, B.B.N., Obersteiner, M., Kapos, V., Burgess, N., Schmidt-Traub, G., Visconti, P., 2021. Areas of global importance for conserving terrestrial biodiversity, carbon and water. Nature Ecology & Evolution 5, 1–11.

Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E.O.C., Berenguer, E., Carmenta, R., Liddy, H.M., Seixas, H., Silva, C.V.J., Silva-Junior, C.H.L., Alencar, A.A.C., Anderson, L.O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M.H., Faria, B.L., Fearnside, P.M., Ferreira, J., Gatti, L., Gutierrez-Velez, V.H., Han, Z., Hibbard, K., Koven, C., Lawrence, P., Pongratz, J., Portela, B.T.T., Rounsevell, M., Ruane, A.C., Schaldach, R., da Silva, S.S., von Randow, C., Walker, W.S., 2023. The drivers and impacts of Amazon forest degradation. Science 379, eabp8622.

Lyra-Jorge, M.C., Ribeiro, M.C., Ciocheti, G., Tambosi, L.R., Pivello, V.R., 2010. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. European Journal of Wildlife Research 56, 359–368.

Magioli, M., Ribeiro, M.C., Ferraz, K.M.P.M.B., Rodrigues, M.G., 2015. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Animal Conservation 18, 499–511.

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V., Edwards, D.P., 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Functional Ecology 31, 542–552.

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V., Meira-Neto, J.A.A., 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodiversity and Conservation 24, 2305–2318.

Marjakangas, E., Abrego, N., Grøtan, V., Lima, R.A.F., Bello, C., Bovendorp, R.S., Culot, L., Hasui, É., Lima, F., Muylaert, R.L., Niebuhr, B.B., Oliveira, A.A., Pereira, L.A., Prado, P.I., Stevens, R.D., Vancine, M.H., Ribeiro, M.C., Galetti, M., Ovaskainen, O., 2020. Fragmented tropical forests lose mutualistic plant–animal interactions. Diversity and Distribution 26, 154–168.

Marques, M.C.M., Trindade, W., Bohn, A., Grelle, C.E.V., 2021. The Atlantic Forest: An Introduction to the Megadiverse Forest of South America, 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. 3–23.

Martinez Pardo, J., Saura, S., Insaurralde, A., Di Bitetti, M.S., Paviolo, A., De Angelo, C., 2023. Much more than forest loss: four decades of habitat connectivity decline for Atlantic Forest jaguars. Landscape Ecology, 38, 41-57.

Melo, F.P.L., Mazzochini, G.G., Guidotti, V., Manhães, A.P., 2023. Using land inequality to inform restoration strategies for the Brazilian dry forest. Landscape and Urban Planning 239, 104844.

Melo, F.P.L., Pinto, S.R.R., Brancalion, P.H.S., Castro, P.S., Rodrigues, R.R., Aronson, J., Tabarelli, M., 2013. Priority setting for scaling-up tropical forest restoration projects: Early lessons from the Atlantic Forest Restoration Pact. Environmental Science &

Policy 33, 395–404.

Mohebalian, P.M., Lopez, L.N., Tischner, A.B., Aguilar, F.X., 2022. Deforestation in South America's tri-national Paraná Atlantic Forest: Trends and associational factors. Forest Policy and Economics 137, 102697.

Morante-Filho, J.C., Arroyo-Rodríguez, V., Pessoa, M. de S., Cazetta, E., Faria, D., 2018. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. Ecological Applications 28, 2024–2032.

Muylaert, R.L., Stevens, R.D., Ribeiro, M.C., 2016. Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. Ecological Applications 26, 1854–1867.

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B., Ribeiro, M.C., 2018. Uma nota sobre os limites territoriais da Mata Atlântica. Oecologia Australis 22, 302–311.

Niebuhr, B.B.S., Vancine, M.H., Martello, F., Ribeiro, J.W., Muylaert, R.L., Campos, V.E.W., Santos, J.S., Tonetti, V.R., Ribeiro, M.C. Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics. In preparation. https://github.com/LEEClab/LS_METRICS.

Neteler, M., Bowman, M.H., Landa, M., Metz, M., 2012. GRASS GIS: A multi-purpose open source GIS. Environmental Modelling & Software 31, 124–130.

Parra-Sanchez, E., Banks-Leite, C., 2020. The magnitude and extent of edge effects on vascular epiphytes across the Brazilian Atlantic Forest. Scientific Reports 10, 18847.

Paviolo, A., C. De Angelo, K. M. P. M. B. Ferraz, R. G. Morato, J. Martínez Pardo, A. C. Srbek-Araujo, B. Beisegel, F. Lima, D. Sana, M. Xavier da Silva, M. Velázquez, L. Cullen Jr, P. G. Crawshaw Jr., M. L. S. P. Jorge, P. M. Galetti Jr, M. S. Di Bitetti, R. Cunha de Paula, E. Eizirik, T. M. Aide, M. P. Cruz, M. Perilli, A. S. M. C. Souza, V. A. Quiroga, E. Nakaro, F. Ramírez, S. Fernández, S. A. Costa, E. A. Moraes & F. C. C. Azevedo. 2016. A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. Scientific Reports 6, 37147.

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, Fascinating Life Sciences. Springer International Publishing, Cham, pp. 415–447.

Piffer, P.R., Calaboni, A., Rosa, M.R., Schwartz, N.B., Tambosi, L.R., Uriarte, M., 2022a. Ephemeral forest regeneration limits carbon sequestration potential in the Brazilian Atlantic Forest. Global Change Biology 28, 630–643.

