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Secondary natural vegetation gains in the Atlantic Forest do not offset losses of carbon stocks and conservation of priority areas

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A R T I C L E I N F O

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A B S T R A C T

Since secondary natural vegetation cover (NVC) constitutes an important factor for the provision of ecosystem services (e.g., helping to tackle both the climate and biodiversity crises), understanding its dynamics is essential for effective forest restoration. Yet, this has seldom been evaluated in prior studies. We examined 37 years (1985–2021) of primary NVC loss, secondary NVC dynamics (persistent and ephemeral regeneration), and their impacts on carbon stocks and on the conservation of priority areas in Brazil's Atlantic Forest biome, a global biodiversity hotspot. We developed a new framework analyzing spatial landscape configurations over time, and found that Atlantic Forest NVC decreased by 4.2 Mha driven by a gross loss of 12.8 Mha of primary NVC (~1.4 Gt of carbon lost). Secondary NVC gained 8.6 Mha (~0.170 Gt of carbon, with potential for ~0.987 Gt in 80 years) but ephemeral regeneration (i.e., loss of secondary NVC) resulted in a loss of 3.8 Mha. Deforestation caused a net loss of 1.2 Mha in priority conservation areas. Results of this study demonstrate that understanding the dynamics of ephemeral regeneration is important for evaluating restoration efforts and ecosystem services in the Atlantic Forest. Our study also demonstrates that secondary forest regeneration plays an important role in reconnecting landscapes, although its instability threatens biodiversity and ecosystem services as it fails to offset the loss of primary vegetation. Thus, halting deforestation remains the single most urgent and vital action to prevent irreversible biodiversity loss and reduce carbon emissions.

1. Introduction

Countering the double crises of biodiversity loss and climate change requires urgent work to understand and manage long-term landscape dynamics, particularly to understand the value of secondary regenerating vegetation following removal of primary natural vegetation (Crawford et al., 2024). Many ecosystems in Brazil, such as the highly diverse tropical and subtropical ecosystems in the Amazon and Atlantic forests (Salgado et al., 2019), constitute an important focus for assessing the impacts of biodiversity loss and climate change (Jakovac et al., 2024). Over the last four decades, Brazil experienced a net loss of around 96 Mha (MapBiomas, 2023) of natural vegetation cover (NVC), representing the country's major contribution to greenhouse gas emissions (Zimbres et al., 2024) and an important threat to global biodiversity (Zalles et al., 2021). However, analysis of the Atlantic Forest biome has shown a shift, in the 2010s, from a trajectory of net loss of NVC to one of net gain (Rosa et al., 2021; Vancine et al., 2024; Silva et al., 2023a), known as 'forest transition'. While remnants of primary vegetation from

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centuries of deforestation continue to be lost in the biome, new areas of secondary vegetation are also establishing, forming new landscape mosaics composed of NVC patches of varying successional stages (Silva et al., 2017a; Rosa et al., 2021). Globally, forest transition is primarily driven by land abandonment due to socioeconomic shifts (Crawford et al., 2024), and this is particularly the case in Brazil's Atlantic Forest (Silva et al., 2017b).

While the recovery of natural vegetation through secondary regeneration during forest transition may provide carbon and biodiversity benefits, the value will vary depending on the spatial pattern and temporal duration. Secondary vegetation may reduce spatial fragmentation and patch isolation in degraded landscapes, while also contributes to carbon sequestration (Pinotti et al., 2012; Matos et al., 2019; Rosenfield et al., 2023; Crawford et al., 2024). However, it can take many decades for secondary vegetation to attain the functional value of primary NVC areas (hereafter areas of 'maximal provision'; Safar et al., 2020; Poorter et al., 2021; Chazdon et al., 2025). Some patches of secondary NVC in the Atlantic Forest have not persisted but have returned to non-NVC, a phenomenon known as ephemeral regeneration (Piffer et al., 2022). From global (Crawford et al., 2024; Bousfield and Edwards, 2025) to regional scales (Rosa et al., 2021) the ephemerality of secondary NVC creates large uncertainty in the future conservation value of forest restoration and regeneration.

Analyses of spatiotemporal variation in landscape composition and configuration are thus vital for comprehensive sustainability assessments, while also enabling examination of the dynamics of NVC ecosystem services (Fig. 1). Such multidimensional approaches are currently prominent in landscape sustainability science, which has used approaches including land optimization, quantitative modeling and participatory approaches to highlight the pressing challenges of reconciling the expectations and aspirations of different stakeholders within biophysical planetary boundaries (Huang et al., 2024; Wang, 2024; Estrada-Carmona et al., 2024). The multidimensional approaches highlighted in Fig. 1b and c (contrasting with a simple land change accounting in Fig. 1a) allow the investigation of questions such as: (*i*) Where land changes are occurring? (*ii*) What are the assets or biophysical features that define the focal area/region of change? (*iii*) What are the impacts on the provision of ecosystem services due to the observed land changes? Hence, quantifying spatiotemporal landscape patterns in relation to specific biophysical features (Fig. 1b) can substantially enhance the understanding of the multiple impacts of various land change scenarios, including biodiversity conservation and climate

