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# Post-fire trajectories in atlantic forest regeneration: a case study in fragmented landscapes

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FOREST ECOLOGY

## ABSTRACT

**Background:** Forests in the Atlantic Forest Domain are increasingly threatened by fire, which disrupts their structure, biodiversity, and resilience. This study investigates how fire impacts functional diversity, community structure, and regeneration in fragmented forest patches near urban areas.

**Results:** We analyzed three types of forest patches: Closed Forest, Perturbed Forest (Once-burned Forest), and Burned Forest (Twice-burned Forest). Significant differences were found in species composition, diversity, and structural parameters among these vegetation types. Closed Forests exhibited the highest levels of functional diversity, structural complexity, and species richness. In contrast, Perturbed and Burned Forests showed reduced functional diversity, lower community-level traits, and diminished resilience. Functional metrics, such as functional divergence (Fdiv) and functional richness (Fric), were notably lower in fire-affected areas. Additionally, fire occurrence influenced dispersal modes, with animal-dispersed species predominating and a notable absence of large-seeded species.

**Conclusion:** The study highlights the significant impact of fire on forest regeneration. Recurrent fires lead to decreased species diversity and functional redundancy, transforming closed-canopy forests into more open, savanna-like landscapes. The absence of large-seeded and animal-dispersed species further impedes the regeneration and resilience of fragmented Atlantic Forests. These findings underscore the need for targeted conservation and management strategies to support forest recovery and maintain biodiversity in fire-prone regions.

**Keywords:** Functional Diversity; Forest Resilience; Wildfires; Forest seeds.

## HIGHLIGHTS

Fire reduces functional diversity and resilience in Atlantic Forest fragments.
Closed Forests show the highest structural and functional diversity post-fire.
Fires hinder forest recovery, harm biodiversity, and reduce shade-tolerant species.
Fragmented forests lack large-seeded species and animal dispersal for recovery.

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## INTRODUCTION

In recent years, wildfires have become increasingly frequent, with growing intensity, greater destructiveness, and expansion to larger areas (Rodrigues et al., 2024). Experts attribute this trend to several factors, including climate warming, accumulation of combustible material from tree mortality, landscape homogenization, fragmentation, and inadequate management of remaining forest areas (Rodrigues et al., 2024). Wildfires significantly impact the distribution and composition of plant communities (van Nes et al., 2018). The rising frequency of wildfires, coupled with global temperature increases, introduces uncertainties about the recovery of forest ecosystems from disturbances (Stevens-Rumann et al., 2019). Forest resilience, defined as the ability to return to a pre-disturbance state, is heavily reliant on effective tree regeneration (Johnstone et al., 2016). This highlights the critical role of tree regeneration in ecosystem recovery.

In tropical landscapes, the transition from old-growth to degraded forests is increasingly driven by human activities such as deforestation and wildfires, leading to significant habitat and biodiversity loss. Wildfires, in particular, alter the fire regime, making fire-sensitive rainforests like the Atlantic Forest more susceptible to disturbances that result in dramatic changes in species composition and tree regeneration (Prieto et al., 2017).

The Atlantic Forest Domain is a critical biodiversity hotspot (Lima et al. 2020), critically endangered and highly fragmented, remaining about 13% of native vegetation (Haddad et al. 2015). The increasing frequency of wildfires, coupled with ongoing fragmentation and the progressive loss of primary forests due to deforestation (Rosa et al., 2021), aggravate the vulnerability of this already threatened hotspot. Between 2019 and 2023, data from MapBiomas indicate that an average of 10,096.95 hectares of forested areas within the Atlantic Forest biome were burned annually, with 56% of these fires occurring in the state of Minas Gerais (MapBiomas, 2024). These conditions increase its susceptibility to additional impacts such as selective logging, hunting, species extinction, and biological invasions, which can be as detrimental as deforestation itself (Lima et al., 2020).

These compounded threats not only accelerate biodiversity loss but also hinder the natural recovery processes of disturbed ecosystems. The recently enacted Brazilian National Integrated Fire Management Policy (Law No. 14,944/2024) emphasizes the importance of reducing wildfire incidence and impacts while seeking to promote prevention, control and ecosystem restoration. In this context, the recovery of burned forest areas relies heavily on large-seeded species and animal-mediated seed dispersal, which are critical for the regeneration of late-successional species and the restoration of ecosystem functions, both of which are increasingly jeopardized in fragmented and degraded landscapes.

Post-fire monitoring is a valuable tool for identifying trends in fire-vegetation feedback processes (Araujo et al., 2017). Frequent fires tend to filter out fire-intolerant species, leading to more open, degraded forests with lower plant diversity (Charles-Dominique et al., 2017). Canopy openings caused by fires alter microclimatic conditions, favoring the colonization of C4 grasses and other flammable plants over C3 tree species. This shift increases fire frequency and reinforces fire-prone vegetation (Pausas & Dantas, 2017; Sansevero et al., 2020). In contrast, effective fire suppression facilitates the expansion of closed forests with diverse and well-structured plant communities, which enhances forest resilience (Pausas & Dantas, 2017).