Piffer, P.R., Rosa, M.R., Tambosi, L.R., Metzger, J.P., Uriarte, M., 2022b. Turnover rates of regenerated forests challenge restoration efforts in the Brazilian Atlantic forest. Environmental Research Letters 17, 045009.

Pinto, S.R., Melo, F., Tabarelli, M., Padovesi, A., Mesquita, C.A., De Mattos Scaramuzza, C.A., Castro, P., Carrascosa, H., Calmon, M., Rodrigues, R., César, R.G., Brancalion, P.H.S., 2014. Governing and Delivering a Biome-Wide Restoration Initiative: The Case of Atlantic Forest Restoration Pact in Brazil. Forests 5, 2212–2229.

Pivello, V.R., Vieira, I., Christianini, A.V., Ribeiro, D.B., da Silva Menezes, L., Berlinck, C.N., Melo, F.P.L., Marengo, J.A., Tornquist, C.G., Tomas, W.M., Overbeck, G.E., 2021. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspectives in Ecology and Conservation 19, 233–255.

Pompeu, J., Assis, T.O., Ometto, J.P., 2024. Landscape changes in the Cerrado: Challenges of land clearing, fragmentation and land tenure for biological conservation. Science of The Total Environment 906, 167581.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., Pardini, R., Vieira, M.V., Banks-Leite, C., Fonseca, C.R., Metzger, J.P., Accacio, G.M., Alexandrino, E.R., Barros, C.S., Bogoni, J.A., Boscolo, D., Brancalion, P.H.S., Bueno, A.A., Cambui, E.C.B., Canale, G.R., Cerqueira, R., Cesar, R.G., Colletta, G.D., Delciellos, A.C., Dixo, M., Estavillo, C., Esteves, C.F., Falcão, F., Farah, F.T., Faria, D., Ferraz, K.M.P.M.B., Ferraz, S.F.B., Ferreira, P.A., Graipel, M.E., Grelle, C.E.V., Hernández, M.I.M., Ivanauskas, N., Laps, R.R., Leal, I.R., Lima, M.M., Lion, M.B., Magioli, M., Magnago, L.F.S., Mangueira, J.R.A.S., Marciano-Jr, E., Mariano-Neto, E., Marques, M.C.M., Martins, S.V., Matos, M.A., Matos, F.A.R., Miachir, J.I., Morante-Filho, J.M., Olifiers, N., Oliveira-Santos, L.G.R., Paciencia, M.L.B., Paglia, A.P., Passamani, M., Peres, C.A., Pinto Leite, C.M., Porto, T.J., Querido, L.C.A., Reis, L.C., Rezende, A.A., Rigueira, D.M.G., Rocha, P.L.B., Rocha-Santos, L., Rodrigues, R.R., Santos, R.A.S., Santos, J.S., Silveira, M.S., Simonelli, M., Tabarelli, M., Vasconcelos, R.N., Viana, B.F., Vieira, E.M., Prevedello, J.A., 2020. Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. Biological Conservation 241, 108368.

QGIS Development Team, 2023. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rambaldi, D M., Fernandes, R.V., Schmidt, M.A.R., 2005. Private protected areas and their key role in the conservation of the Atlantic Forest biodiversity hotspot, Brazil. Parks 15, 30–38.

Reis, R.E., Albert, J.S., Di Dario, F., Mincarone, M.M., Petry, P., Rocha, L.A., 2016. Fish biodiversity and conservation in South America. Journal of Fish Biology 89, 12–47.

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 hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16, 208–214.

Ribeiro, M.C., Martensen, A.C., Metzger, J.P., Tabarelli, M., Scarano, F., Fortin, M.-J., 2011. The Brazilian Atlantic Forest: A Shrinking Biodiversity Hotspot, in: Zachos, F.E., Habel, J.C. (Eds.), Biodiversity Hotspots. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 405–434.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142, 1141–1153.

Riva, F., Nielsen, S.E., 2020. Six key steps for functional landscape analyses of habitat change. Landscape Ecology 35, 1495–1504.

Rosa, M.R., Brancalion, P.H.S., Crouzeilles, R., Tambosi, L.R., Piffer, P.R., Lenti, F.E.B., Hirota, M., Santiami, E., Metzger, J.P., 2021. Hidden destruction of older forests threatens Brazil’s Atlantic Forest and challenges restoration programs. Scientific Advances 7, eabc4547.

Rudel, T.K., Coomes, O.T., Moran, E., Achard, F., Angelsen, A., Xu, J., Lambin, E., 2005. Forest transitions: towards a global understanding of land use change. Global Environmental Change 15, 23–31.

Ruggiero, P.G.C., Metzger, J.P., Reverberi Tambosi, L., Nichols, E., 2019. Payment for ecosystem services programs in the Brazilian Atlantic Forest: Effective but not enough. Land Use Policy 82, 283–291.

Scarano, F.R., 2002. Structure, Function and Floristic Relationships of Plant Communities in Stressful Habitats Marginal to the Brazilian Atlantic Rainforest. Annual of Botany 90, 517–524.

Silva, R.F.B. da, Batistella, M., Moran, E.F., 2017. Socioeconomic changes and environmental policies as dimensions of regional land transitions in the Atlantic Forest, Brazil. Environmental Science & Policy 74, 14–22.

Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L.A., Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. Biological Conservation 177, 12–24.

Song, X.-P., Hansen, M.C., Stehman, S.V., Potapov, P.V., Tyukavina, A., Vermote, E.F., Townshend, J.R., 2018. Global land change from 1982 to 2016. Nature 560, 639–643.

Solórzano, A., Brasil, L.S.C. de A., 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.