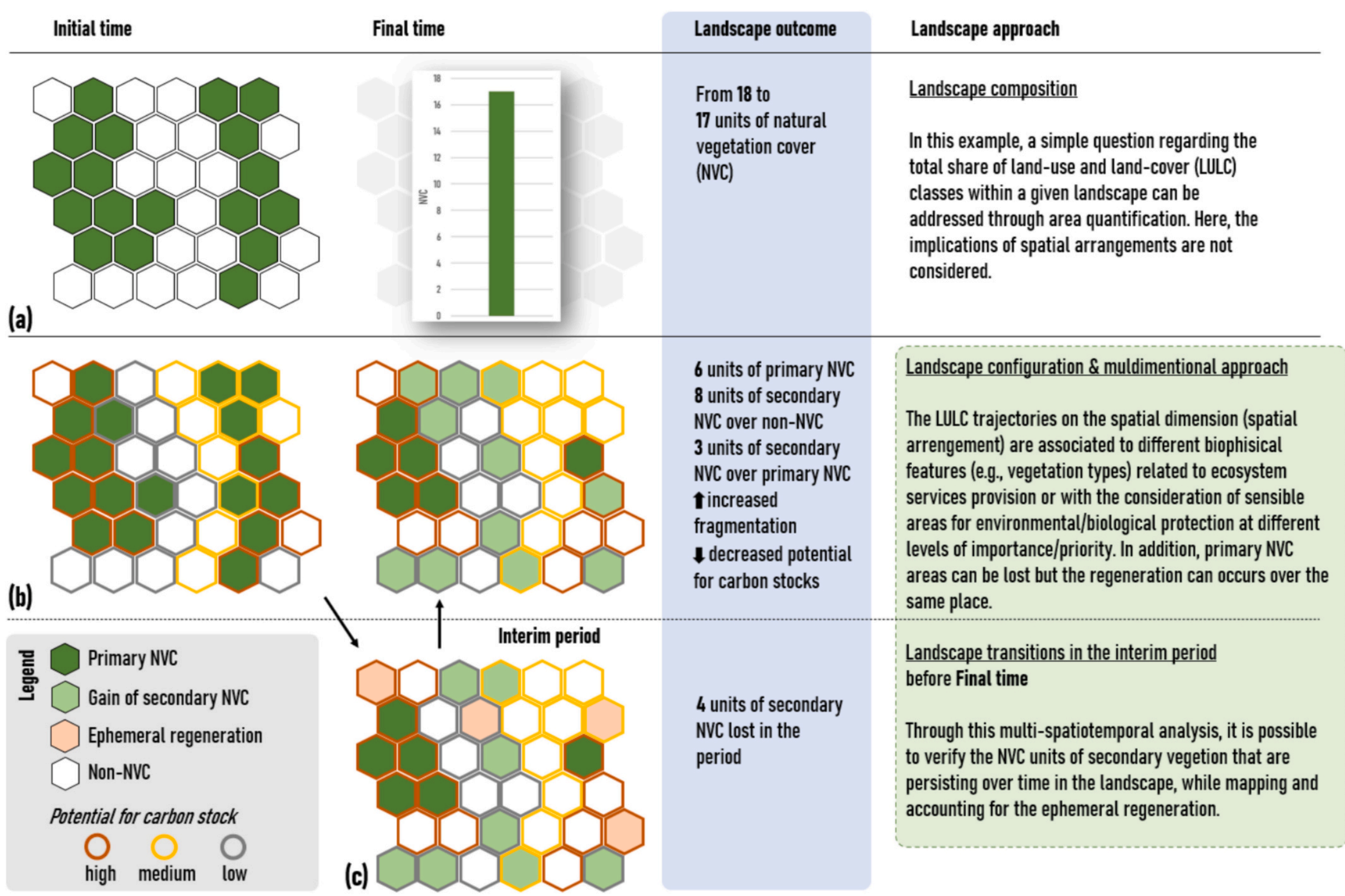


Fig. 1. Changes in landscape composition and configuration over time, highlighting the dynamics of primary and secondary natural vegetation cover (NVC) and their implications for carbon stocks. At the initial time-point **(a)**, the landscape comprises 18 units of NVC, differentiated into primary NVC (green hexagons, indicating areas of varying carbon stock potential) and non-NVC areas (white hexagons). By the final time-point, only one hexagon of NVC is lost indicating a small change to this land cover category. In **(b)**, the initial state has the same 18 units of NVC but additionally the contour colors (orange, yellow, and gray) indicating potential of carbon stock. By the final time-point, significant changes are observed: 11 units of primary NVC are lost, with 3 being replaced by secondary NVC (orange hexagons), while 8 units transitioned from NVC to non-NVC. Despite the apparent stability in the total share of NVC (17 units), the loss of primary NVC in areas critical for carbon stock is not fully offset by the growth of secondary NVC, which typically emerges in less suitable locations. This leads to fragmentation and a decline, for example, in the landscape's overall carbon stock potential. During the interim period **(c)**, 4 units of secondary NVC are lost, illustrating the high turnover and ephemeral nature of regeneration processes. These dynamics highlight the transient contribution of secondary NVC to carbon stock (affecting the provision of a regulating ecosystem service by NVC), which is still lower compared to those provided by primary NVC areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

change mitigation (Silva et al., 2023b). While several studies have described some potential sustainability outcomes of changes in landscape configuration, such outcomes are seldom explicitly addressed (Metzger et al., 2021; Owens et al., 2024).

Building on recent efforts mapping deforestation in the Atlantic Forest (Amaral et al., 2025), here we take a multidimensional landscape approach to build new knowledge about NVC trends and address the key issue of ephemeral regeneration of secondary NVC (Fig. 1c; Crawford et al., 2024). The Atlantic Forest is Brazil's most endangered biome with only about 35 % of primary NVC remaining (Vancine et al., 2024), while it is home to around 70 % of the country's human population (Marques et al., 2021; Costa et al., 2024). Using nearly four decades (1985 to 2021—37 years) of native vegetation cover change data, we developed a spatiotemporal analysis of NVC trends (loss of primary NVC, persistent gain, and ephemeral regeneration) to evaluate the dynamics of key landscape metrics along with potential impacts on carbon stocks and priority areas for biodiversity conservation. We refer to gains in carbon and priority conservation areas as 'potential', recognizing the limited capacity of secondary vegetation to match primary forest values, together with the decades required to achieve 'maximal provision' (Poorter et al., 2016; Rozendaal et al., 2019; Jakovac et al., 2024). Although previous authors have indicated that biodiversity recovery could take around five decades to reach high values (Rozendaal et al., 2019), there is an alarming expert consensus on the irreversibility of biodiversity loss in highly degraded tropical ecosystems, particularly where species extinctions have already occurred like in the Atlantic Forest (Isbell et al., 2023). Our results demonstrate that secondary forest regeneration plays an important role in reconnecting landscapes, although its instability threatens biodiversity and carbon sequestration as it fails to offset the loss of primary vegetation. Thus, halting deforestation remains the single most urgent and vital action to prevent irreversible biodiversity loss and reduce carbon emissions. Subsequently, we discuss the implications of our results for policy and management interventions.

2. Methods

This study analyses the Atlantic Forest as defined by the *Brazilian Institute of Geography and Statistics* (IBGE) biome boundaries (IBGE, 2024), covering 13 % of Brazil's territory. We use the IBGE definition, rather than the one established by the Atlantic Forest Law 11.428/2006, to ensure consistency with other datasets used in the study, i.e., land use/cover and associated accuracy assessments from MapBiomas and the priority areas for biological conservation defined by the *Brazilian Ministry of Environment and Climate Change*. Although we used the biome's biophysical definition rather than the political one, our study area has an 85 % overlap with the political boundary. Thus, the study provides a robust dataset and analytical approaches to support policy recommendations.