Numerous studies have detailed the role of fire in maintaining functional diversity in diverse ecosystems (Loiola et al., 2010; Carvalho et al., 2014; Mata et al., 2022; Senande-Rivera et al., 2022; Ssekuubwa et al., 2023). In general, the Brazilian savannah areas, fire maintains high functional diversity within plant communities, as species have developed fire-tolerant traits such as resprouting and thick bark to coexist with or resist fire. There is a positive relationship between resprouting and fire as a persistence strategy, with savanna trees and shrubs tending to be smaller and investing in thicker bark, while rainforest species typically have thin bark and tall trees with closed canopies (Ondei et al., 2016; Charles-Dominique et al., 2017). However, the increased stress due to the high frequency of fires in a short period can impair the ability of even fire-adapted species to recover.

The impact of fire on non-adaptive forest communities, such as Atlantic Forest fragments, and their functional thresholds when interacting with fire-prone vegetation like savannas, remains uncertain. Assessing functional diversity is an effective approach to understanding fire effects in fragmented forests, as it reflects species characteristics and their functional responses within a community. Functional traits are related to ecosystem functions like forest resilience and productivity (Sakschewski et al., 2016) and comprise dispersal, establishment, and persistence traits (Zambrano et al., 2019). Post-fire changes in plant communities involve critical life-history traits like resprouting, recruitment from seed banks, growth rates, and dispersal syndromes (Ondei et al., 2016).

Although post-fire regeneration has been well-studied in tropical forests (Balch et al., 2013; Araujo et al., 2017), the functional diversity in fragmented Atlantic Forests following fire requires further investigation. In this study, we assessed how fire affects functional diversity and structure in fragmented patches of Atlantic Forest remnants near urban areas. We hypothesized that anthropogenic fire negatively impacts natural regeneration, structure, and functional diversity. We predicted changes in floristic composition, reduced structural values (basal area and richness), altered community-level traits (height and stem number), and decreased functional diversity parameters in patches affected by fire. The expected negative relationship between fire and functional diversity is attributed to the filtering out of fire-intolerant species.

## MATERIAL AND METHODS

### Study site and sampling

This study was conducted in the Santa Cândida Municipal Biological Reserve, which covers an area of 113 hectares and is considered a protected area in the municipality of Juiz de Fora, state of Minas Gerais, Brazil (21º 41' S and 43º 20' W) (Figure 1). Remnants of the fragmented Atlantic Forest landscape characterize the area. The predominant trees in this area belong to the Submontane Semideciduous Seasonal Forest category (Eisenlohr & Oliveira-Filho 2015). This fragment hosts old-growth rainforest tree families such as Annonaceae, Lauraceae, and Euphorbiaceae. The average temperature is 19.3 °C, and the annual rainfall is 1,983.1 mm. According to the Köppen classification, the climate is categorized as Cwa, with very hot and typically rainy summers (Martins et al., 2018).

Urbanization has substantially increased over the last twenty years, gradually surrounding the Reserve and leading to a rise in anthropogenic fires. In March 2019 a significant fire occurred in the area, followed by another four and a half years later, in September 2023. The last fire burned the vegetation, eliminating seedlings and seeds, and killing some shrubs and trees. We established three grids in the area six months after the second fire. One grid was allocated in a forest patch that burned in both events (referred to as the "Twice-burned Forest" or "Burned Forest"). Another grid was located in an area affected only by the first fire (referred to as the "Once-burned Forest" or "Perturbed Forest"). The last grid was positioned inside the Reserve, showing no signs of fire impact (referred to as the "Closed Forest"), where large trees provide dense canopy coverage.

To evaluate the influence of fire on the heterogeneity of tree and shrub regeneration, each grid was subdivided into 30 subplots measuring 2 x 2 m (4 m2) each, with a total sampling area of 120 m² per vegetation type (conglomerate or cluster sampling). All seedlings and saplings with heights between 0.50 and 5 m (0.50 m ≤ h ≤ 5 m) were counted in the sampling units. Each individual was marked with numbered aluminum tags, and its height was measured and species identified. Fertile collected specimens were deposited in the collection of the Leopoldo Krieger Herbarium (Herbário Leopoldo Krieguer - CESJ) at the Federal University of Juiz de Fora (Universidade Federal de Juiz de Fora – UFJF). Species nomenclature followed the Angiosperm Phylogeny Group (APG IV, 2016).