Souza, C.M., Z. Shimbo, J., Rosa, M.R., Parente, L.L., A. Alencar, A., Rudorff, B.F.T., Hasenack, H., Matsumoto, M., G. Ferreira, L., Souza-Filho, P.W.M., de Oliveira, S.W., Rocha, W.F., Fonseca, A.V., Marques, C.B., Diniz, C.G., Costa, D., Monteiro, D., Rosa, E.R., Vélez-Martin, E., Weber, E.J., Lenti, F.E.B., Paternost, F.F., Pareyn, F.G.C., Siqueira, J.V., Viera, J.L., Neto, L.C.F., Saraiva, M.M., Sales, M.H., Salgado, M.P.G., Vasconcelos, R., Galano, S., Mesquita, V.V., Azevedo, T., 2020. Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. Remote Sensing 12, 2735.

Sparovek, G., Berndes, G., Barretto, A.G.D.O.P., Klug, I.L.F., 2012. The revision of the Brazilian Forest Act: increased deforestation or a historic step towards balancing agricultural development and nature conservation? Environmental Science & Policy 16, 65–72.

Sparovek, G., Reydon, B.P., Guedes Pinto, L.F., Faria, V., de Freitas, F.L.M.,Azevedo-Ramos, C., Gardner, T., Hamamura, C., Rajão, R., Cerignoni, F., Siqueira,G.P., Carvalho, T., Alencar, A., Ribeiro, V., 2019. Who owns Brazilian lands? Land Use Policy 87, 104062.

Szangolies, L., Rohwäder, M.-S., Jeltsch, F., 2022. Single large AND several small habitat patches: A community perspective on their importance for biodiversity. Basic and Applied Ecology 65, 16–27.

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. Biological Conservation 143, 2328–2340.

Tambosi, L.R., Martensen, A.C., Ribeiro, M.C., Metzger, J.P., 2014. A Framework to Optimize Biodiversity Restoration Efforts Based on Habitat Amount and Landscape Connectivity: Optimizing Restoration Based on Landscape Resilience. Restoration Ecology 22, 169–177.

Tavares, A., Beiroz, W., Fialho, A., Frazão, F., Macedo, R., Louzada, J., Audino, L., 2019. Eucalyptus plantations as hybrid ecosystems: Implications for species conservation in the Brazilian Atlantic forest. Forest Ecology and Management 433, 131–139.

Teixeira, F.Z., Kindel, A., Hartz, S.M., Mitchell, S., Fahrig, L., 2017. When road-kill hotspots do not indicate the best sites for road-kill mitigation. Journal of Applied Ecology 54, 1544–1551.

Teixeira, F.Z., Silva, L.G. da, Abra, F., Rosa, C., Buss, G., Guerreiro, M., Costa, E.R., Medeiros, A.S. de M., Gordo, M., Secco, H., 2022. A review of the application of canopy bridges in the conservation of primates and other arboreal animals across Brazil. Folia Primatologica 93, 479–492.

Tubenchlak, F., Badari, C.G., de Freitas Strauch, G., de Moraes, L.F.D., 2021. Changing the Agriculture Paradigm in the Brazilian Atlantic Forest: The Importance of Agroforestry, in: Marques, M.C.M., Grelle, C.E.V. (Eds.), The Atlantic Forest. Springer International Publishing, Cham, pp. 369–388.

Turner, M.G., Gardner, R.H., 2015. Landscape Ecology in Theory and Practice. Springer New York, New York, NY.

Vale, M.M., Arias, P.A., Ortega, G., Cardoso, M., Oliveira, B.F.A., Loyola, R., Scarano, F.R., 2021. Climate Change and Biodiversity in the Atlantic Forest: Best Climatic Models, Predicted Changes and Impacts, and Adaptation Options, 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. 253–267.

Vancine, M. H., Niebuhr B. B., Muylaert R. L., Oshima J. E. F., Tonetti V., Bernardo R., Alves R. S. C., Zanette E. M., Souza V. C., Giovanelli J. G. R., Grohmann C. H., Galetti M., Ribeiro, M. C. 2023. ATLANTIC SPATIAL: a data set of landscape, topographic, hydrologic and anthropogenic metrics for the Atlantic Forest. EcoEvoRxiv. https://doi.org/10.32942/X26P58.

Varassin, I.G., Agostini, K., Wolowski, M., Freitas, L., 2021. Pollination Systems in the Atlantic Forest: Characterisation, Threats, and Opportunities, 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. 325–344.

van Moorter, B., Kivimäki, I., Panzacchi, M., Saura, S., Niebuhr, B. B., Strand, O., Saerens, M. 2023. Habitat functionality: Integrating environmental and geographic space in niche modeling for conservation planning. Ecology 104, e4105.

Zalles, V., Hansen, M.C., Potapov, P.V., Parker, D., Stehman, S.V., Pickens, A.H., Parente, L.L., Ferreira, L.G., Song, X.-P., Hernandez-Serna, A., Kommareddy, I., 2021. Rapid expansion of human impact on natural land in South America since 1985. Science Advances 7, eabg1620.