2.1. Data

For the analyses of NVC, the study relied on the land-use and land-cover mapping and the *Secondary vegetation* product, both from MapBiomas Brazil v.9 (https://brasil.mapbiomas.org). The MapBiomas Brazil v.9 has an overall accuracy of 93.1 % and was developed using Landsat imagery with a 30 m/pixel resolution (Souza et al., 2020). The MapBiomas product *Secondary vegetation* accounts for the number of consecutive years a given pixel transitioned from anthropic use to NVC, using a persistent classification method and spatial filters for a minimum mapping area of 1 ha (MapBiomas, 2025). It then attributes the secondary NVC age within the time-span of interest to each mapped area (e.g., a pixel transitioned to NVC in 1986 and persistently observed as NVC until 2021 will be assigned as 36 years old). Hence, for MapBiomas collection (v.9), regeneration is accounted for until 2021 due to temporal filters (MapBiomas, 2025). For measuring potential impacts on carbon stocks according to different NVC trends, the study used the *Potential carbon stocks* map from Silva et al. (2023c). Impacts on biodiversity are evaluated through the assessment of NVC trends within the *Priority Areas for Biodiversity Conservation* v.2 dataset, developed by the *Brazilian Ministry of Environment*. In the study, we considered all-natural vegetation cover (NVC) classes observed in the biome to represent the class of interest [NVC = "forest formation", "savanna formation", "mangrove", "wooded sandbank vegetation", "wetland", "grassland", "hypersaline tidal flat", and "herbaceous sandbank vegetation" following Vancine et al., 2024]. This is consistent with the *Secondary vegetation* product from MapBiomas. The MapBiomas collection v.9, together with the carbon stocks map derived from the IBGE's vegetation map, and the priority conservation areas where all developed at a 1:2500,000 scale.

2.2. Trends in natural vegetation cover

The land cover trajectories are known to be dynamic and susceptible to different change intensities over time (Aldwaik and Pontius Jr., 2012; Li et al., 2020) given to varying sets of socio-environmental factors and contexts (Lambin and Meyfroidt, 2010; Silva et al., 2023a; Dembélé et al., 2024). These multiple trends have impacts on carbon stocks associated with soil and vegetation components (Chang et al., 2022), and in this case the trajectories of land-use and land-cover classes, mainly NVC, are key aspects of carbon dynamics and with implications to climate change (Piffer et al., 2022). Stability of NVC trends of regeneration is also important to enhance ecosystem services and landscape connectivity, which influences biodiversity (Metzger et al., 2021). For the purpose of the analyses of carbon and biodiversity in 2021, we consider the secondary NVC pixels that transitioned from other classes to NVC since 1985 and that persisted until 2021—i.e., *NVC persistent regeneration*. Alternatively, pixels of secondary NVC that turned over in subsequent years to other classes were considered ephemeral regeneration (Piffer et al., 2022). In this case, we did not estimate potential carbon stocks or the effects on conservation priority areas (from the ephemeral regeneration areas) for 2021, but rather examined a 'what if' scenario where all ephemeral pixels would remain as persistent (i.e., to estimate the magnitude of the effects on ecosystems services by the loss of secondary NVC). Additionally, for the NVC class in 1985 and 2021 we evaluated five landscape metrics of configuration using the *landscapemetrics R* package (Hesselbarth et al., 2019; R Core Team, 2025): *Aggregation Index*, *Number of Patches*, *Euclidean Nearest Neighbor Distance* (in meters), *Mean Patch Size* (in hectares), and *Total Edge* (in km). For this analysis we considered two additional scenarios, one without secondary NVC—i.e., only NVC remnants of 1985 observed in 2021—and another including the ephemeral regeneration in the NVC of 2021. Due to computational constraints, for the landscape metrics we created a random sample ($n = 100$) consisting of circular areas with 30 km of radius each, rendering an area of ~28Mha (25 % of the biome's area). This approach has been previously applied to analyze land-use and land-cover dynamics in Brazilian biomes to support inferential statistics (Silva et al., 2023c).

2.2.1. Persistent regeneration of natural vegetation cover

To generate the *NVC persistent regeneration* data we used the secondary NVC data of 2021 from the *Secondary vegetation* MapBiomas product plus the disregarded pixels from its method (i.e., areas smaller than 1 ha) as follows: (*i*) *difference map of NVC—gain* (No Data = non-NVC, and 1 = NVC) between 1985 (*1985 NVC*) and 2021 (*2021 NVC*); (*ii*) new pixels of NVC in 2021 from step (*i*) but not mapped by the *Secondary vegetation* product were added to the final data *NVC persistent regeneration* (i.e., gross gain of NVC). In Supplementary Information (SI-Fig. 1a) we present the step-wise approach for generating these data.

2.2.2. Loss of primary natural vegetation cover

The *primary NVC loss* data were derived from the *Secondary vegetation* and the *difference map of NVC—loss* [same as in step (*i*) above but to return pixels of NVC loss from 1985] datasets. Here, the idea was to consider only the pixels of NVC that existed in 1985 and that transitioned to other classes. In the Atlantic Forest these are considered as primary NVC, as defined by previous studies (Silva et al., 2017a; Rosa et al., 2021). A full mapping of NVC loss in 1985 is crucial due to the vital role of primary vegetation in maintaining carbon stocks. Deforestation in these tropical ecosystems has disproportionately significant impacts on greenhouse gas emissions and biodiversity (Lima et al., 2020; Bello et al., 2024). Hence, to reach the *primary NVC loss* (i.e., gross loss of primary NVC) we (*i*) extracted all pixels of secondary NVC in 2021 observed in the *Secondary vegetation* data from the *1985 NVC* data (*extracted secondary NVC*), and (*ii*) summed these pixels with those observed in the *difference map of NVC—loss*. The step-wise approach in SI-Fig. 1b.

2.2.3. Loss of secondary natural vegetation cover

We analyzed the last 36 years (from 1986 to 2021) of *Secondary vegetation* data to understand what regeneration ages are more susceptible to undergoing new deforestation cycles (i.e., ephemeral regeneration), and how much this turnover represents the total area regenerated over the same period. This is key to support new understanding about the complex and dynamic persistence and ephemeral trajectories of NVC in the Atlantic Forest (Piffer et al., 2022). To develop this analysis, the secondary NVC observed in one year (e.g., 2018) that did not persist in the next year (i.e., 2019) was extracted from the original dataset. This process extracted only the ephemeral regeneration pixels while retaining their regeneration age information and location. Based on the age information, this method allowed assessing the susceptibility of each class age to become deforested again and allowed obtaining the proportion of secondary NVC lost after the initial regeneration. Fig. 2 explains the step-wise approach to map ephemeral regeneration from the *Secondary vegetation* data of MapBiomas. All area calculations, in hectares (ha), from the MapBiomas data were conducted by multiplying the number of pixels by 0.09 (the equivalent in hectares to a pixel resolution of 30 m—using Albers Equal Area Conic Projection). Considering trends and potential impacts of ephemeral regeneration on ecosystem services, we compared results by creating two scenarios: (*i*) to estimate the net balance considering the *NVC persistent regeneration* vs. *primary NVC loss*, and (*ii*) to estimate a scenario without ephemeral regeneration—in this case we sum the observed areas of secondary NVC lost within the period with the *NVC persistent regeneration* data.

