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Atlantic Forest Regeneration Dynamics Following Human Disturbance Cessation in Brazil

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Abstract: The Brazilian Atlantic Forest (BAF) is one of the most important biodiversity hotspots and species-rich ecosystems globally. Due to human activities, it has been significantly reduced and fragmented. This study examined both biotic (floristic composition, diversity, and structure) and abiotic (topographic and soil) factors in BAF fragments undergoing varying levels and durations of human disturbance cessation: approximately 20 years (20 y), ~30 years (30 y), and over 40 years (>40 y). We aimed to understand the recovery dynamics of floristic composition, diversity, and structure in BAF fragments in relation to abiotic factors. Several statistical tools were employed to examine similarities/differences and relationships. Forests of the 30 y group exhibit significantly greater homogeneity in terms of floristic composition, while forests of the 20 y group are characterized by lower species abundance and diversity. The floristic composition was primarily influenced by soil features and the time of disturbance. Under "Environmental Protection Areas", soil–vegetation recovery can occur more swiftly than usually observed for BAF. A significant BAF recovery was observed approximately 40 years after the end of human disturbance. A partial recovery featured 30 y disturbed areas, while in 20 y forests, recovery is in its early stages. Human-disturbed BAF can gradually rebound when effective management practices are implemented.

Keywords: vegetation; soil; indicator species; multivariate statistics; conservation and management; environmental protection areas

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1. Introduction

Tropical forests play a crucial role in regulating global climate, conserving biodiversity, and providing essential ecosystem services. They are biodiversity hotspots, home to the majority of Earth's plant and animal species, preserving genetic diversity, essential for ecosystem resilience and adaptation [1].

Tropical forests are under threat due to deforestation and degradation, primarily driven by human activities (such as agriculture, logging, harvesting, mining, climate change, etc.). Thus, protection and, when necessary, recovery actions are strongly recommended. For instance, the Bonn Challenge is a global initiative to restore 150 million hectares of degraded and deforested land by 2020 and 350 million hectares by 2030. Recovery actions are needed to address the threats to tropical forests and achieve the Bonn Challenge goals (reducing biodiversity loss, climate change mitigation, water cycle regulation, soil erosion prevention, economic benefits) [2].

The Atlantic Forest (also known as *Mata Atlântica*) extends along the eastern coast of South America, primarily in Brazil (92% of the total area), with smaller portions in Paraguay (6%) and Argentina (2%) [3]. This vast, fragmented biome of tropical and subtropical forests once covered 130–150 million hectares before Portuguese colonization in 1500 [4]. Over 70% of its original extent has been destroyed, leaving 26–28% highly fragmented and in various stages of regeneration [5]. Despite this, it remains the fourth most important biodiversity hotspot on Earth, due to its crucial ecological role in providing high biodiversity [6], carbon storage [7], rainfall, and deepwater resources [8]. Therefore, its conservation and effective management offer significant global benefits [9].

Following the initial devastation by the Portuguese, the Brazilian Atlantic Forest (BAF) faced another significant loss during the 1970s and 1980s due to its presence in fertile lands, which were affected by selective logging, agriculture, and urbanization [5]. In fact, the Brazilian and global agroeconomies are heavily reliant on the BAF, where numerous commodities (coffee, corn, ethanol, meat, soybeans, sugarcane, biodiesel, etc.) are produced and exported worldwide. As a result, there are no BAF fragments that have remained entirely untouched over time [10].

However, a substantial portion of the remaining forest formations is currently confined to areas that are difficult to access, such as rugged terrain, hilltops, mountain peaks, and steep slopes, making them less suitable for agricultural or other human activities. Moreover, many of these fragments are now protected by state and federal laws, ensuring permanent conservation in accordance with the Brazilian Forest Code (Law No. 4771 of 15 September 1965).

The preservation of these areas is crucial to prevent further degradation. However, effective conservation necessitates understanding their response to natural factors and anthropogenic disturbances. Human activities alter environmental conditions, such as vegetation and soil characteristics, and determine the presence of forest legacies (e.g., remnant trees, soil seed bank, and tree stump regrowth) that influence natural succession [11,12].

Isolation, selective logging, fires, and the impacts of agriculture, industry, and urbanization [13] currently shape BAF fragments. In landscapes characterized by mosaics of native vegetation and anthropogenic cover types, changes occur through direct impacts, including habitat destruction due to fragmentation, edge effects, the introduction of exotic species, and reduced gene flow (leading to inbreeding of some species). The intensity of these factors is related to the surrounding environment and influences landscape dynamics [11–13].

Even altered from their original structure and functions, these BAF fragments possess significant conservation value due to their unique habitat and specialized biodiversity or endemic species. Analyzing species richness and composition, resulting from disturbance and environmental interactions, will enable the design of conservation strategies that balance species preservation with disturbance processes [10].

Although studies have demonstrated clear differences in physiognomy, structure, and diversity, a lack of predictive studies has been identified as a limitation. The advancements in science and ecosystem conservation have been slower than desirable, contrasting with the rapid acceleration of degradation, especially in the face of impending global climate change [14]. Despite the complexities of comparing natural regeneration processes under varying human disturbances within the same site, these studies remain limited. The novelty of our research lies in its dual focus on soil and plant interactions, as well as their feedback loops, within a globally significant and threatened forest ecosystem. This investigation will provide crucial insights into how human disturbances influence BAF ecosystems.

Furthermore, biodiversity recovery rates in secondary forests are crucial to the success of restoration programs. These rates may vary depending on resource availability—water and soil fertility—and the severity of human impact on the forest. Faster growth rates driven, for example, by higher nutrient availability are likely to occur in forest areas with high conservation value and low disturbance. Disturbance history can significantly influence ecological legacies that affect the rate and trajectory of succession. For example, remnant trees serve as seed sources and modify the microclimate [15].

The study was conducted in three distinct BAF areas with varying levels and cessation time of human disturbance history (*vide infra*): approximately 20 years (20 y), ~30 years (30 y), and over 40 years (>40 y). We examined their structural and floristic characteristics, along with soil and morphological features. We hypothesized that (i) abiotic factors (such as soil nutrients, fertility, water availability, etc.) will influence the BAF recovery process, and (ii) this recovery will be more rapid and extensive in less degraded areas. Consequently, our objective was to analyze: (i) how the BAF floristic composition, diversity, and structure recover during secondary succession in fragments with different levels of human disturbance; and (ii) the influence of environmental features on their recovery.