### Functional diversity and structural regeneration measures

To evaluate the impact of burns on natural regeneration, we assessed structural parameters, abundance, and species richness for each vegetation type. Additionally, we calculated Community-Weighted Means (CWM) for height (CWMh) and multistem (CWMms), which are plot-level functional measures (Muscarella & Uriarte, 2016). CWM traits provide insights into the functional response of natural regeneration (functional regeneration). We also measured functional traits related to the regeneration process to compute functional diversity metrics (see Table 1). Based on field observations, voucher

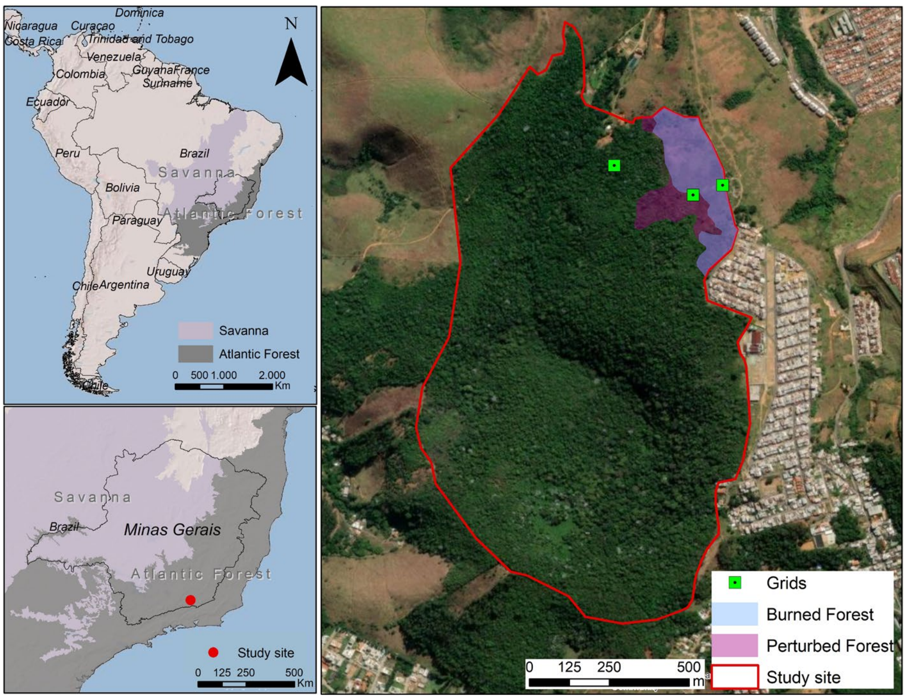


**Figure 1:** Studied site (red circle) in Juiz de Fora, Minas Gerais State, Brazil. The fragment is located in the Atlantic Forest, near the transition with the Savanna domains.

specimens, and material identification, we classified species according to their dispersal mode, fruit size, and seed size. Fruits (including pseudofruits) were categorized into five size classes: very small (≤ 0.2 cm), small (0.2 < small ≤ 2 cm), middle (2 < middle ≤ 5 cm), large (5 < large ≤ 10 cm), and very large (> 10 cm). Seed sizes were classified into three size classes: small (≤ 0.2 cm), middle (0.2 < middle ≤ 2 cm), and large (2 < large ≤ 5 cm). These size classes are useful because many Atlantic Forest plant species exhibit intra-specific variation within these ranges (Tabarelli et al., 2003). We categorized all dispersal modes into these classes to understand the relationship between fruit/seed size and dispersal mode comprehensively.

The functional diversity metrics calculated include functional dispersion (Fdis), which measures the dispersion of communities from a centroid; functional divergence (Fdiv), which quantifies the divergence weighted by species abundance in multivariate trait space; functional evenness (Feve), representing the distribution of species abundances across trait multi-space; and functional richness (Fric), which assesses the whole functional space occupied by species. These metrics collectively account for various dimensions of trait diversity in multivariate space. The functional diversity metrics were computed using the "FD" package, version:1.0-12.3 (Laliberté & Legendre, 2010; Laliberté et al., 2014) within the R software environment (R Development Core Team, 2024).

### Data analysis

Using the "Bray-Curtis" dissimilarity index with abundance data, we ordinated plot-level species through non-metric multidimensional scaling (NMDS) to explore the impact of fire on regeneration composition. The "MetaMDS" function from the "vegan" package (Oksanen et al., 2016) was used in this analysis. To investigate how fire influences functional community structure and diversity metrics across three vegetation types, we employed global linear models (GLMs) with vegetation type as a fixed effect. Abundance, species richness, CWMh, CWMms, Fric, Feve, Fdiv, and Fdis were included as response variables. Gaussian family errors were applied to CWMh and CWMms due to their normal distribution after log transformation. Negative Binomial distribution corrected for overdispersion was used for abundance, and Poisson family errors were applied for species richness. Model fitting utilized the "glm" function from the "lme4" package and "glm.nb" function from the "MASS" package (Bates et al., 2015). Multiple comparisons across vegetation types were conducted using the "glht" function from the "multcomp" package (Hothorn et al., 2008). Considering the proximity of plots (between 90 and 300 meters) and vegetation types, we accounted for spatial autocorrelation in testing fire effects across vegetation types.