Figures

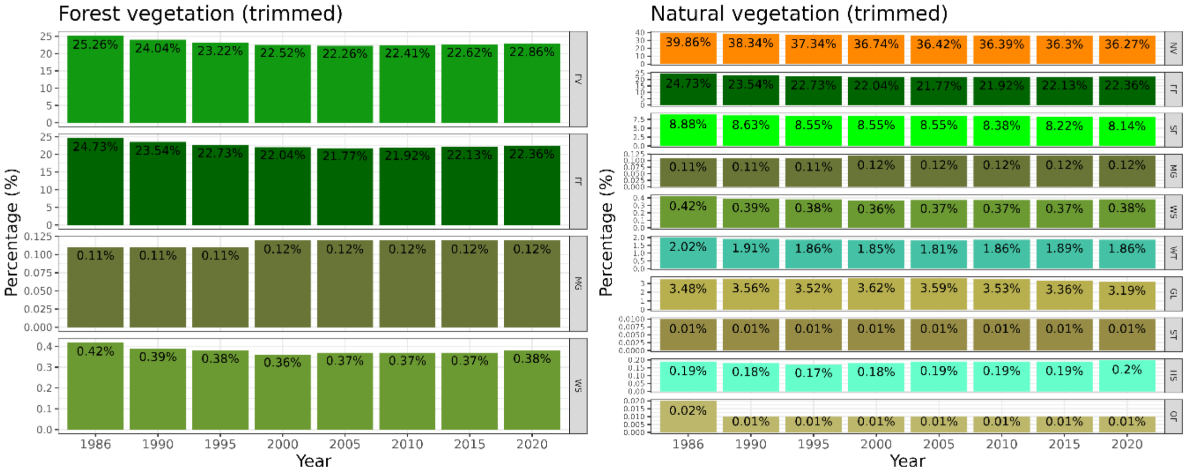
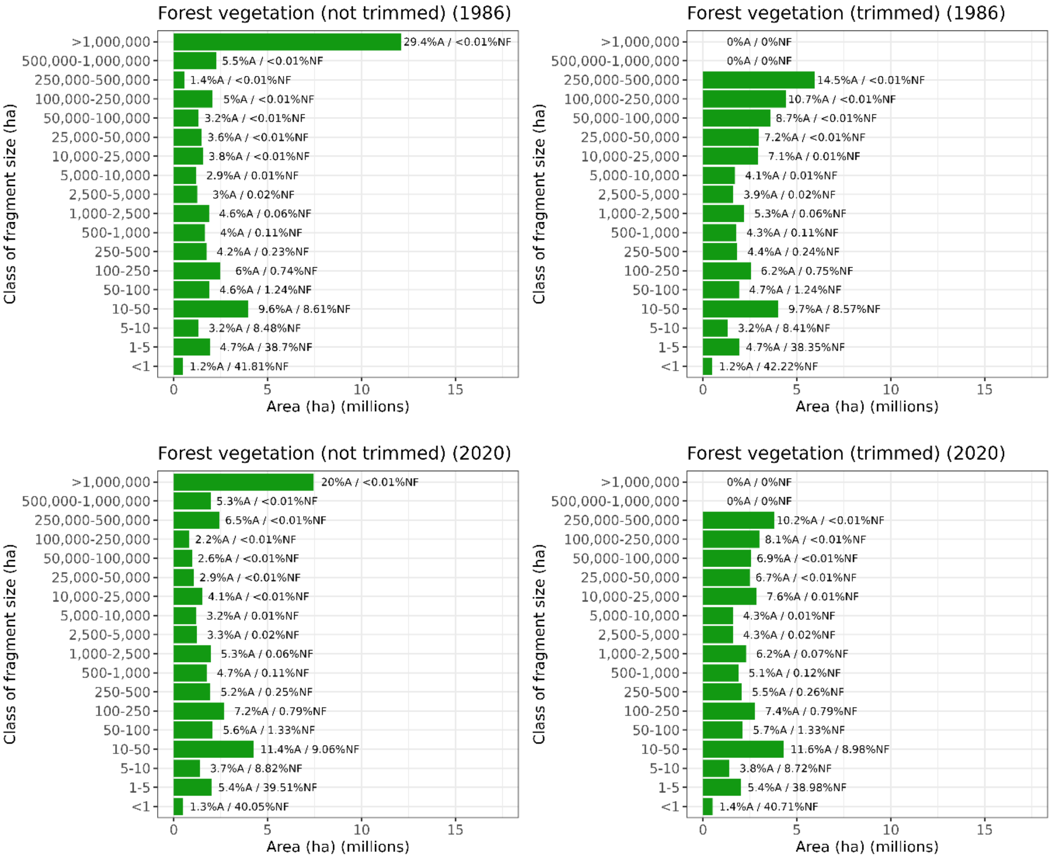


Figure 1. Vegetation cover for Forest Vegetation (FV) and Natural Vegetation (NV) through the years for the whole Atlantic Forest limit, trimmed by roads and railways. Abbreviations: Forest Formation (FF), Mangrove (MG), Wooded Sandbank Vegetation (*restinga*) (WS), Savanna Formation (SF), Wetland (WT), Grassland (GL), Salt Flat (ST), Herbaceous Sandbank Vegetation (HS), Other Non-Forest Formations (OF).