2.3. Impacts of natural vegetation cover trends on carbon stocks

The ‘potential carbon stocks’ data (SI-Fig. 2a) is key to identify the potential of carbon associated with each type of natural vegetation (including above- and below-ground, litter, and dead wood) in the Brazilian territory, the stocks representing the outcomes of carbon sequestration (Yin et al., 2023). Considering the vast territorial extent and different climate and environmental settings, there are varying degrees of carbon stocks associated with the different vegetation types and biomes of Brazil (Jakovac et al., 2024). The Brazilian Institute of Geography and Statistics (IBGE) vegetation map (IBGE, 2012), version of 2021, was used as the reference to spatialize carbon stock rates for each vegetation type from the Third National Inventory (SEEG, 2020). This procedure resulted in a spatial map of ‘potential carbon stocks’ (tC/ha; Silva et al., 2023c). This ‘potential carbon stocks’ map serves as a

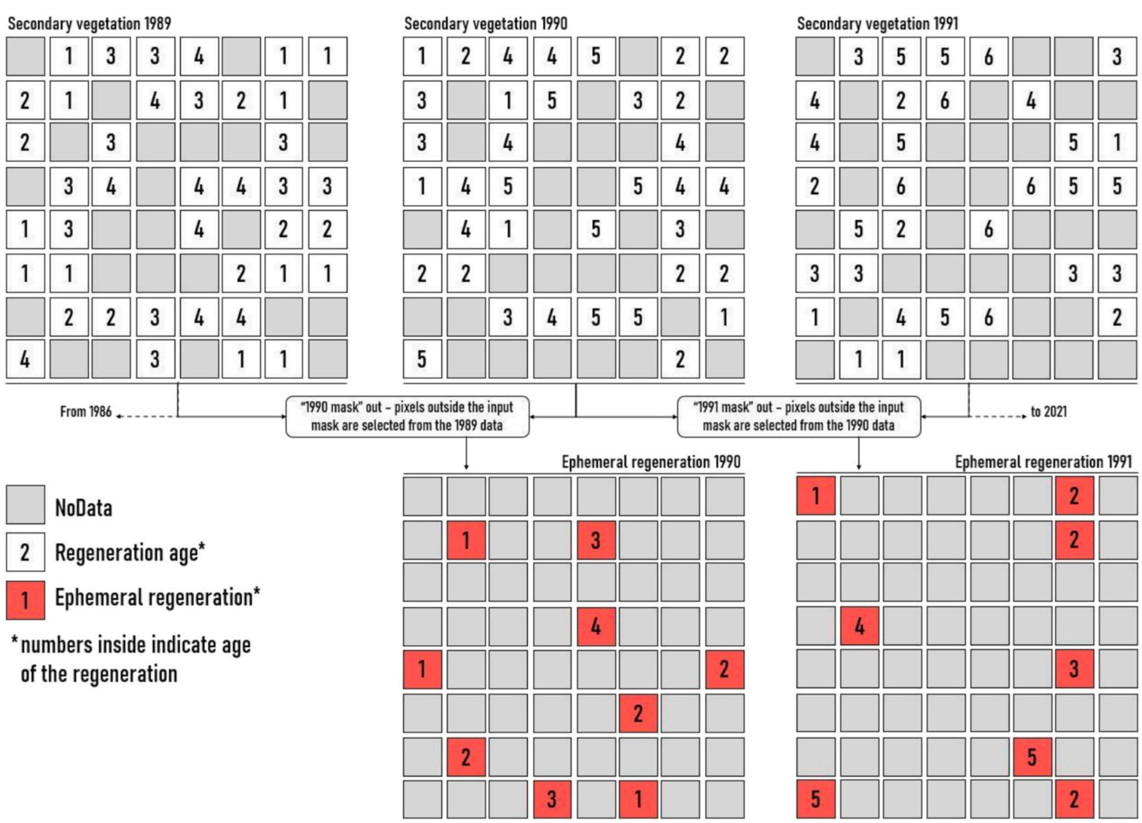


Fig. 2. Dynamics of secondary natural vegetation cover (NVC), highlighting ephemeral regeneration. The secondary NVC maps (1989–1991) show the regeneration age of NVC (in years) within each white grid cell—numbers indicating the time elapsed since regeneration began. Gray cells represent areas with no data (No Data), excluded from the analysis. The ephemeral regeneration maps (1990–1991) highlight areas where regeneration was temporary and did not persist in subsequent years. These areas are shown as red cells, with numbers indicating the age of the ephemeral vegetation before loss. Masks are applied for each year (1989, 1990, 1991) to exclude pixels outside the respective year's dataset, ensuring consistency in comparisons over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surrogate for estimating the amount of carbon stored per hectare of NVC, based on the original distribution and territorial extent of each vegetation type within the biome. To calculate the loss and 'potential' gain of carbon stocks associated with NVC trends, we used the *primary NVC loss* and *NVC persistent regeneration* datasets. Zonal statistics were applied to calculate the sum of pixels for each vegetation type for both loss and gain of NVC, and the resulting areas (ha) were used to estimate the total carbon stocks in each vegetation type. Previous studies have estimated that carbon stocks recover to achieve reference values (equivalent to primary vegetation) at around ~66 (Poorter et al., 2016) to ~80 years (Safar et al., 2020). Consequently, we used the *Secondary vegetation* product to calculate the area of each age and within each vegetation type, and adopted 80 years as the targeted age for full recovery—i.e., 'maximal provision'. By doing this we calculated the linear annual gains of carbon through sequestration to estimate the carbon stocks in the secondary NVC in 2021. For example, a vegetation type with potential carbon stock of 177.75 tC/ha is assumed to sequester 2.22 tC/yr, meaning that a one-hectare 33-year old plot of this secondary vegetation is estimated to store ~73.3 tC. In addition, we calculated the total area of ephemeral regeneration between 1986 and 2021 to assess the association of this specific NVC trend in the 'potential carbon stocks' data.