## RESULTS

The sampling of shrub and tree species resulted in 1,189 individuals, encompassing 104 species from 71 genera and 35 families (Supplementary material 1). NMDS analysis identified three distinct floristic communities based on fire occurrence (Figure 2). The first axis primarily differentiated the Burned Forest (Twice-burned Forest) from the Perturbed Forest (Once-burned Forest) and Closed Forest. The second axis further distinguished the Perturbed Forest from the Closed Forest.

Among the different vegetation types, Fdiv and Fric exhibited significant variations, with Closed Forests showing the highest values and Burned Forests the lowest, respectively (see Figure 3; Table 2). Fdis showed significantly lower values in the Perturbed Forest than the other vegetation types, while Feve indicated that the Burned Forest had the lowest values (see Figure 3; Table 2). The remaining response variables (abundance, richness, CWMh, and CWMms) were also significantly influenced by vegetation type, with the Closed Forest consistently showing higher values (see Figure 3; Table 2).

Tree life forms were more abundant across all vegetation types, particularly in the Closed Forest (Figure 4a). Animal-mediated dispersal was higher in all vegetation types, with a predominance in the Closed Forest. Wind dispersal was more pronounced in the Burned Forest, while self-dispersal was emphasized in the Perturbed Forest (Figure 4b). Fruit and seed sizes exhibited similar patterns across the different vegetation types. Small and medium-sized fruits were present in all vegetation types, but large fruits were absent in the Burned Forest. Similarly, large seeds were absent in both the Burned and Perturbed Forests (Figure 4c, d).

Notably, the largest fruits (very large class) were found in *Schizolobium parahyba* (Vell.) (FABACEAE) in the Burned Forest and *Piptadenia gonoacantha* (Mart.) J.F.Macbr (FABACEAE) in the Closed Forest, with wind and self-dispersal modes, respectively.

**Table 1:** Functional traits identity, function and unit of natural regeneration species.

| Trait | Regeneration function | Definition |
|---|---|---|
| Maximum Height | Resilience/ Competition ability | Continuous (m) |
| Resprout | Persistence/ Resistance ability | Continuous (number) |
| Life form | Establishment ability | Categories (tree or shrub) |
| Dispersal mode | Dispersal ability | Categories (wind, self or animal dispersal) |
| Fruit size | Dispersal ability | *Categories (very small, small, middle, large or very large) |
| Seed size | Dispersal ability | *Categories (small, middle or large) |

* - See methods to range of the size classes.

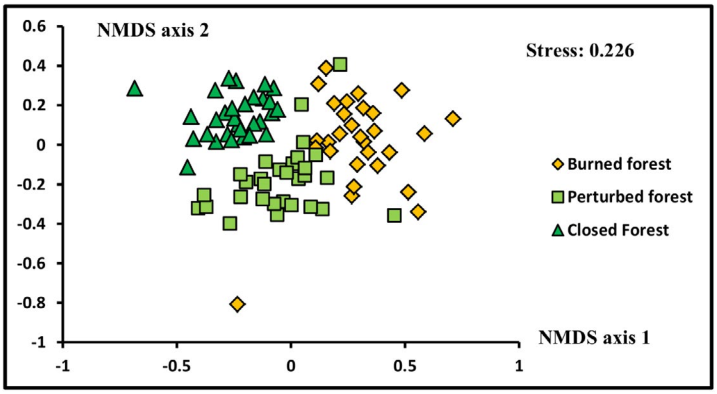


**Figure 2:** Non-Metric Multidimensional Scaling (NMDS) plotted with community-level composition dissimilarity of the three vegetation types (Burned Forest – yellow diamond, Perturbed Forest – light green square, and Closed Forest – dark green triangle).