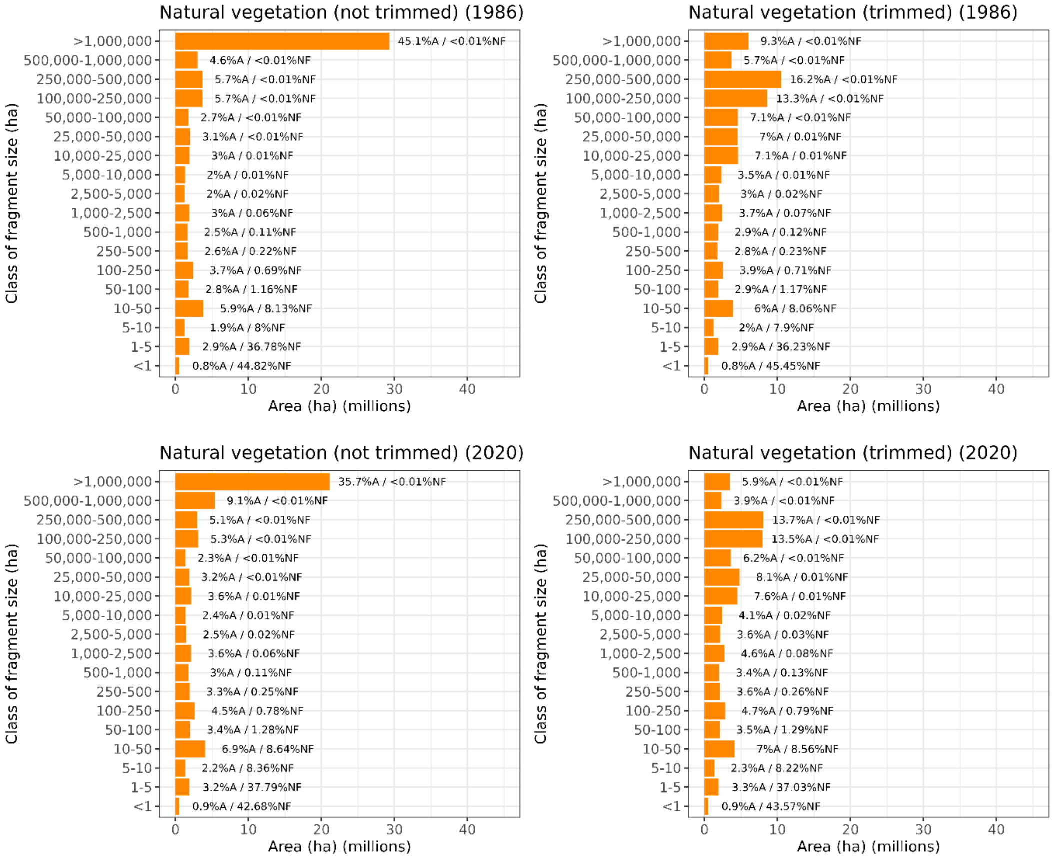


Figure 2. Distribution of Forest Vegetation (FV) and Natural Vegetation (NV) fragment sizes across the AF (1986 and 2020), trimmed and not trimmed by linear infrastructure. %A: percentage of the total area; %NF: percentage of the number of fragments. See Fig. 3S for other years (1990–2015). Please note the difference scales in the x-axis between the FV and NV plots.

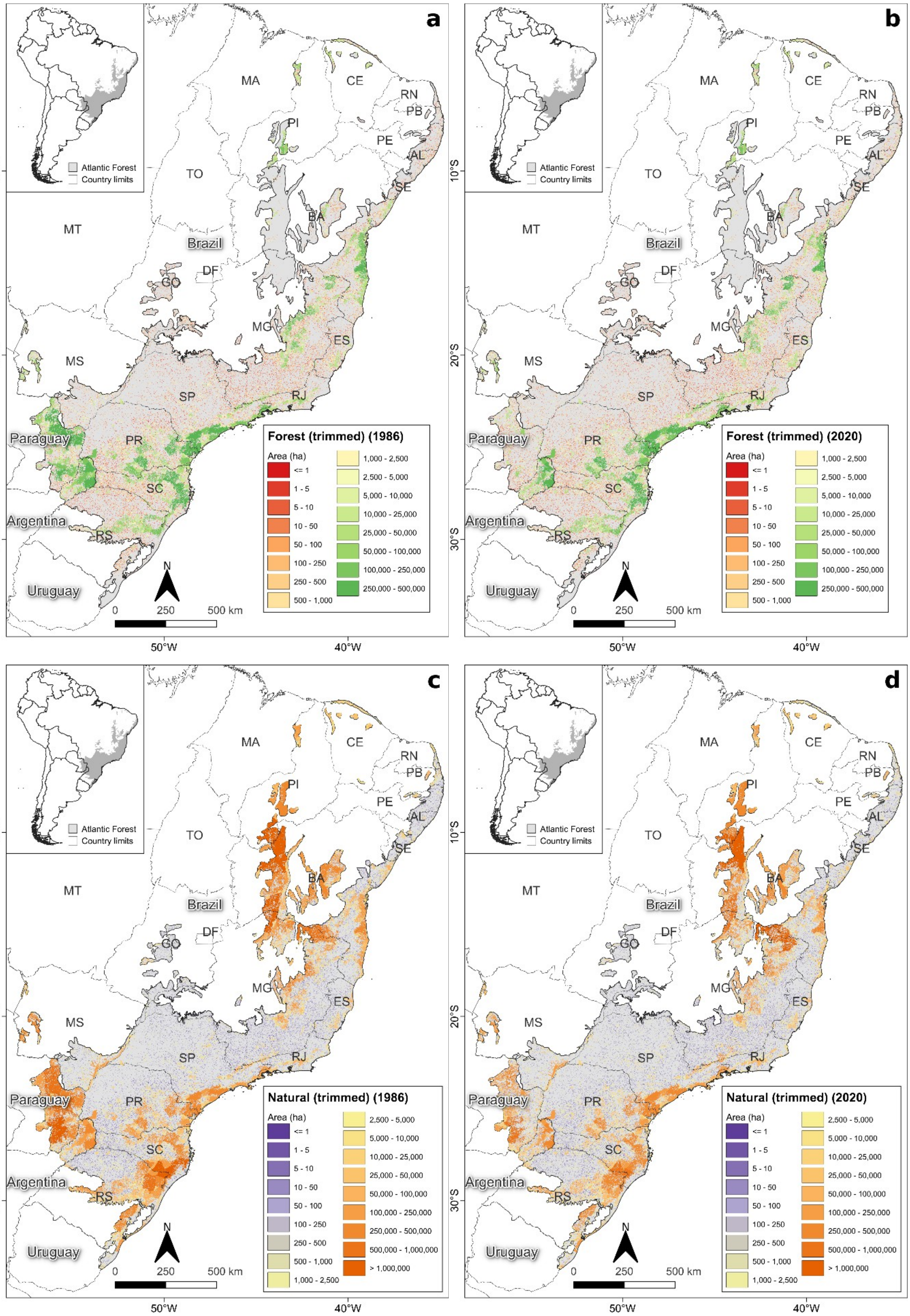


Figure 3. Fragment area for Forest Vegetation (FV) in 1986 (a) and 2020 (b), and for Natural Vegetation (NV) in 1986 (c) and 2020 (d), trimmed by roads and railways for the entire AF.