2.4. Impacts of natural vegetation cover trends on biodiversity (conservation priority areas)

The *Priority Areas for Biodiversity Conservation* is a national effort led by the *Brazilian Ministry of Environment and Climate Change* with the aim of mapping and classifying the most appropriate regions across Brazil to be targeted as priorities to conserve biodiversity. The areas identified by a panel of specialists (including NGOs, public servants, universities and private sector) are categorized (ranked) according to their biological importance (Brock et al., 2021). The *Priority Areas for Biodiversity Conservation* is in its second edition of 2018 and is freely available in shapefile format (MMA, 2021). Following the same procedures applied to analyze carbon stocks, the deforestation, persistent regeneration, and ephemeral regeneration were computed by zonal statistics (sum operator), for all areas identified as being of conservation priority and according to each category of biological importance (high, very high, and extremely high; SI-Fig. 2b). This calculation is intended to retrospectively quantify the effects of NVC trends on conservation priority areas, as it was performed in the analysis of carbon stocks. However, we underline that this approach should not be interpreted in any way as an endorsement of biodiversity offsetting, which remains both, scientifically and ethically contentious (Zu Ermgassen et al., 2019; Karlsson and Edvardsson Björnberg, 2021)—particularly in biodiversity hotspots like the Atlantic Forest (Souza et al., 2023).

3. Results

3.1. Effects of vegetation change on carbon and conservation priority areas

The total NVC area in the Atlantic Forest decreased by 4.2 Mha (net balance) over a period of 37 years, which is equivalent to about 10 % of the primary NVC present in 1985. This process resulted in a landscape composition change of 3 % in the NVC class (28.7 % in 1985, and 25.7 % in 2021). Interestingly, in 2005, the NVC class reached its lowest extent (36.5 Mha), followed by a general increasing trend until 2021, reaching 36.7 Mha. However, when calculating gross change over the 37 years period, it was observed that the biome lost 12.8 Mha of primary NVC (10.6 Mha from the *difference map of NVC—loss*, and 2.2 Mha from the *extracted secondary NVC*) while gaining 8.6 Mha of secondary NVC (7.8 Mha from the *Secondary vegetation* 2021, and an additional amount of 0.8 Mha when mosaicking with the *difference map of NVC—gain*). These changes have resulted in a share of 23.5 % of secondary vegetation to the NVC class in 2021. In addition, in 2021 we found that 65 % of the secondary NVC was more than eight years old.

The cumulative impact of the spatial distribution of deforestation of primary vegetation indicates a declining trend of carbon stock and conservation priority areas (Fig. 3a). For instance, considering the actual 2021 NVC, while the reductions of primary vegetation resulted in a loss of ~1.4 Gt (gigaton) of carbon (mean of 114 tons per ha), the new NVC areas under regeneration (secondary NVC) indicate a potential gain of ~0.987 Gt of carbon (mean of 114 tons per ha). These results indicate that the increase in secondary NVC did not offset the carbon stock lost due to deforestation, although it may compensate it by 70 % (net balance of −0.413 Gt) if the observed secondary NVC remains preserved over the next decades (because it might take about 80 years for the secondary NVC to reach 'maximal provision').

In addition to the potential gain estimates, we estimated the carbon stocks currently provided by secondary NVC in 2021, considering the 80 years period for 'maximal provision'. Our findings indicate that stocks in 2021 amounted to 0.170 Gt—representing only 17 % of 'maximal provision'. Hence, the Atlantic Forest's carbon stocks in 2021 totaled 3.131 Gt (remaining primary NVC plus secondary NVC stocks). The result from the potential carbon gain is similar to the net balance between gross change in loss and gain of primary and secondary NVC, respectively, with a compensation of 67 %. According to the carbon stocks data—considering the fifty-one classes of NVC in the Atlantic Forest biome with stocks ranging from 2.12 tC/ha to 177.75 tC/ha— around 62 % of the potential gains in carbon stocks were estimated from just five classes [*Floresta Estacional Semidecidual* (98.34 tC/ha), *Floresta Ombrofila Mista* (142.66 tC/ha), *Floresta Ombrófila Densa* (147.39 tC/ha), *Floresta Ombrófila Densa Submontana* (151.42 tC/ha), and *Floresta Ombrófila Mista Montana* (142.66 tC/ha)]. These five classes combined represent 53 % of the Atlantic Forest area. Similarly, 63 % of the carbon stocks lost by deforestation of primary vegetation occurred within the same five classes. While deforestation reached 6.8 Mha within these five classes, regeneration accounted for 5 Mha.

Results for the spatial distribution of deforestation and secondary NVC within the *Priority Areas for Biodiversity Conservation* indicate a net loss of 1.2 Mha in NVC, composed of a total loss of 3.1 Mha of primary NVC and a gain of 1.9 Mha of secondary NVC (i.e., 61 % compensation gain). Consequently, the gains in secondary NVC within these priority areas are being compensated at lower rates compared to those observed at the biome level, which stands at 67 %. In the Atlantic Forest, there are 77 *Priority Areas* classified as of 'high' biological importance, 100 as 'very high', and 88 as 'extremely high', with net balances between gain and loss of NVC at −109 kha (compensation of 64 %), −473 kha (69 %), and − 612 kha (53 %), for each class respectively. These results indicate a declining trend in crucial areas for biological conservation, revealing that the rates of secondary NVC replacement in these areas are lower than those observed at the biome level, particularly in areas of extremely high biological importance.

3.2. Ephemeral regeneration dynamics

Our approach identified 3.8Mha of ephemeral regeneration from 1986 to 2021 within a total area of 3.5 Mha. This means that approximately 0.3 Mha of the area was classified as ephemeral regeneration at least twice during the 37-year period (e.g., conversion between agriculture and secondary NVC happened multiple times over the study period). However, it is important to highlight that about 0.8 Mha of the observed ephemeral regeneration is found in locations classified as NVC in 2021, indicating that secondary NVC that was established during that period persisted until the end of the time series. Conversely, the area of ephemeral regeneration that was non-NVC in 2021 was equivalent to 2.7 Mha (this was the area used for calculations shown in Fig. 3a). The highest annual rate of increase in ephemeral regeneration was found between 1986 and 1997, and with the largest area of secondary NVC lost in 2021 being around 185,000 ha (Fig. 3b). Considering the age of