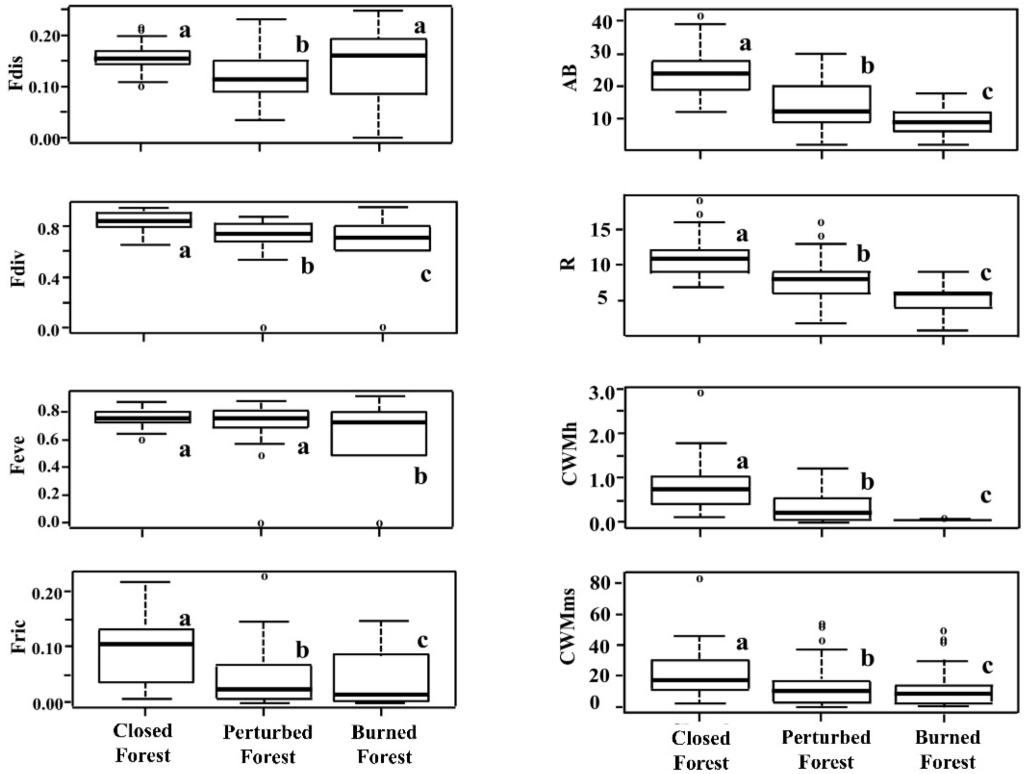


**Figure 3:** Boxplots showing variations of all analyzed variables for the three vegetation types: Closed, Perturbed, and Burned Forest. On the left, the variables are functional diversity metrics (functional dispersion - Fdis; functional divergence – Fdiv; functional evenness – Feve; functional richness – Fric) and on the right, are the abundance (AB), richness (R), and community-level traits of height (CWMh) and multistemmed (resprouting ability – CWMms). Significant differences between vegetation types were indicated by letters created using multiple comparisons analysis (see methods). "n.s" indicates no significant comparison between vegetation types with 95% confidence.

## DISCUSSION

Monitoring and analyzing post-fire trajectories in forest communities is crucial for understanding growth mechanisms and the provision of critical ecosystem services. These findings can help plan recovery actions for impacted areas (Andrade et al. 2020), especially in fragments of the Atlantic Forest. Our observations indicate that fire occurrence affects functional diversity, CWM traits, structural parameters, community-level composition, and species diversity across different vegetation types.

**Table 2:** Results of the generalized linear effects models for natural regeneration across the three vegetation types showed significant influences of the fixed effects (vegetation types) on various functional diversity metrics and other response variables. The response variables included functional dispersion (Fdis), functional divergence (Fdiv), functional evenness (Feve), functional richness (Fric), abundance (AB), richness (R), and community-level traits such as height (CWMh) and multistemmed (CWMms, indicating resprouting ability).

| Variable | Vegetation type | Estimate | SE | t-value | p-value | Random residual | AIC |
|---|---|---|---|---|---|---|---|
| Fdis | Intercept | 0.158 | 0.009 | 18.187 | <0.001* | 0.198 | -287.18 |
| | Perturbed | -0.036 | 0.012 | -2.931 | 0.004* | | |
| | Burned | -0.017 | 0.012 | -1.425 | 0.16 | | |
| Fdiv | Intercept | 0.84 | 0.045 | 18.766 | <0.001* | 5.225 | 7.2377 |
| | Perturbed | -0.168 | 0.063 | -2.656 | 0.009* | | |
| | Burned | -0.252 | 0.063 | -3.978 | >0.001* | | |
| Feve | Intercept | 0.75 | 0.044 | 16.85 | <0.001* | 5.168 | 6.227 |
| | Perturbed | -0.067 | 0.063 | -1.065 | 0.29 | | |
| | Burned | -0.174 | 0.063 | -2.776 | 0.007* | | |
| Fric | Intercept | 0.095 | 0.01 | 9.057 | <0.001* | 0.286 | -254.13 |
| | Perturbed | -0.042 | 0.015 | -2.855 | >0.001* | | |
| | Burned | -0.053 | 0.015 | -3.610 | >0.001* | | |
| AB* | Intercept | 3.199 | 0.068 | 47.036 | <0.001* | 96.694 | 582.48 |
| | Perturbed | -0.576 | 0.101 | -5.677 | <0.001* | | |
| | Burned | -0.994 | 0.107 | -9.244 | <0.011* | | |
| R | Intercept | 2.389 | 0.055 | 43.196 | <0.001* | 94.217 | 445.16 |
| | Perturbed | -0.305 | 0.085 | -3.595 | >0.001* | | |
| | Burned | -0.745 | 0.096 | -7.409 | <0.001* | | |
| CWMh | Intercept | -0.491 | 0.291 | -1.688 | 0.095 | 220.79 | 344.17 |
| | Perturbed | -1.461 | 0.411 | -3.552 | >0.001* | | |
| | Burned | -4.394 | 0.411 | -10.682 | <0.001* | | |
| CWMms | Intercept | 2.881 | 0.246 | 11.718 | <0.001* | 157.82 | 313.93 |
| | Perturbed | -0.904 | 0.348 | -3.469 | 0.011* | | |
| | Burned | -1.206 | 0.348 | -3.469 | >0.001* | | |