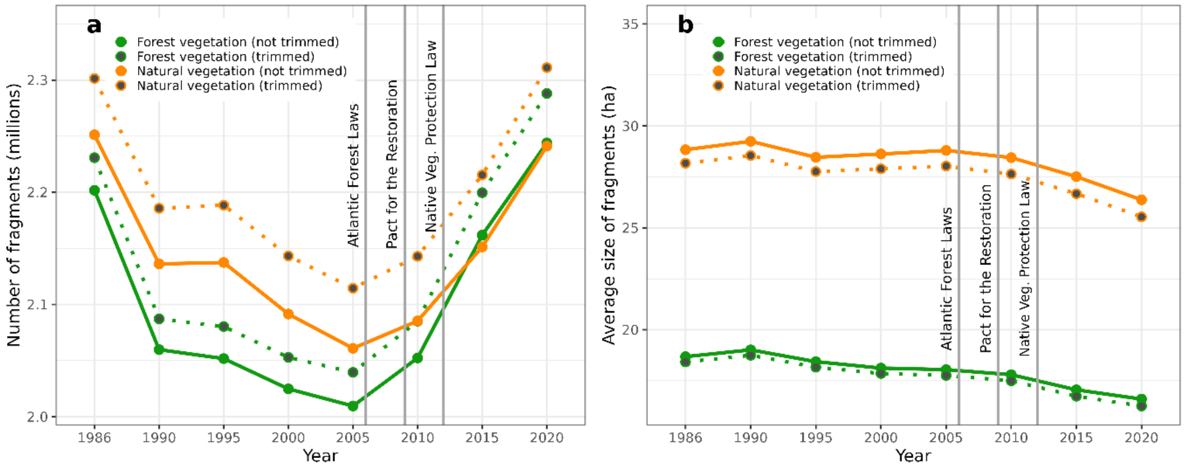


Figure 4. Distribution of (a) number of fragments and (b) average fragment sizes of Forest Vegetation (FV) and Natural Vegetation (NV) across the AF from 1986 to 2020, trimmed and not trimmed by roads and railways. The gray lines represent reference years when important legislation and restoration programs were created in Brazil (See Discussion for details).