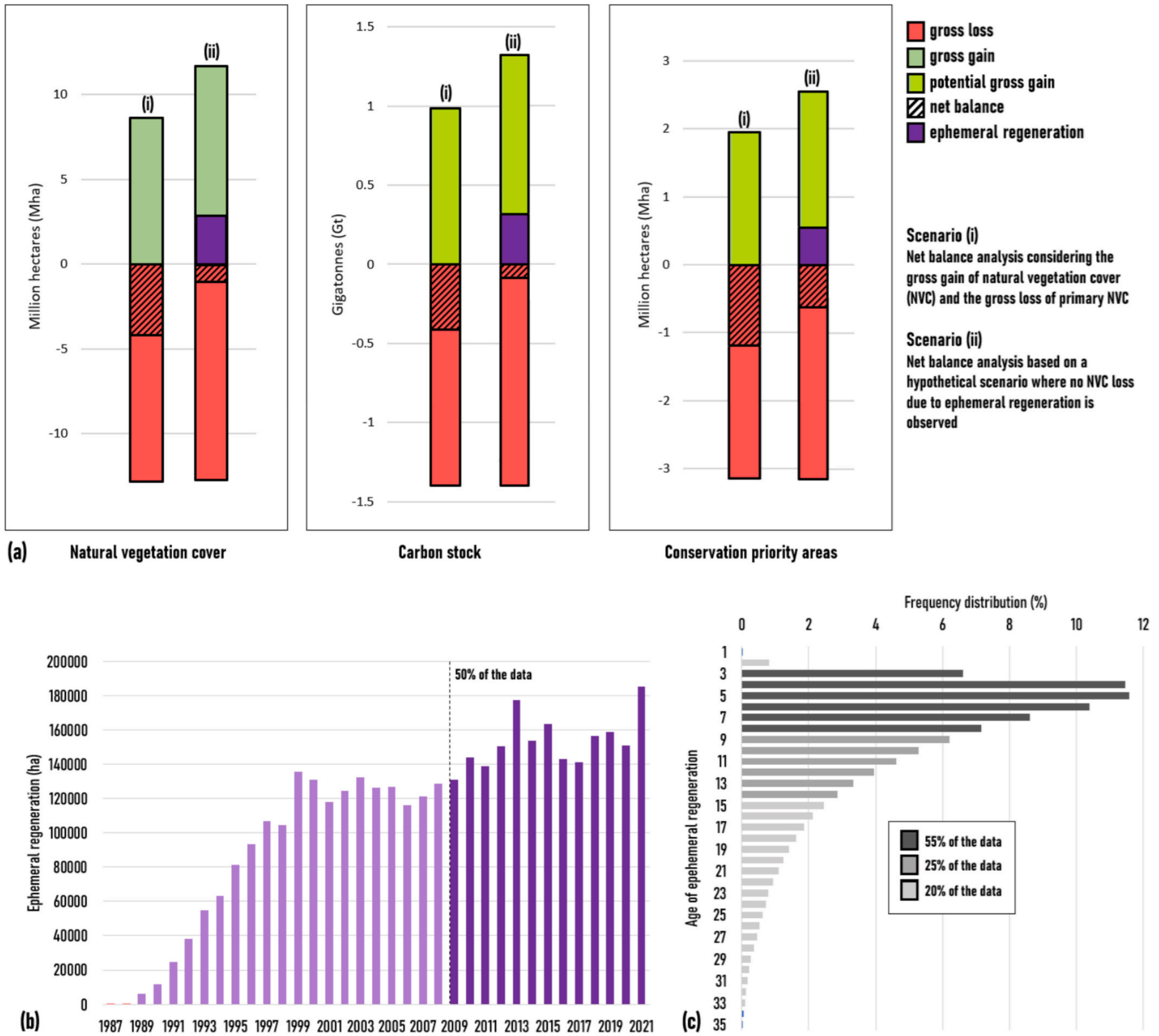
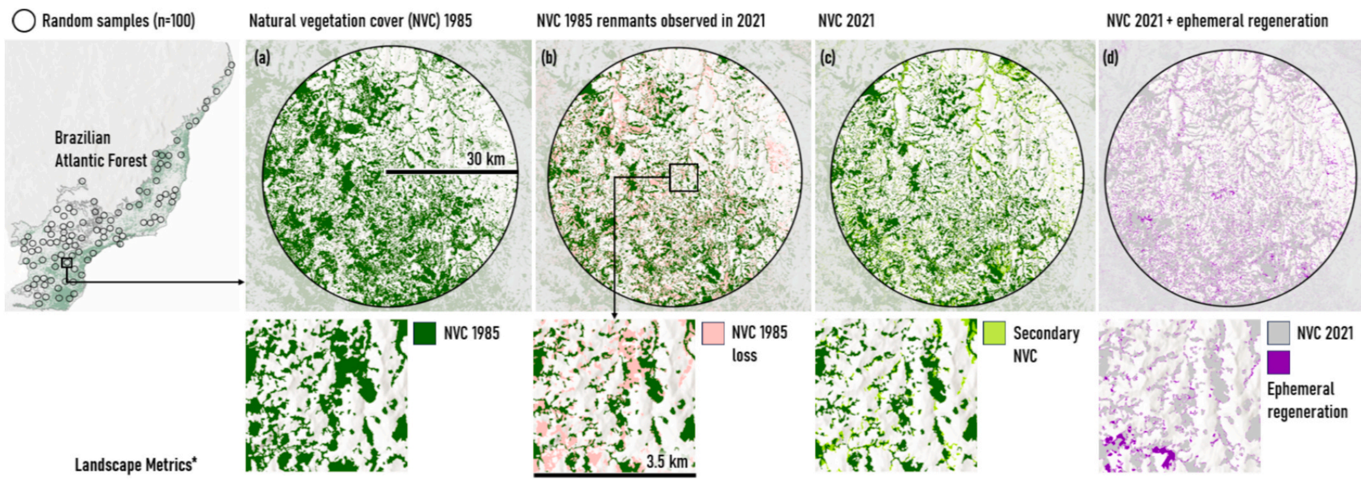


Fig. 3. Analysis of natural vegetation cover (NVC), carbon stock, conservation priority areas, and ephemeral regeneration in different scenarios. Panel **(a)** presents the net balance of NVC, carbon stock, and conservation priority areas under two scenarios: scenario (i) considers the gross gain of secondary NVC and the gross loss of primary NVC, while scenario (ii) assumes a hypothetical situation where primary NVC loss is additionally compensated by ephemeral regeneration (in this case no loss of secondary NVC). For all three components, the bar segments represent gross loss (red), gross gain (green), potential gross gain (light green), net balance (diagonal hatching), and compensation by ephemeral regeneration (purple). Panel **(b)** shows the temporal annual trend (area per year) of ephemeral regeneration from 1987 to 2021, expressed in hectares, with darker purple indicating more recent years. A vertical dashed line marks the year dividing 50 % of the data distribution. Panel **(c)** displays the frequency distribution of ephemeral regeneration by age (over all 35 years), expressed as a percentage, with bars divided into three groups: 55 % of the data (dark gray), 25 % of the data (medium gray), and 20 % of the data (light gray). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ephemeral regeneration, we found that 55 % was between 3 and 8 years old over the entire period. Interestingly, the older the regeneration, the lower the probability of turning over to non-NVC—i.e., the ephemeral regeneration was significantly associated with secondary areas that are less than 10 years old (Fig. 3c). The total area lost by ephemeral regeneration represented 44 % of the gross gain of NVC during the same period. Estimates of the effects of ephemeral regeneration on carbon stocks and conservation priority areas showed a loss of 0.313 Gt of carbon and of around −580 kha, respectively (i.e., the potential gains that carbon stocks and priority areas would benefit if no loss in secondary NVC was observed). These results indicate that deforestation of secondary NVC had important negative impacts on carbon and priority areas—without ephemeral regeneration, the gains in conservation priority areas may have been 2.5 Mha, while potential gains of carbon stocks may have reached 1.3 Gt after ~80 years of regeneration.