2. Materials and Methods

2.1. Study Area

The study was conducted in fragments of the BAF domain, totaling 938 hectares. These fragments are part of the UNESP "Edgardia and Lageado" Experimental Farms (Municipality of Botucatu, São Paulo State, southeastern Brazil; 22°47′30″–22°50′ S and 48°26′15″–48°22′30″ W).

Igneous rocks are the primary geological substrate, while the morphology is shaped by the presence of the typical basaltic cuesta formation; a homoclinal ridge, characterized by alternating cliffs or escarpments and gentle slopes [5].

Soil horizons are primarily of the A-B_{o1}-…-C (Oxisols) or A-B_{t1}-…-C (Alfisols and Ultisols) types [16]. Topography significantly influences soil depth, with the deepest soils found at the summit of the *cuesta* formation and along the backslope, while the shallowest are located on the steep slope (shoulder) [10].

The climate is classified as hot and humid subtropical (Cfa) according to Köppen criteria [17]. Based on meteorological data from 1997 to 2018 collected at the Faculty of Agronomic Sciences—UNESP (Botucatu Campus) weather station, the mean annual rainfall (P) is 1494 mm, concentrated primarily between October and March. The mean annual temperature (T) is 20.5 °C, with lower monthly values in July (17.5 °C) and higher in February (23 °C).

2.2. Experimental Area and Permanent Plots

The entire area has a long history of human impact, with varying degrees and types of disturbance. Due to extensive scientific research in the experimental area, we can accurately map all the fragments, allowing us to classify them into three distinct successional stages of recovery (Figure 1). Specifically, they can be categorized as follows:

- BAF fragments where human disturbance ceased over 40 years ago (>40 y, hereafter): representing the fragment with the highest naturalness, as it is characterized by native vegetation dating back over 40 years [5,10]. These lush, well-structured forests (with tall trees and abundant species diversity) are typically located in inaccessible areas, making them, at least currently, isolated and distant from human disturbance [18];
- BAF fragments where human disturbance ceased approximately 30 years ago (30 y): where vegetation was affected by human disturbance until 30 years ago [18]. Specifically, the last intervention involved the selective exploitation of tree species [19];
- BAF fragments where human disturbance ceased approximately ~20 years ago (20 y): these are the most disturbed fragments, with human influence persisting until 20 years ago, primarily related to grazing [18,19].

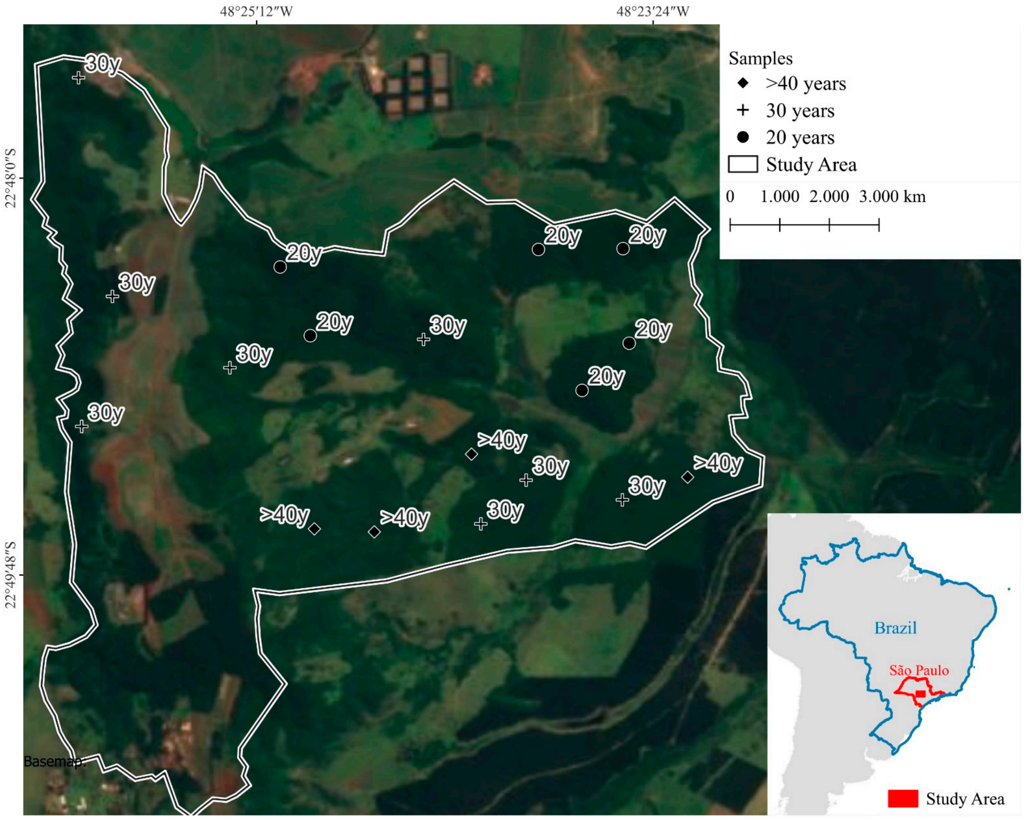


Figure 1. Study area and BAF fragment locations ("Edgardia and Lageado" Experimental Farm, University of São Paulo State (UNESP), Botucatu, São Paulo State). Sentinel-2 cloudless—https://s2maps.eu by EOX IT Services GmbH, (accessed on 31 August 2024). (Contains modified Copernicus Sentinel data 2016 and 2017). License: http://creativecommons.org/licenses/by/4.0/, accessed on 10 September 2024.

Eighteen permanent plots of 2000 m^2 (20 m × 100 m) were randomly distributed (Figure 1), with 6, 8, and 4 plots in >40 y, 30 y, and 20 y fragments, respectively. An uneven distribution was necessary to capture differences in size, environmental features, slope, and other characteristics among the investigated fragments.

Using the Milliren et al. [20] method, we assessed whether uneven plot distribution could affect observed variance and outcomes due to biased random effect estimation. We found that the chosen plot distribution implied a completely random effect with high statistical significance ($p < 0.05$). To reduce edge effects, permanent plots were located at least 500 m apart and 200 m from the fragment borders.