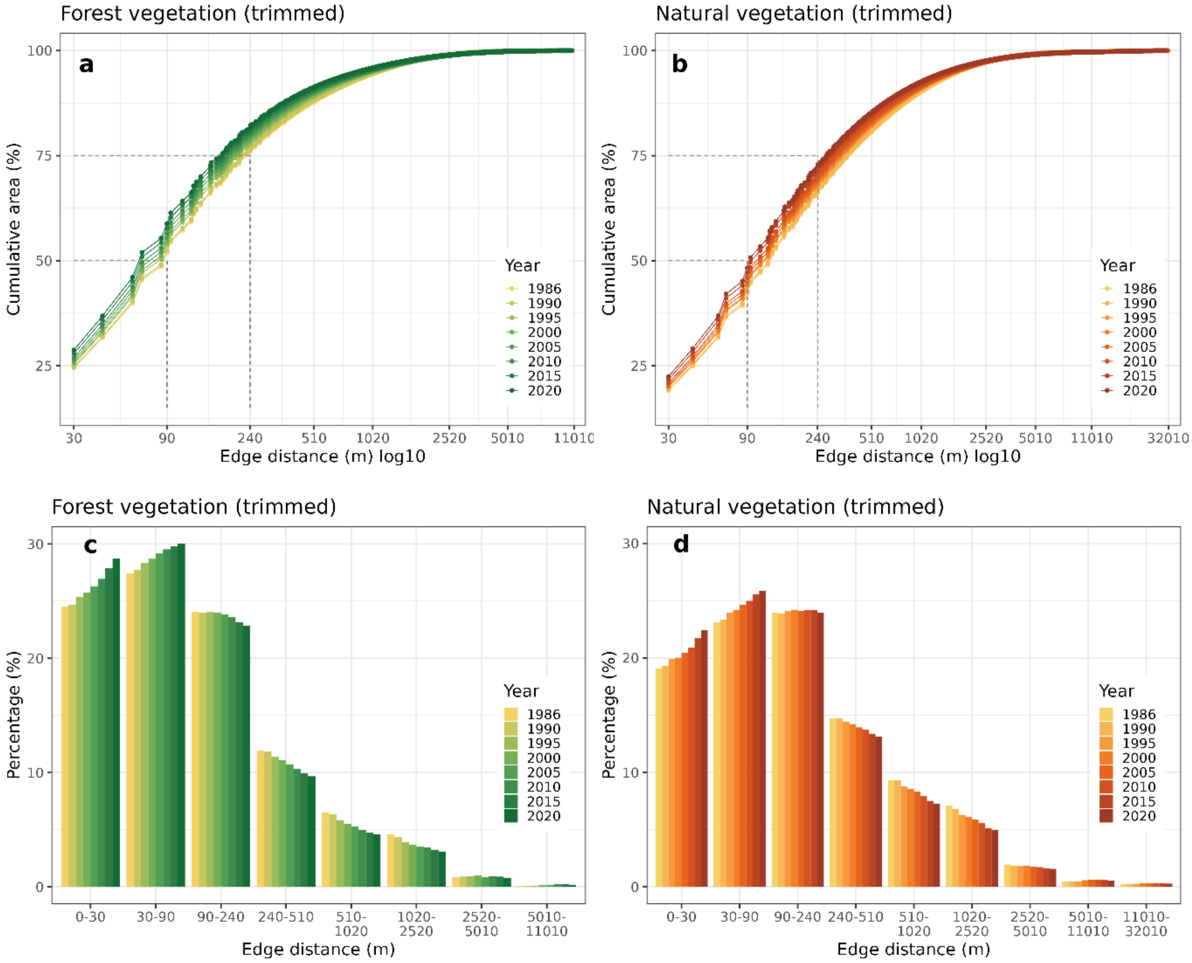


Figure 5. Cumulative (a and b) and per class (c and d) area under edge effect at different depths for the Forest Vegetation (FV) and Natural Vegetation (NV) in the AF trimmed by roads and railways. See Fig. S6 for not trimmed scenario.

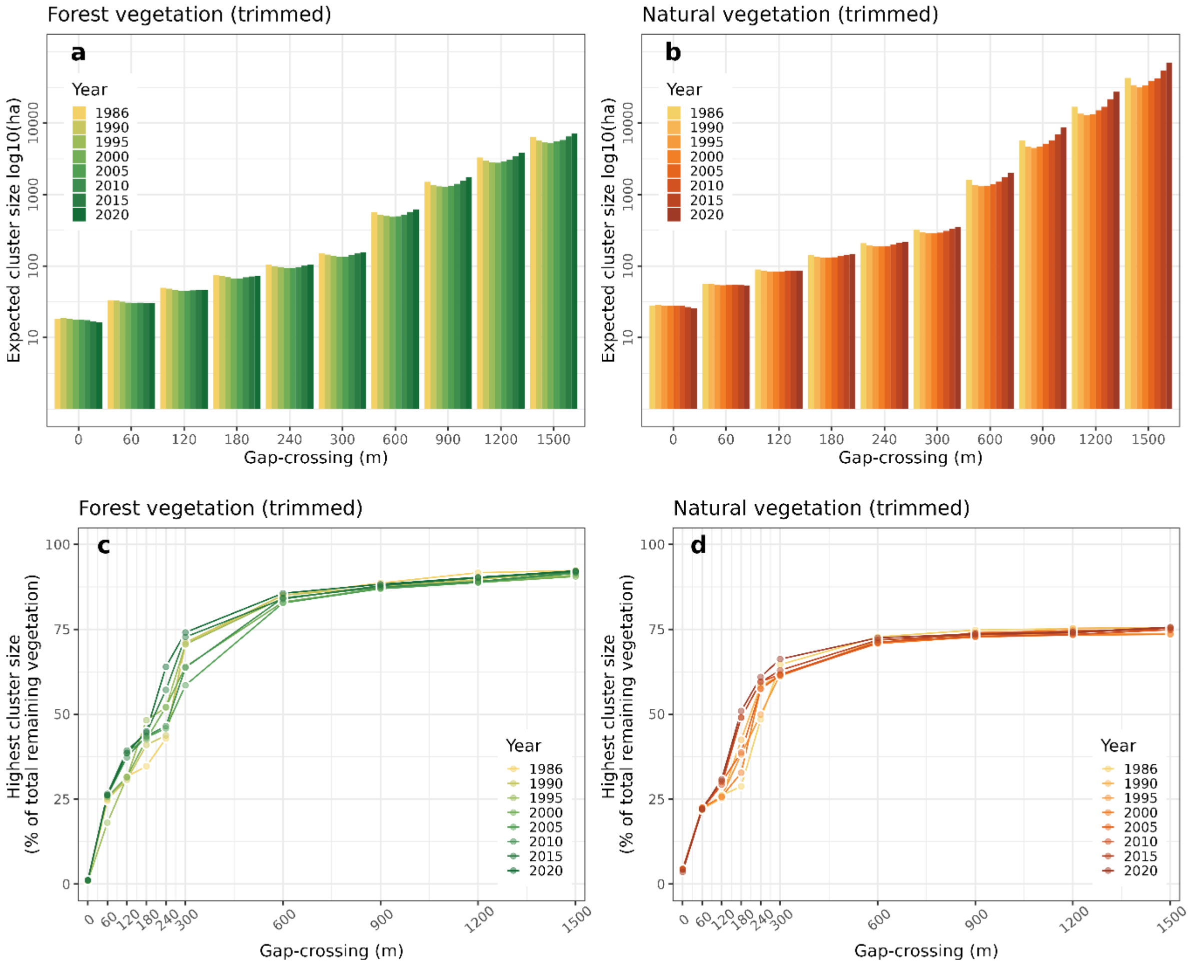


Figure 6. Expected cluster size (a-b) (average functional size; ha) of functionally connected fragments of Forest Vegetation (FV) and Natural Vegetation (NV) for different functional distance values (meters) for the AF trimmed by roads and railways. Highest functionally connected vegetation cluster (c-d) (% of total cover of FV and NV) estimated across varying functional distances (meters) for the AF. See Fig. S7 for not trimmed scenario.