3.3. *Landscape configuration outcomes*

Results from five metrics of landscape pattern [*Aggregation Index*, *Number of Patches*, *Euclidean Nearest Neighbor Distance* (meters), *Mean Patch Size* (hectares), and *Total Edge* (km)] highlight the concerning situation of primary NVC in 2021 (Fig. 4b), which has fragmented into a greater number of smaller patches than in 1985 (Fig. 3a). At the same time, the secondary NVC demonstrates the importance of regenerating



Landscape Metrics*				
Aggregation Index (%)ᵃ	87.1	84.9	85.9	86.7
Euclidean Distance (m)	136.1	152.1	123.8	118.5
Mean Patch Size (ha)	46.3	18.7	32.2	37.8
Number of Patches (n)	4190	5055	4696	4288
Total Edge (km)	11,086	9,469	11,520	12,702

* Mean values represeting the total sampling area. [a] The index ranges from 0% (fully disaggregated) to 100% (maximally aggregated)

Fig. 4. Spatial patterns of natural vegetation cover in the Brazilian Atlantic Forest from 1985 to 2021, showing changes in natural vegetation cover (NVC) and regeneration processes with effects on landscape metrics of configuration. Panel **(a)** represents Natural Vegetation Cover (NVC) in 1985, highlighting areas of preserved NVC (dark green). Panel **(b)** shows NVC remnants from 1985 observed in 2021, with areas of loss marked in pink. In panel **(c)** NVC in 2021 illustrates secondary NVC (light green). Panel **(d)** shows NVC in 2021 with ephemeral regeneration areas highlighted in purple. The landscape metrics below the maps [aggregation index, Euclidean distance (m), mean patch size (ha), number of patches, and total edge (km)] summarize structural changes across the landscape. These metrics represent mean values for 100 random sampling areas (30 km radius). Insets (3.5 km scale) provide detailed views of spatial changes at finer resolutions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

areas to buffer some of the negative impacts of deforestation, by increasing mean patch size and reducing the distance among patches of natural vegetation (Fig. 4c). Taking the metric values of 1985 as a reference (Fig. 4a), if accounting for the effect of ephemeral regeneration areas in the landscape metrics of NVC would result in even higher benefits from a landscape configuration perspective (e.g., lower Euclidean distance, higher mean patch size; Fig. 4d). This result suggests that if all secondary NVC persisted—i.e., in this case assuming all pixels of ephemeral regeneration as being persistent regeneration, no loss of regeneration areas—the newly established areas of NVC would play a crucial role in enhancing connectivity and increasing patch area, thus strengthening biodiversity conservation. Of the five metrics, the mean patch size was the most sensitive to the NVC changes in comparison to 1985 (Fig. 4a)—ranging from −59 % (Fig. 4b), −30 % (Fig. 4c), and −18 % (Fig. 4d).

4. Discussion

Our study demonstrates that a more complete understanding of forest recovery emerges when examining trends of increase and decrease of NVC together with their effects on carbon stocks and conservation priority areas. This perspective is important for improving estimates of the potential gains and losses under different future scenarios of landscape change (Poorter et al., 2016; Rozendaal et al., 2019; Jakovac et al., 2024). Similar evidence has been reported for the Amazon, where secondary forests offset less than 10 % of deforestation-related carbon emissions (Smith et al., 2020) and where old-growth forest loss has far exceeded secondary forest recovery across the basin (Smith et al., 2021). In our case, we examined the current persistent gains in NVC for future scenarios of carbon stocks after evaluating the ephemeral trends over the same time period. In doing this, we found that around 65 % of secondary NVC older than 8 years exhibited a lower turnover probability, thereby increasing the odds of attaining maximal provision under a scenario of persistent NVC regeneration [after around 80 years of regeneration (Poorter et al., 2016; Safar et al., 2020)]. The findings of Bousfield and Edwards (2025) reinforce this result, as they show that the oldest secondary forests at the global scale are highly concentrated in the Brazilian Atlantic Forest, highlighting the potential of these regenerating areas to persist and mature over time.

Our results also show that between 1985 and 2021 the Atlantic Forest's primary NVC landscape lost connectivity, increased fragmentation, and faced a significant reduction in mean patch size. The mean patch size metric is an important indicator because a larger patch area is important for conservation priority areas and carbon stock dynamics, while smaller patches lead to heightened edge effects and negatively impact the amount of conservation priority areas (Vancine et al., 2024) and carbon stocks (Bello et al., 2024; Lima et al., 2020). Conversely, ephemeral regeneration represents a missed opportunity for the Atlantic Forest, as the combined potential of these areas with persistent regeneration could greatly enhance landscape connectivity and reduce fragmentation. In this context, the biome's regenerating areas are an important focus for bringing it to a higher level of conservation. However, the loss of regeneration areas presents a significant contradiction, with substantial economic implications, as those areas represent lower-cost restoration opportunities. This is primarily due to the high costs of restoration and labor efforts needed (Brancalion et al., 2019).

It is particularly important to note that, although natural regeneration is a valuable and cost-effective restoration strategy in the Atlantic Forest—especially where ecological resilience, seed sources, and soil conditions remain favorable—this approach is not universally applicable across the biome. In severely and long-term degraded areas spontaneous regeneration is unlikely (Brancalion et al., 2016). These areas require active interventions, such as planting of native species (Rodrigues et al., 2009). Hence, a strategic mix of passive and active restoration is widely recommended to ensure biome-wide recovery and prevent neglecting the most degraded landscapes (Crouzeilles et al., 2017).

Prices under the Voluntary Carbon Market in 2025—estimated at US

\$4.8 per ton of carbon removed from the atmosphere (international carbon market average; Systemica, 2025)—could favor a carbon-based market to support restoration and conservation efforts in this unique biome. Based on this number, the estimated 0.170 Gt of carbon removed between 1985 and 2021 could translate into an economic value of approximately US\$816 million. In this sense, securing the current secondary NVC to ensure persistent regeneration areas could still render a US\$3.88 billion over the next ~80 years, necessary to reach a total of 0.98 Gt by the time of 'maximal provision'. Although this value represents just an estimation [carbon markets are volatile, with prices ranging greatly from a few dollars to several hundred dollars (Systemica, 2025)], it is worth driving attention to the importance of current secondary NVC given the high occurrence of ephemeral regeneration. Assuming the regenerating areas are not only of intrinsic conservation value but also of economic value, public policies and national-international fund initiatives should sharply engage with a focus on financial mechanisms such as payment for ecosystem services in areas under current regeneration, while also targeting newly regenerated areas (younger than eight years), as these are more susceptible to turnover (Fig. 3c).