2.3. Vegetation, Topographic, and Soil Sampling

In each plot, all trees with a diameter exceeding 5 cm were measured for diameter at breast height (DBH, 1.30 m). Each individual was labeled and identified in the field using the APG (Angiosperm Phylogeny Group) III system [21]. This classification was refined using the "Flora do Brazil" website [22], the most comprehensive and up-to-date database of Brazilian flora.

Topographic variables were calculated for each plot, including altitude, slope, and Topographic Moisture Index (TMI). It indicates the soil's water retention capacity [23].

Surface soil samples (A horizon, 0–20 cm) were randomly collected from each plot. The 18 permanent plots were divided into 20 subplots of 100 m^2 (10 × 10 m). Five subplots were randomly selected, and three sub-samples were collected to create a composite sample. This resulted in 90 soil samples (5 subplots × 18 permanent plots).

Soil chemical analysis was conducted at the Laboratory of the Department of Forest, Soil, and Environmental Sciences, Faculty of Agronomic Sciences, UNESP, Botucatu campus.

Analyses were performed on air-dried soil (<2 mm) using Brazilian official procedures [24]. pH-$CaCl_2$ was determined potentiometrically, and Ca and Mg through extraction in 1 M Potassium Chloride. Aluminum, B, Cu, Fe, K, Mn, P, and Zn were extracted using modified Olsen procedures (at pH 8.5). Sulfur (S) was measured using the colorimetric method. Cation-exchange capacity (CEC) was assessed via saturation with $BaCl_2$ (pH 8.2). Accordingly, the sum of bases (SB) and base saturation (BS) were also calculated. Soil carbon (thus organic matter (OM)) and nitrogen (N) were determined by dry combustion using a CHN analyzer.

2.4. Statistical Analysis

Statistical analyses were conducted using R Statistical Software, version 4.4.1 [25]. To examine interrelationships among plant species across sampled plots, non-metric multidimensional scaling (NMDS) was employed using Bray–Curtis distance. It grouped plots based on species abundance similarity and identified distinct forest areas [26–28]. Analysis of similarity (ANOSIM) with Bray–Curtis dissimilarity (1000 randomizations) verified statistical differences between these areas. Both NMDS and ANOSIM were performed using the “vegan” R package, version 2.5 [26]. Indicator species analysis (indicator value (IV) $\geq$ 0.70; $p < 0.05$) was conducted to identify characteristic species within each forest area using the “indicspecies” R package, version 1.7.7 [29].

To analyze differences in species richness across sites, an ANOVA on a matrix of Euclidean distances with 999 permutations was performed, followed by a multiple comparison of means using the Tukey HSD test (95% confidence) [26]. Data on species and abundance were grouped by forest type. Species diversity of each forest area was characterized using interpolation rarefaction curves based on the first three Hill numbers (^0D, ^1D, ^2D). The first-order richness (^0D) represents the number of detected species, while the ^1D estimator is sensitive to low- or medium-abundance species. The ^2D estimator is sensitive to common and dominant species [29,30]. Hill’s numbers are true diversities representing the number of species in a community [29]. Rarefaction curves were generated with confidence intervals constructed using the bootstrap resampling method for ^0D, ^1D, and ^2D. The extrapolation curve’s asymptote estimates the proportion of species captured by the sample relative to the total potential richness. Interpolation/extrapolation analyses were performed on the iNEXT online platform [30] in the R Statistics environment.

Vegetation structure was analyzed by comparing structural variables: density, basal area, mean diameter, canopy height, and individual and basal area distribution by size classes. Generalized linear models (GLM) with gamma-distributed and logarithmic-link functions were used to compare structural variables with forest areas as a factor [31]. The genmod procedure was performed for GLM analysis, and the Tukey–Kramer test was used for comparisons among fragment types [32]. Standardized Pearson residuals assessed the fit of all GLMs.

Redundancy analysis with variance partitioning (VARPART) was used to investigate the relationship between floristic composition and environmental variables. Hellinger’s transformation was applied to the composition matrix to reduce the weight of abundant species [33]. Geographical coordinates were transformed into a geographic distance matrix using principal coordinates of neighboring matrices (PCNM) and incorporated as an explanatory variable [34]. Forward selection was applied to soil features, elevation, and topographic variables to identify significant contributors to floristic variation (1000 randomizations; $p < 0.05$). Canonical correspondence analysis (CCA) was performed to detect the main environmental variables influencing floristic composition. Spearman correlation was used to identify and eliminate redundant environmental variables ($p < 0.05$). Altitude was excluded due to a high correlation with slope. Predictive variables included pH, N, Fe, CEC, slope, TMI, and time since disturbance. A PERMANOVA test evaluated the significance of CCA for each axis and predictor variable. The “vegan” R package was used for CCA analysis [26].

3. Results

3.1. Richness and Diversity

In total, 4265 individuals representing 178 distinct species across 44 botanical families were identified within the studied forest areas (Table S1). The five most abundant families were Fabaceae (22.5%), Meliaceae (10.8%), Rutaceae (8.8%), Euphorbiaceae (6.1%), and Apocynaceae (5.4%), collectively accounting for 54% of the total sampled individuals. Fabaceae exhibited the highest species richness with 37 species, followed by Myrtaceae (17) and Rutaceae (15). The dominant species, based on the greatest coverage in the forest areas, were *Gallesia integrifolia* (Spreng.) Harms in >40 y and 20 y fragments, *Astronium graveolens* Jacq. in 20 y, and *Parapiptadenia rigida* (Benth.) Brenan in 30 y and 20 y fragments.

Non-metric multidimensional scaling (NMDS) analysis revealed the arrangement of the three BAF fragments (Figure 2), with ANOSIM confirming statistically significant differences in species composition among these areas ($p = 0.001$). The NMDS analysis stress value of 13% ($p < 0.01$) indicates an explained variance of 87%, suggesting that the diagram is statistically appropriate for interpretation. In the NMDS, the BAF of the 20 y group clearly differs from those of the 30 y. Fragments where human disturbance ceased over 40 years ago (>40 y) differ in species composition from those belonging to the 20 y group while showing partial similarity to those of the 30 y group. Fragments of the >40 y group tended to be more homogeneous and occupy a smaller area of ordination space compared to the other BAF fragments.