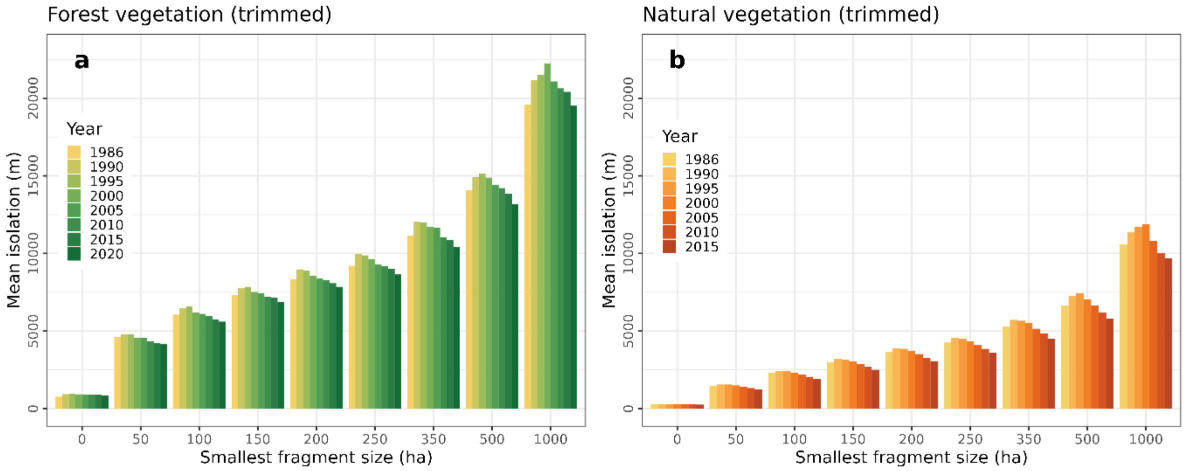


Figure 7. Mean isolation between fragments of Forest Vegetation (FV) and Natural Vegetation (NV) trimmed for the AF trimmed by roads and railways. Smallest fragments size: 0 ha (all fragments), 50 ha, 100 ha, 150 ha, 200 ha, 250 ha, 350 ha, 500 ha, and 1000 ha. See Fig. S8 for not trimmed scenario.

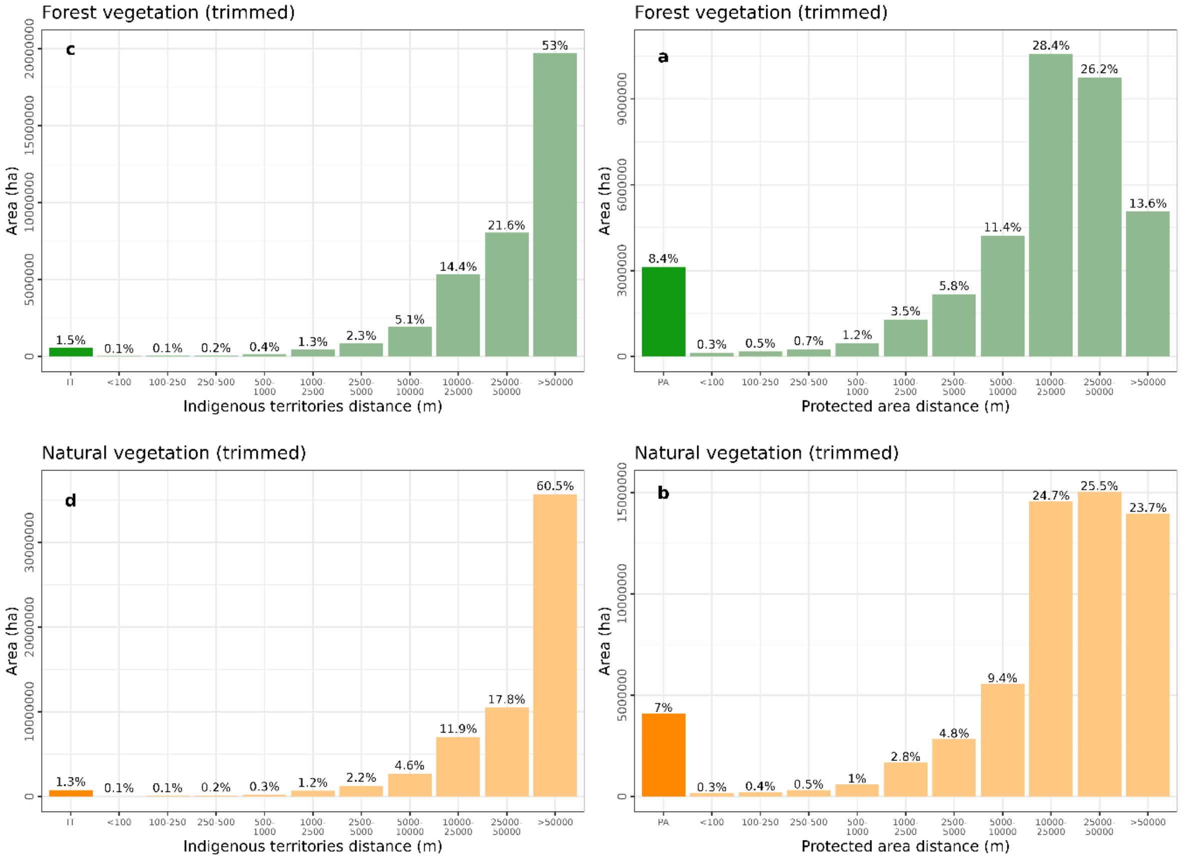


Figure 8. Amount of AF vegetation trimmed by roads and railways (area and percentage) and their distance (meters) from protected areas (PA; a – FV and b – NV) and indigenous territories (IT; c – FV and d – NV) per class. See Fig. S9 for not trimmed scenario.