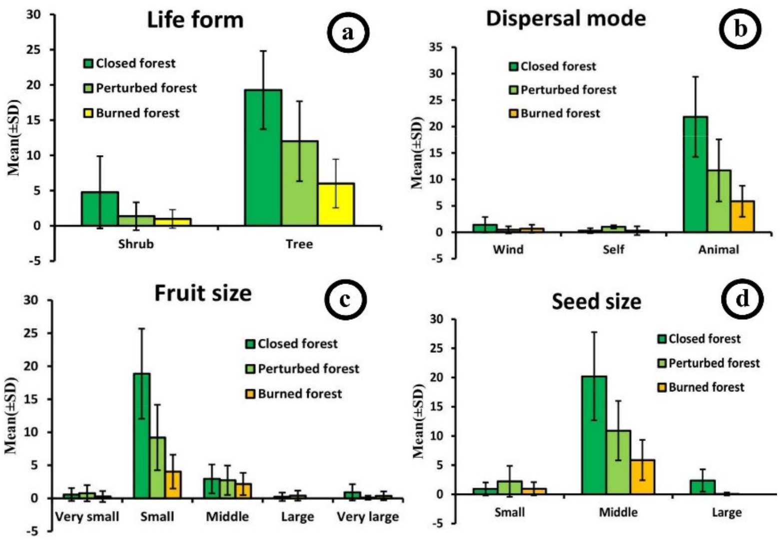


**Figure 4:** Bar plots of regeneration traits illustrate the mean values with standard deviations (± SD) for life form (shrub and tree) (a), dispersal mode (wind, self, and animal dispersal) (b), number of fruits across different size classes (five size classes ranging from very small to very large) (c), and number of seeds in different size classes (three size classes ranging from small to large) (d) among the three vegetation types (Closed – dark green bars, Perturbed Forest – light green bars, and Burned Forest – yellow bars).

The Closed Forest exhibited the highest functional diversity and values for structural and functional parameters compared to vegetation impacted by fire. Closed forests maintain a high canopy cover, which regulates the understory's temperature, humidity, and solar radiation (Cleary & Eichhorn, 2018). These microclimatic conditions favor the regeneration of plant species associated with more advanced successional stages, fulfilling complementary ecological functions within the ecosystem. In this context, fire act as an environmental filter (Andrade et al., 2020), preventing the coexistence of fire-intolerant species alongside fire-tolerant ones. Consequently, the absence of disturbances such as wildfires contributes to higher functional diversity by the coexistence of species with complementary ecologically attributes, enabling closed forests to evolve continuously (Araujo et al., 2017). This process enhances soil nutrient accumulation and carbon sequestration, improves the efficiency of organic matter cycling, and stabilizes ecological processes such as seed dispersal and seed bank maintenance. These conditions are conducive to the growth of more resource-demanding species, facilitating species recruitment across various ecological guilds.

On the other hand, burned areas present a functional dominance that compromises these services, reducing the ecosystem's capacity to regulate the local climate and maintain processes such as nutrient cycling and water retention. In addition, the loss of key species associated with the reduction of functional uniformity (Feve) in burned areas can significantly impact cultural or support services, such as seed dispersal and pollination, essential for natural regeneration and ecosystem resilience. The reduction of these services can result in limited ecosystem functionality, hindering its recovery and long-term sustainability.

Expected was a similarity in regeneration patterns between the Perturbed and Burned forests due to their spatial proximity (approximately 100 m), but due to the double fire occurrence, the Burned Forest was found to be significantly different. The Perturbed Forest has not fully recovered from the first fire occurred. Studies focusing on the reproductive characteristics of communities from an ecological perspective have reported long recovery periods, where tree communities may require approximately 25 years to recover from a fire, reaching a state similar to that of unburned communities, particularly after high-severity fires (Rodrigues et al., 2024). Andrade et al. (2020) identified differences in forest structure, mortality, and recruitment rates 11 and 15 years after a fire, reinforcing the understanding that the time since the fire has been insufficient for full recovery. The three vegetation types differed in species composition, diversity, and structure, consistent with reports in the literature about changes in composition (Cleary & Eichhorn, 2018) and structure (Balch et al., 2013) between burned and unburned landscapes.