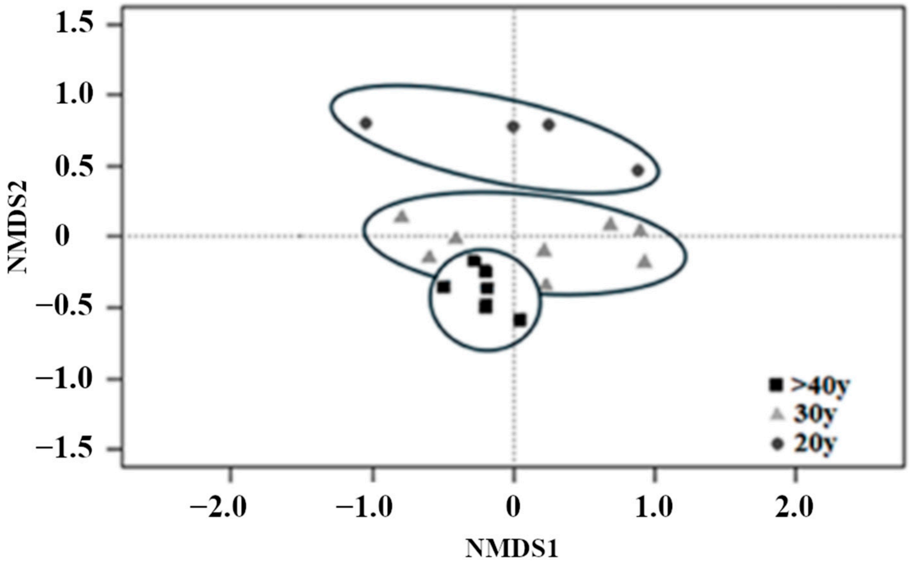


Figure 2. Non-metric multidimensional scaling (NMDS, Stress: 0.13; $p < 0.01$) revealed the distribution of 2000 m^2 plots based on Bray–Curtis similarity indices of floristic composition within the investigated BAF fragments.

In BAF of the 20 y group, 38% of the abundance was due to five species only, i.e., *Trichilia pallida* Sw. (11%), *Machaerium scleroxylon* Tul. (8%), *Parapiptadenia rigida* (Benth.) Brenan (8%), *Myrciaria floribunda* (H.West ex Willd.) O.Berg (6%), and *Cordia americana* (L.) Gottschling and J.S.Mill. (5%) (Table S1).

The analysis of the species indicator showed a total of fourteen species with an indicator value (IV) ≥ 0.70 ($p < 0.05$) for the three investigated BAF fragments (Table 1). In particular, nine species belonged to the >40 y group, and five to the 30 y and 20 y groups. The species with the highest indicator value were *Casearia gossypiosperma* Briq. in >40 y and 30 y fragments, and *Casearia sylvestris* Sw. in 20 y group.

Table 1. Indicator values (IV ≥ 0.70; $p < 0.05$) for species within BAF fragments.

Family	Indicators Species	Indicator Value		
		>40 y [1]	30 y [2]	20 y [3]
Apocynaceae	*Aspidosperma polyneuron* Müll. Arg.	0.89	0.89	
Salicaceae	*Casearia gossypiosperma* Briq.	0.94	0.94	
Salicaceae	*Casearia sylvestris* Sw.			0.90
Sapindaceae	*Diatenopteryx sorbifolia* Radlk.	0.77		
Rutaceae	*Esenbeckia densiflora* (Chodat and Hassl.) Hassl.			0.71
Fabaceae	*Holocalyx balansae* Micheli	0.90		
Caricaceae	*Jacaratia spinosa* (Aubl.) A.DC.	0.78		
Fabaceae	*Machaerium brasiliense* Vogel		0.86	0.86
Fabaceae	*Machaerium villosulum* Mart.			0.87
Rutaceae	*Metrodorea nigra* A. St.-Hil.	0.88	0.88	
Fabaceae	*Pterogyne nitens* Tul.			0.68
Moraceae	*Sorocea bonplandii* (Baill.) W.C.Burger et al.	0.82		
Meliaceae	*Trichilia claussenii* C. DC.	0.79		
Urticaceae	*Urera baccifera* (L.) Gaudich. ex Wedd.	0.89	0.89	

[1–3] BAF fragments where human disturbance ceased over 40 (>40 y), approximately 30 (30 y), and ~20 (20 y) years ago, respectively.

The species abundance across the investigated BAF fragments varied, reflecting the heterogeneity of the study areas, likely due to differing histories of human disturbance (Table S1). In the >40 y group, *Metrodorea nigra* A. St.-Hil. (13%), *Trichilia claussenii* C. DC. (9%), *Trichilia catigua* A. Juss. (8%), *Astronium graveolens* Jacq. (7%), and *Gallesia integrifolia* (Spreng.) Harms (5%) were the most abundant species, collectively accounting for 42% of the relative abundance among 112 species. In the 30 y group, *Metrodorea nigra* A. St.-Hil. (8%), *Tecoma stans* (L.) Juss. ex Kunth (7%), *Parapiptadenia rigida* (Benth.) Brenan (7%), *Urera baccifera* (L.) Gaudich. ex Wedd. (5%), and *Senegalia polyphylla* (DC.) Britton and Rose (4%) dominated, comprising 30% of the total species abundance. In the 20 y group, 38% of the abundance was concentrated in five species: *Trichilia pallida* Sw. (11%), *Machaerium scleroxylon* Tul. (8%), *Parapiptadenia rigida* (Benth.) Brenan (8%), *Myrciaria floribunda* (H.West ex Willd.) O.Berg (6%), and *Cordia americana* (L.) Gottschling and J.S.Mill. (5%) (Table S1).

Indicator species analysis identified fourteen species with an indicator value (IV) ≥ 0.70 ($p < 0.05$) for the three BAF fragments (Table 1). Nine of these species were associated with the >40 y group, while five were indicative of the 30 y and 20 y groups. *Casearia gossypiosperma* Briq. was the most strongly associated species with both >40 y and 30 y fragments, while *Casearia sylvestris* Sw. was characteristic of 20 y fragments.

The species diversity analysis revealed a significantly lower arboreal species diversity (${}^{0}D$) in 20 y (83) compared to both >40 (${}^{0}D = 112$) and 30 y fragments (${}^{0}D = 123$) (Figure 3).