There are criticisms of markets and offsets for ecosystem services across many perspectives, ranging from efficacy (West et al., 2023; Brancalion et al., 2024), to justice (Redvers et al., 2025), to governance (Damiens et al., 2021). In Brazil, the law that established the Brazilian Emissions Trading System (SBCE 15042/2024) requires carbon credits to be both, additional and permanent. Yet, Bishop et al. (2025) recently showed that 73 of 114 REDD+ carbon projects in Brazil overlap to some extent on areas with mining concessions (meaning permission to clear forest for operations), questioning the validity of the associated carbon credits. Our analysis quantifies the balance of carbon stocks according to NVC trends based on the assumption that they will persist into the future. Furthermore, our analysis did not examine biodiversity offsetting but rather, exposed the ecological imbalance caused by historical trajectories. This is because we recognize that many biodiversity losses—particularly of endemic species (Isbell et al., 2023)—are irreplaceable and cannot be compensated through equivalent gains elsewhere.

Thus, our study highlights the potential benefits of regeneration processes in the Atlantic Forest, while underscoring the dynamic and spatial trends of natural vegetation cover. Although mitigating climate change and reducing biodiversity loss through nature-based solutions is scientifically sound, it is essential to acknowledge the limitations. For example, relying solely on natural regeneration to enhance landscape connectivity and carbon storage capacity may be insufficient and even risky. However, the new insights provided in this study can guide the development of policies and strategies to maximize regeneration potential. By focusing on increasing the resilience of regeneration processes, we can promote a sustained expansion of persistent regeneration areas while reducing the prevalence of ephemeral regeneration (Chazdon, 2025).

4.1. Implications for conservation and policy

The findings of this study underscore an urgent need to recalibrate conservation and restoration policies by integrating regeneration stability and spatial configuration metrics into monitoring and planning frameworks. As well as reinforcing the importance of avoiding deforestation of primary vegetation, public policies such as Brazil's Forest Code and payment for ecosystem service programs must also prioritize the consolidation of persistent secondary vegetation, especially in areas of high ecological value. The recovery goal cannot be merely to expand forest cover area, but to ensure the persistence of regeneration.

Additionally, planning efforts should explicitly target younger regenerating areas (particularly those under 8 years of age) that exhibit high turnover rates, with interventions aimed at reducing the risk of reclearance. Conservation investments and carbon-based funding mechanisms should also shift focus toward ensuring the ecological maturation of these landscapes, recognizing the economic and environmental opportunity costs associated with ephemeral regeneration. Strategic prioritization of areas with high potential for long-term stability and ecosystem service delivery will be essential to maximize the benefits of natural regeneration, especially when complemented by assisted approaches such as enrichment planting or secondary forest management, which can enhance persistence and generate additional returns through carbon or biodiversity credits (Oliveira et al., 2018; Fantini et al., 2019).

More importantly, the Atlantic Forest is the only biome in Brazil governed by a specific and targeted legal framework—the Atlantic Forest Law (Federal Law 11,428/2006 and Decree 6660/2008)—which classifies any deforestation as a legal violation, except under very specific circumstances and with formal approval by environmental authorities. Therefore, the deforestation trends observed within this biome represent clear infractions of current legislation (Amaral et al., 2025). For a highly threatened biodiversity hotspot like the Atlantic Forest, deforestation is unacceptable—not only from a legal standpoint, but also on ethical and scientific grounds.

While we advocate for policy efforts that promote regeneration and restoration, zero-deforestation efforts such as the Glasgow Declaration on Forests and Land Use of 2021 (to halt forest loss by 2030) must also be firmly enforced to halt any further loss within the biome. The remaining fragments of primary or old-growth native vegetation in the Atlantic Forest are critically scarce, and their loss can no longer be tolerated. Even when considering potential compensation through restoration or regeneration, these remnants of primary native vegetation constitute the most valuable providers of ecosystem services and the last strongholds of the biome's biodiversity.

5. Concluding remarks

This study found that secondary natural vegetation gains are insufficient to offset the ecological and functional losses caused by primary vegetation loss in the Brazilian Atlantic Forest, consistent with the results of other studies (Bousfield and Edwards, 2025; Chazdon, 2025; Robinson et al., 2025). This trend compounds the alarming losses of primary natural vegetation over recent decades and re-emphasizes the importance of halting deforestation, which must be the top priority for policy and conservation mechanisms. Despite signs of a forest transition, ephemeral regeneration and fragmentation threaten to undermine the biome's potential for long-term carbon stocks recovery. Our findings highlight the importance of avoiding deforestation but also suggest the need for a paradigm shift regarding vegetation recovery and regeneration—moving from static metrics of forest cover to dynamic monitoring of vegetation persistence, ecological maturity, and spatial integration. By incorporating the temporality and fragility of regeneration into the conservation framework, we provide a more realistic baseline for assessing restoration outcomes.

In a time of planetary urgency, the ephemerality of regeneration in deforested areas cannot be viewed as a simple land change process. We must move from assuming the persistence of forest recovery to proactively ensuring ecosystem permanence. This requires cross-scale policy instruments that reward the ecological persistence and spatial connectivity of regenerating forests—not just their initial appearance in the landscape. Ultimately, our results suggest that the future of the Atlantic Forest—and other tropical landscapes—depends not only on how much regenerating vegetation is gained. It also depends on society investing to ensure the permanence and vitality of the regenerating vegetation, and more important, to avoid the loss of the remaining primary vegetation. Such actions can be supported by mechanisms that increase the value of young regenerating forests for landowners and communities, including payments for ecosystem services, enrichment planting, and secondary forest management.

CRediT authorship contribution statement

Ramon Felipe Bicudo da Silva: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **James D.A. Millington:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Dou Yue:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Maurício Humberto Vancine:** Writing – review & editing, Methodology, Investigation. **Luiz Fernando Silva Magnago:** Writing – review & editing, Validation, Supervision. **Andrés Viña:** Writing – review & editing, Validation, Supervision, Conceptualization. **Fu Bin:** Writing – review & editing, Validation, Supervision. **Margarita Huesca:** Writing – review & editing, Validation, Supervision, Conceptualization. **Simone Aparecida Viera:** Writing – review & editing, Validation, Conceptualization. **Jianguo Liu:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111512.

Data availability

Data will be made available on request.

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