Fires pose a significant threat to forest resilience (Andrade et al., 2020). In the Atlantic Forest, fires affect secondary succession by altering floristic composition, decreasing richness, reducing the prevalence of animal-dispersed trees, lowering abundance, and diminishing aboveground biomass, all of which contribute to low resilience in this rainforest compared to savannas (Sansevero et al., 2017, Abbas et al., 2023). Additionally, in our study sites, fire effects reduced basal area, height, and stem number weighted by community means, which are critical indicators of forest resilience. These patterns could be attributed to the increased mortality rate of fire-intolerant Atlantic Forest species due to selective pressure (Araujo et al., 2017). Recurrent fires, occurring two or more times in a short period, can decrease the abundance and diversity of slow-growing, shade-tolerant species typical of well-preserved climax forests. This can lead to the transformation of closed-canopy forests into more open forests dominated by secondary forest species (Andrade et al., 2020), a critical factor in highly fragmented environments and areas close to urban centers.

Closed Forests and Perturbed Forests remain distinct in composition, structure, and diversity. Fire also impacted functional diversity, with the lowest values of functional divergence (Fdiv) indicating losses in functional redundancy and resilience in Perturbed and Burned Forests, besides the lowest values in CWM traits (CWMh and CWMms). Where fire was most recent, functional evenness (Feve) was lower, indicating functional dominance. This occurs when a species disproportionately influences ecosystem functioning due to its abundance. Overall, we observed a gradual loss of functional groups and an increase in functional dominance from Closed to Burned Forests. In this case, functional dominance arises from the proliferation of species with fire-adaptive functional traits, as these species typically have adaptive advantages that allow them to monopolize available resources. This reduces functional diversity, leaving only species with similar attributes to dominate the community, thereby decreasing Feve. This process may lead to the loss of species associated with complementary ecosystem functions or even the disappearance of keystone species that support ecological processes such as seed dispersal or pollinator attraction, particularly in fragmented and degraded landscapes. Therefore, management and recovery strategies for burned areas must prioritize the reintroduction of species that perform complementary functions. Promoting structural and functional heterogeneity is thus essential to mitigating functional dominance and restoring ecosystem health (Charles-Dominique et al., 2017).

Functional richness (Fric) across vegetation types indicated that they differ in several traits within a multivariate space. The lowest values of functional dispersion (Fdis) in Perturbed Forests suggest a loss of diversity and potential resilience (Cooke et al., 2019). Despite the correlation between Fdis and richness, Burned Forests showed higher Fdis values than Perturbed Forests, even with lower richness. This suggests that an area with greater functional dispersion and lower richness can maintain ecosystem functionality due to the wide range of ecological functions performed by the few species present (Zhang & Zang, 2021). This functional diversity allows the ecosystem to sustain its functionality despite environmental changes or disturbances, due to the presence of species that can play complementary roles or replace each other in their ecological functions (Cooke et al., 2019).

The Closed Forest exhibited the highest functional diversity values, indicating that the best scenario for Atlantic Forest fragments is the absence of fire (Sakschewski et al., 2016). Empirical evidence demonstrates that fire alters the composition of functional traits, selecting traits that confer resistance to fire-induced disturbances, reducing the variability and thereby, influencing successional trajectories (Mata et al., 2022). Consequently, the natural regeneration of the Atlantic Forest following fire may be constrained by reductions in resilience (Cooke et al., 2019; Zhang & Zang, 2021).

Dispersal ability appears to be filtered within the fragment. Animal dispersal predominates across all vegetation types, with middle-sized fruit and seed classes being the most common. These results suggest that the fragment primarily contains species with middle-sized fruits and seed dispersers Fragmented forests in the Atlantic Forest Domain have only 13% tree cover and lack large-seed and late-successional species, hindering the development of old-growth forest stages (Costa et al., 2012). The defaunation process has been recognized as a significant driver of this pattern (Carvalho et al., 2016), not only in our studied remnant but throughout the entire Atlantic Forest Domain. Large-fruited and seeded dispersers like large mammals are missing (Jorge et al., 2013). Thus, defaunation could contribute to limiting fruit/seed sizes and dispersion and ecosystem functions like natural regeneration, which may be an indirect effect of fire, especially in Atlantic Forest fragments (Galetti et al., 2021). Seed sizes also may be influenced by seed banks and seed rain sources, which are reduced with fire occurrence (Cury et al., 2020). Finally, trees were the predominant life form in all vegetation types, suggesting that even the Burned Forest, the most affected by fire, remains in a forest state, still within the forest-savanna mosaic's alternative states.