The diversity of moderately abundant species (${}^{1}D$) was 37 and 34 species for the >40 y and 20 y BAF fragments, respectively, while 53 species were observed in the 30 y group (Figure 3). Similarly, the dominance values (${}^{2}D$) indicate that the 30 y fragments have the highest number of dominant species (${}^{2}D = 33$), which is significantly different from the >40 y and 20 y groups that presented a diversity of dominant species of approximately 20 species (Figure 3). Overall, based on the first-order Hill numbers (without considering species abundance), the most diverse area was the 30 y one (${}^{0}D = 123$). The >40 y fragment had 11 fewer species (${}^{0}D = 112$), and the 20 y had 29 fewer species (${}^{0}D = 83$) than the 30 y one.

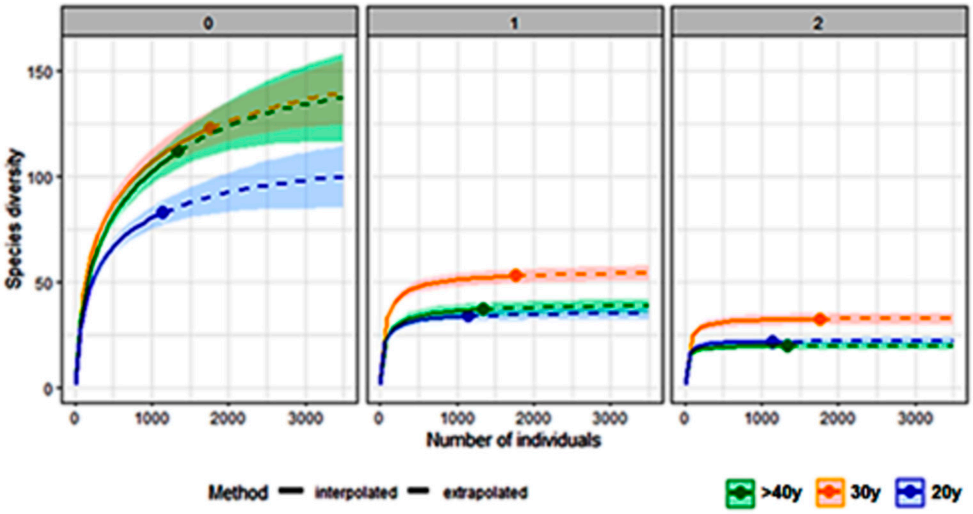


Figure 3. Integrated rarefaction/extrapolation curves, plotted as a function of the number of individuals in three BAF fragments: human disturbance ceased over 40 (>40 y), approximately 30 (30 y), and ~20 (20 y) years ago. q^0: species richness (effective number of species), q^1: Shannon diversity exponent, q^2: inverse Simpson's diversity index (solid lines: interpolation; dashed lines: extrapolation; shaded area: 95% confidence intervals).

No significant difference in diversity was observed between the >40 y and 30 y fragments. However, a significant difference was found between 30 y and 20 y fragments (Figure 3). When weighting species abundance, the 30 y fragment emerged as the most diverse in terms of ^1D diversity. The >40 y and 20 y fragments exhibited similar ^1D values, which differed significantly from the 30 y group (Figure 3). The same pattern was observed for dominant species diversity (^2D).

3.2. Structure

According to the results obtained from the GLM and the test of comparison of means of the structural variables in the forest areas, tree density (number of individuals ha^{-1}), the basal area (m^2 ha^{-1}), and the canopy height (m) did not present significant statistical difference among the BAF fragments (Figure 4). The forest areas showed a mean of 1185 individuals per hectare and 25 m^2 ha^{-1} basal area. However, the mean diameter of the >40 y BAF fragments showed a significant difference with the 20 y, a difference not observed in this variable with the 30 y fragment (Figure 4).

All diameter classes were present in the three BAF fragments, albeit in varying proportions (Figure 5). The basal area did not differ significantly among the three forest areas for the five diameter classes (Figure 5A). The 20 y fragments exhibited the highest basal area values in the first three diametric classes (trees 5–30 cm). The >40 y fragments were characterized by the highest basal area values in the last three diametric classes (trees > 30 cm). The basal area per diameter class was significantly different only between the >40 y and 20 y fragments in the last diameter class (trees > 50 cm) (Figure 5A). The number of individuals per diameter class differed significantly only in the last diameter class (>50 cm) among all three investigated BAF fragments ($p < 0.001$). The most abundant diameter class in all BAF fragments was group I (5–10 cm), whose abundance was notably distinct from the other classes (Figure 5B). In all investigated BAF fragments, a gradual decline in abundance was observed as tree size increased (Figure 5B).

