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

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A B S T R A C T

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.

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 km² (Marques et al., 2021). Due to its high environmental heterogeneity, topographic

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variability, and pre-historic process of formation, the AF has high species diversity and endemicity (Peres et al., 2020). With >18,000 species of plants (Flora e Funga do Brasil, 2023) and 3500 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 (sugar cane and coffee), extensive cattle production, energy demand (charcoal), fires, mining, and urban and industrial growth (Solorzano et al., 2021). These landscape modifications have affected the biodiversity in the AF for different taxonomic groups (Pütter et al., 2020) and ecological processes, such as seed dispersal (Marjakangas et al., 2020), carbon storage (de Lima et al., 2020), pollination (Varasin 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 3° S to 33° S, and from 35° W to 58° W 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 picture in ecological and evolutionary terms, we used an integrative delimitation adapted from Mylalta 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-c] 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 Atlântico 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
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 proportionally 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 Casteleto (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 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 less than 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 nonlinearly 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—cabrucas 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.
The percentage of FV and NV located less than 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% for 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. 8[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...
Fig. 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. 3 S for other years (1990–2015). Please note the difference scales in the x-axis between the FV and NV plots.
Fig. 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.
Fig. 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).

Fig. 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.
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 1400 ha (8.6%), followed by restinga with 22,000 ha (3.6%), and Mangrove with 4600 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
Fig. 7. Mean isolation between fragments of Forest Vegetation (FV) and Natural Vegetation (NV) when fragments smaller than a given threshold (x-axis) are removed, 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.

Fig. 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.
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 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 Paraguay (The Zero Deforestation Law in 2004) (da Silva et al., 2017; van 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 1986, 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 (APPR; https://pactomataatlantica.org.br) has been encouraging restoration with the goal to restore 15 Mha by 2050 (Melo et al., 2015), with about 700,000 ha forest restored between 2011 and 2015 (Crouzille 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 2005–2015, 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 and 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 (Mohelbian 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; Fundacion Vida Silvestre Argentina and WWF, 2017).

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; Martínez 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).

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 (Sanzgories 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 protect endangered species (Rambaldi et al., 2005). Drastically changes in the vegetation configuration of the AF nowadays are highly unlikely in agricultural land, pasture and urban areas are already established in flatter terrains. 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, 2026; 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. (2022) 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. 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 (Martínez 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

Alarmingy, 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 (Benezve 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 IT (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 IT (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; Benezve 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. (2023) 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://c onexaomataatlantica.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 spatio-temporal 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.

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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.

Declaration of competing interest

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

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) (doi: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) (doi:10.17605/OSF.IO/AJUMC).

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Appendix A. Supplementary data

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