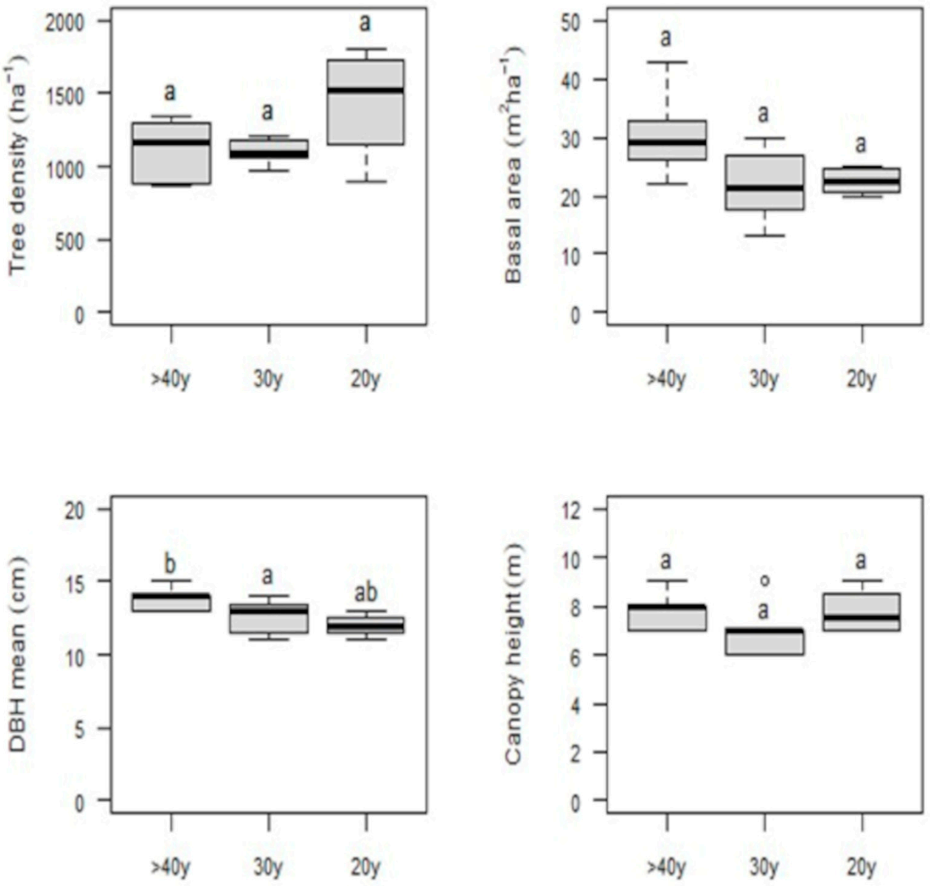
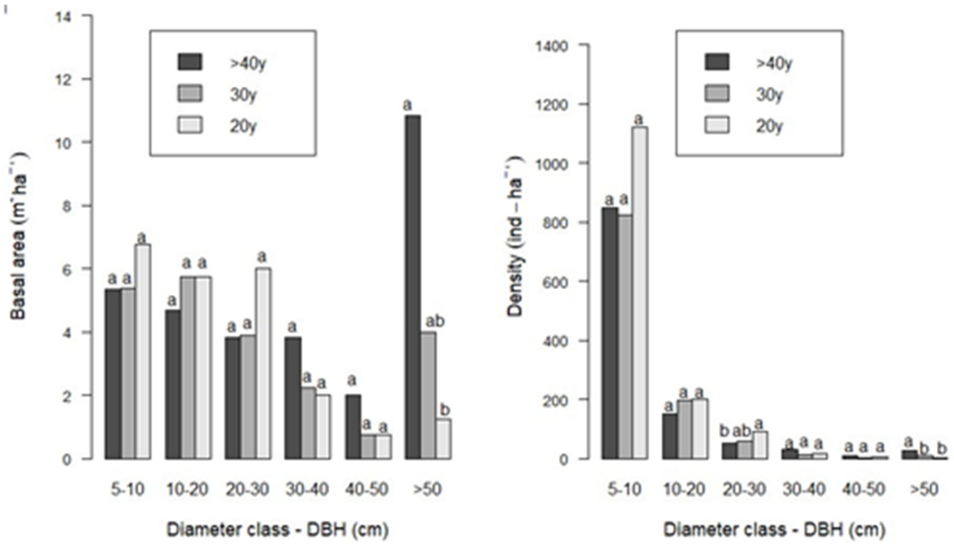


Figure 4. Comparison of structural variables among different BAF fragments. Different letters indicate significant differences ($p < 0.05$) among BAF fragments based on the Generalized Linear Model (GLM) analysis and Tukey–Kramer test. >40 y, 30 y, 20 y: human disturbance ceased over 40, approximately 30, and ~20 years ago, respectively.



(**A**) (**B**)

Figure 5. Basal area distribution per hectare (**A**) and total number of individuals per hectare (**B**) by diameter class for trees ≥ 5 cm DBH. >40 y, 30 y, 20 y: human disturbance ceased over 40, approximately 30, and ~20 years ago, respectively. Different letters derived from the generalized linear model (GLM) analysis and the Tukey–Kramer test, $p < 0.05$, indicate significant statistical differences between the areas per diameter class.

3.3. Floristic Composition and Environmental Variables

The redundancy analysis revealed that the soil, geographical, elevation, and topographic variables selected through forward selection accounted for 40% of the variation in floristic composition (Table 2). Specifically, soil chemical properties (pH, OM, CEC, BS, SB, N, P, K, Ca, Mg, S, Fe, B, Cu, Zn, Mn, Al) were the primary drivers of floristic variation in all investigated BAF fragments, surpassing the influence of elevation and topographic variables (Table 2). Notably, P, Al, and BS explained a substantial portion of the variation in floristic composition.

Table 2. Independent contribution to variance explained (F; $p < 0.05$) of the environmental variables and the floristic composition in the investigated BAF fragments.

Environmental Variables	**Floristic Composition**			
	Variable	**% Variation**	**F**	***p*-Value**
Soil	P, Al, BS [1]	0.37	2.70	0.001 ***
Geographic	UTM Coordinates	0.09	1.66	0.048 *
Elevation	Altitude	0.11	2.01	0.017 *
Topographic	Slope, TMI [2]	0.10	1.77	0.027 *
All		0.40	1.19	0.033 *

* < 0.05; *** < 0.001. [1] base saturation. [2] topographic moisture index.

The CCA explained a total variance of 51% (F = 1.3959, $p = 0.012$) (Figure 6). We found a significant correlation between species abundance and environmental variables along the first two axes. Fragments of the >40 y and 30 y groups were positively correlated with the TMI and forest age (EStime), but negatively correlated with pH, N, Fe, and CEC. Conversely, these soil and topographic variables were positively correlated with 20 y fragments (Figure 6). The species distribution among the investigated BAF fragments (CCA of all species included) was primarily influenced by soil pH along the first axis (F = 2.07; $p = 0.001$), while CEC and forest age (EStime) were significant factors along the second axis (F = 1.58; $p = 0.04$, F = 1.82; $p = 0.002$, respectively) (Figure 6).

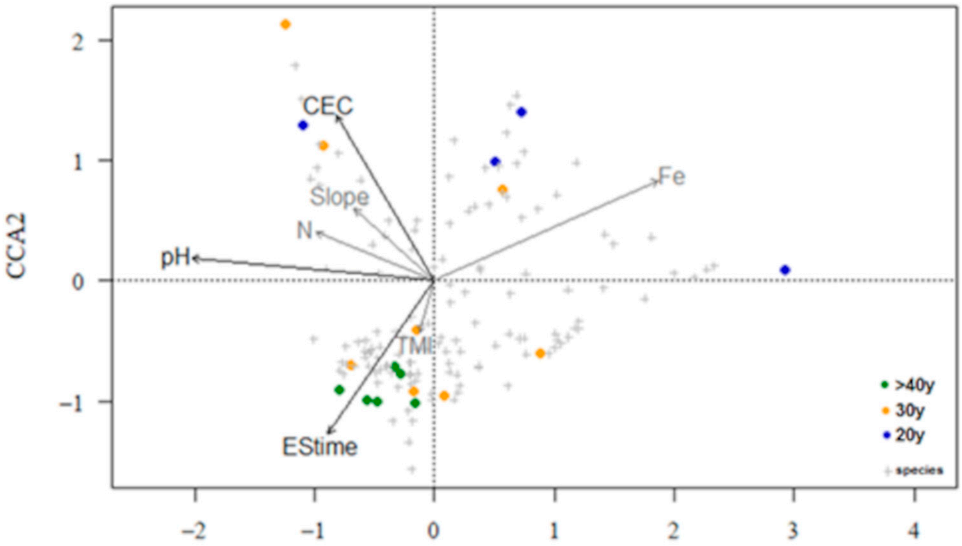


Figure 6. Canonical Correspondence Analysis (CCA) of factors influencing species distribution among the investigated BAF fragments. Colored points represent forest areas: >40 y (green), 30 y (yellow), 20 y (blue): human disturbance ceased over 40, approximately 30, and ~20 years ago, respectively. Arrows indicate factors with a significant correlation ($p < 0.05$) with the floristic composition of the sampled units. CEC: cation-exchange capacity; TMI: topographic moisture index; EStime: age of forest areas.

4. Discussion

4.1. Floristic Composition, Richness, Diversity, and Structure

Fragments where human disturbance ceased over 40 years ago (>40 y) exhibited a significantly different floristic composition compared to the most disturbed fragments, i.e., those where disturbance ended approximately 20 years ago (20 y). Interestingly, >40 y fragments showed some similarities with the 30 y one, suggesting that 30 y fragments represent a transitional stage in forest recovery. This aligns with previous findings [5,10] indicating that 30 y fragments are not fully recovered floristically but are closer to 40 y than 20 y fragments.

Fabaceae, Meliaceae, and Rutaceae were predominant families in the arboreal communities of all fragments, reflecting their characteristic presence in the Brazilian Atlantic Forest. Fabaceae, the largest family in Brazilian flora, is especially rich in species, including large trees [35,36].

Certain arborescent species could be valuable for conservation or as indicators of forest change. Indicator species were identified in all fragments, revealing their conservation status [27]. *Holocalyx balansae*, *Aspidosperma polyneuron*, and *Metrodorea nigra* were exclusive to >40 y fragments, indicative of high conservation value [37–39]. These BAF fragments (>40 y) also featured climax species like *Trichilia*, confirming an advanced species recovery. In 30 y BAF fragments, *Machaerium brasiliense* and *Senegalia polyphylla*, generalist species with high ecological plasticity, were indicators of the transitional stage [38]. *Casearia sylvestris*, a pioneer species typical of altered primary forests where it readily colonizes disturbed areas such as pastures, was the dominant indicator in 20 y fragments.

Species diversity and total richness were strongly influenced by human disturbance. The 20 y fragments, previously pasture, had low diversity and high abundance, coinciding with low richness, canopy cover, and alteration. This pattern aligns with prior studies [12,40,41]. The slower recovery of floristic composition compared to structure [42,43] and the low dispersal ability of late secondary species contribute to 20 y fragments' low diversity. The 30 y fragments exhibited greater richness and diversity, as observed in other BAF studies [40]. This indicates good recovery from both conservation and restoration perspectives. It seems that these fragments likely maintain natural succession processes, improving landscape connectivity [12,44]. Forest legacies and available propagules in the landscape matrix facilitate species richness recovery [11]. The >40 y fragments, with minimal alteration, had a low diversity of abundant species but a high diversity of dominant species. Its high tree richness suggests an advanced successional stage with higher environmental quality [45]. The complexity and heterogeneity of >40 y fragments promote higher diversity, though further collection efforts may be needed. Its arborescent diversity exceeds that of 20 y fragments.

Regarding structure, 20 y BAF fragments had the highest basal area in smaller diameter classes (5–30 cm), while >40 y fragments dominated in larger classes (>30 cm). Basal area per diameter class differed significantly between >40 and 20 y fragments in the largest class (>50 cm). Fragments belonging to the 30 y group did not differ from >40 y or 20 y, confirming its transitional stage. Successional recovery stages in terms of 20 y → 30 y → >40 y were confirmed by i) the differences among all fragments, with the most abundant diameter class being 5–10 cm in all; and ii) a gradual decline in abundance with increasing tree size is typical of growing tropical forests, often represented by an inverted J-shaped curve.

4.2. Floristic Composition and Environmental Variables

Redundancy analysis and partition of variance revealed soil as the primary environmental factor influencing floristic composition in the studied BAF fragments. Our findings indicate that edaphic, topographic, and temporal post-disturbance factors explain 51% of floristic variation. Fragments of the >40 y and 30 y BAF fragments demonstrated significant positive correlations with TMI and successional age, distinguishing them from 20 y fragments. This last exhibited strong associations with soil fertility parameters (CEC, N, pH), suggesting less soil development in BAF environments. Notably, 20 y fragments displayed the lowest floristic diversity. Studies in tropical forests have linked macronutrients (Ca, Mg) to floristic differentiation [46–48], a pattern confirmed in our study, where 20 y fragments pH is highly correlated with Ca (r = 0.73, $p < 0.001$) and Mg (r = 0.72, $p < 0.001$), further explaining floristic variation. In disturbed environments like in 20 y BAF fragments, soils are less developed and more dependent on fertility parameters, as is typically observed in soils at their early stages of evolutionary processes [5,10,12]. As disturbance diminishes and natural conditions prevail, the soil–vegetation relationship becomes more balanced, eliminating the "soil dependency" observed during early recovery stages [5,10]. In such cases, both soil and vegetation reach their climax states ("pedoclimax" for soil, [49]). This explains the lack of significant soil–vegetation relationships in fully recovered fragments (>40 y). The significant correlation between >40 y fragments and time, inversely related to soil parameters and degraded fragments (20 y), further supports these findings. Over time, soil and vegetation recovery progresses, becoming less influenced by specific soil parameters until reaching a sort of climax condition. This aligns with other research [50] showing inverse correlations between soil features and time, impacting floristic composition (decreased endemic species) and ecological guilds (decreased zoochory and non-pioneer/sub-forest species). The positive relationship between >40 y fragments and TMI further supports the previously reported soil–vegetation climax condition. In natural environments with balanced soil–vegetation relationships, plants establish deep root networks, improving overall soil conditions and drainage [51]. These improved soil conditions positively impact vegetation, enhancing nutrient and water exchange and overall edaphic conditions. In summary, vegetation/forest conditions and soil features exhibit a strong, mutually beneficial feedback loop. Several authors have argued that secondary forests can require a different timeframe, spanning from years to decades, depending on several factors, to partially recover in terms of species richness [12,52,53]. The literature also indicates that complete primary forest recovery can take centuries due to the loss of propagules or structural alterations in forest fragments [12,41,53]. However, our study seems to suggest that in inaccessible and isolated areas, far from human disturbance, a high degree of recovery can occur more rapidly in soil, vegetation, and soil–vegetation relationships. We observed a higher recovery in BAF fragments after approximately 40 years of almost complete human disturbance absence (>40 y). Interestingly, partial recovery was noted in areas disturbed approximately 30 years ago (30 y). Complete recovery remains distant in environments where human influence ended within the last 20 years (20 y).

As with many secondary forest studies, it is challenging to completely and accurately separate the effects of time (e.g., abandonment age) from chemical–physical soil features and landscape characteristics. In fact, more preserved fragments are often located in inaccessible areas due to topographic constraints (e.g., steep slopes), where soil properties may differ from less preserved areas. However, our previous studies [7,12] have shown that these confounding factors can be effectively addressed through careful site exploration, data collection, and analysis, thereby minimizing (but not eliminating) their influence on our results and conclusions. The study area is a long-term research site, established in 2008, which allows us to reduce intrinsic variability by limiting, as much as possible, the impact of confounding factors.

4.3. Findings Implications and Application to Forest Management

The findings of this study aim to provide deeper insights into the recovery dynamics of BAF fragments. The observed patterns of floristic composition, richness, diversity, and structural changes can be compared to other tropical and subtropical regions experiencing forest degradation and restoration efforts.

Regarding global implications, the study's findings highlight the importance of time and the cessation of human disturbance for BAF recovery. Our results suggest that even in severely degraded areas, a significant degree of recovery can occur over time if disturbance is strongly reduced, limited, or eliminated. This provides hope for restoration efforts in other tropical and subtropical regions facing similar challenges.

While the general trends observed in this study are likely applicable to other regions, it is essential to consider the specific ecological and socio-economic contexts of different areas. Factors such as climate, soil conditions, and human activities can influence the rate and trajectory of forest recovery.

The study's findings contribute to the growing body of knowledge on tropical forest restoration, such as prioritizing long-term recovery. Indeed, the study emphasizes the importance of long-term commitment to restoration efforts. While significant progress can be made in the early stages, higher and more consistent recovery may take longer times.

Focusing on disturbance reduction, the findings underscore the critical role of reducing human disturbance in facilitating forest recovery. This includes addressing issues such as illegal logging, deforestation, and land conversion.

The study also highlights the importance of landscape-scale approaches to restoration, which involve connecting fragmented forests and promoting ecological connectivity. This can enhance biodiversity and facilitate natural regeneration.

The Atlantic Forest shares many characteristics with other tropical biodiversity hotspots, such as the Amazon rainforest and the Congo Basin [54]. By drawing parallels with these regions, we can gain a broader understanding of the challenges and opportunities for forest restoration. Indeed, many tropical biodiversity hotspots face similar threats, including deforestation, habitat fragmentation, and climate change [54,55]. The findings of this study can inform restoration efforts in these regions by providing insights into the factors that influence forest recovery. Obviously, each hotspot has its own unique ecological and socio-economic characteristics [54], thus it is important to consider these differences when applying the findings of this study to other regions.

This study's findings could inform future management and conservation of BAF fragments by revealing their recovery dynamics. By identifying distinct recovery stages (20 y, 30 y, >40 y), the study underscores the importance of tailoring management strategies to the specific stage of forest regeneration. Additionally, the identification of indicator species highlights the need for targeted conservation efforts to protect these valuable elements of the ecosystem.

Landscape connectivity plays a crucial role in facilitating species richness recovery [54], as evidenced by the study's emphasis on the importance of forest legacies and available propagules in the landscape matrix. Promoting habitat corridors and restoration initiatives can significantly accelerate forest recovery [2]. Moreover, soil conservation is essential for influencing floristic composition and recovery, emphasizing the need to prioritize soil improvement in conservation and restoration efforts [5,10].

The study also provides practical guidance for species selection in restoration efforts, identifying pioneer species (e.g., *Casearia sylvestris*) for early-stage restoration and climax species (e.g., *Trichilia*) for advanced stages. A community-based conservation approach, involving local communities in conservation and restoration efforts, can ensure long-term sustainability and promote local ownership of forest resources.

By incorporating these findings into forest management and conservation strategies, we can develop more effective approaches to support BAF recovery and ensure its long-term sustainability.

5. Conclusions

Floristic dissimilarity was pronounced between older (>40 y) and younger (20 y) BAF fragments but less so between older and 30 y fragments, suggesting slower species recovery in the latter. Older fragments with less disturbance had higher species richness and diversity, likely due to soil characteristics and successional stage. Forest structure recovered quickly in all fragments, demonstrating the potential for biodiversity conservation. However, current conditions still lag behind older, more natural fragments. Overall, the obtained results suggest a positive feedback loop between vegetation/forest conditions and soil features. This relationship seems to be particularly pronounced in fragments older than 40 years (>40 y). Our study indicates that with effective management and conservation practices, recovery in human-impacted BAF fragments can successfully occur. The "Edgardia and Lageado" Experimental Farms offer unique research conditions due to their location within Environmental Protection Areas. These areas have strict conservation practices, limiting human activities and allowing for the study of undisturbed ecosystems. As a result, the farms represent a prime example of how complete recovery of soil, vegetation, and their interactions can occur in the absence of human disturbance. We observed a higher stage of recovery in BAF fragments after approximately 40 years of near-complete human disturbance absence (>40 y). Partial recovery was evident in areas disturbed until approximately 30 years ago (30 y). Conversely, BAF fragments where human influence ceased within the last 20 years (20 y) exhibited a lower level of recovery.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/environments11110243/s1, Table S1: Families and tree species registered in each study area (in alphabetical order by family).

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