These findings underscore the significant implications of fire disturbances in the Atlantic Forest and reinforce the importance of management strategies that promote the structural and functional recovery of degraded areas to ensuring the long-term sustainability of ecosystem services (Charles-Dominique et al., 2017). Closed forests, with their higher functional diversity, are crucial for maintaining critical services such as carbon sequestration, climate regulation, and nutrient cycling. Reintroducing ecologically important species and promoting functional heterogeneity are crucial actions to mitigate the effects of fire and promoting resilience, ensuring the sustainable provision of essential services for human populations and biodiversity associated with the Atlantic Forest.

## CONCLUSIONS

We found that fire occurrence leads to significant differences in natural regeneration patterns, composition, structure, and functional diversity. Vegetation types without fire exhibited the highest regeneration parameters, including functional diversity, community-level traits, diversity, abundance, and richness. In contrast, twice-burned vegetation types showed the lowest values, with few exceptions. Urbanization and anthropogenic fire (e.g., criminal fire, slash-and-burn practices) pose significant threats to preserved forest fragments. Frequent fires can lead to cascading effects on tree cover and natural regeneration, hindering the expansion of forest fragments in the Atlantic Forest. Our study demonstrated that, at the fragment level, the composition, structure, and functional diversity of Atlantic Forest fragments vary with successional changes following fire events. Moreover, the reduction in the abundance of large-seeded and fruited tree species (or even middle-sized ones) could potentially decrease the resilience of the Atlantic Forest. Understanding the effects of fire on functional diversity and natural regeneration patterns is crucial for anticipating the challenges in preserving the ecosystem services and biodiversity of the Atlantic Forest in the context of current fire and climate change scenarios.

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Database: FCA; POG; PCL

Processing: FCA; POG

Analysis: FCA; KJVP; ASM

Writing: FCA; POG; KJVP; ASM

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**Suplementary material 1:** Species list from Atlantic Forest fragment showing ocurrence between the three vegetation types.

| Family | Species | Closed Forest | Perturbed Forest | Burned Forest |
|---|---|---|---|---|
| Euphorbiaceae | *Acalypha brasiliensis* var. brasiliensis Müll.Arg. | x | | |
| Lamiaceae | *Aegiphila sellowiana* Cham. | | | x |
| Euphorbiaceae | *Alchornea glandulosa* Poepp. & Endl. | x | | |
| Euphorbiaceae | *Alchornea triplinervia* (Spreng.) Müll.Arg. | x | | |
| Sapindaceae | *Allophylus sericeus* (Cambess.) Radlk. | x | | |
| Rubiaceae | *Amaioua guianensis* Aubl. | | x | |
| Fabaceae | *Anadenanthera colubrina* (Vell.) Brenan | | x | |
| Fabaceae | *Andira fraxinifolia* Benth. | x | | |
| Lauraceae | *Aniba firmula* (Nees & Mart.) Mez | | x | |
| Annonaceae | *Annona cacans* Warm. | x | | |
| Euphorbiaceae | *Aparisthmium cordatum* (A.Juss.) Baill. | x | x | |
| Apocynaceae | Aspidosperma sp. | x | | |
| Solanaceae | *Athenaea martiana* Sendtn. | | | x |
| Solanaceae | *Aureliana velutina* Sendtn. | | | x |
| Asteraceae | *Baccharis serrulata* DC. | | | x |
| Moraceae | *Brosimum guianense* (Aubl.) Huber | x | | x |
| Solanaceae | *Brunfelsia brasiliensis* (Spreng.) L.B.Sm. & Downs | x | x | x |
| Solanaceae | *Brunfelsia hydrangeiformis* (Pohl) Benth. | x | x | x |
| Salicaceae | *Casearia arborea* (Rich.) Urb. | x | x | x |
| Salicaceae | *Casearia decandra* Jacq. | x | | |
| Salicaceae | *Casearia sylvestris* Sw. | x | | |
| Salicaceae | *Casearia ulmifolia* Vahl ex Vent. | x | | |
| Celastraceae | *Cheiloclinium serratum* (Cambess.) A.C.Sm. | | x | x |
| Primulaceae | *Clavija spinosa* (Vell.) Mez | x | | |
| Rubiaceae | *Coffea arábica* L. | x | | |
| Euphorbiaceae | *Croton salutaris* Casar. | | x | |
| Lauraceae | *Cryptocarya micranta* Meisn. | x | x | |
| Sapindaceae | *Cupania ludowigii* Somner & Ferrucci | x | x | x |
| Sapindaceae | *Cupania oblongifolia* Mart. | x | | |
| Sapindaceae | *Cupania vernalis* Cambess. | x | | |
| Solanaceae | *Cyphomandra* sp. | x | | |
| Fabaceae | *Dalbergia frutescens* (Vell.) Britton | | x | |
| Fabaceae | *Dalbergia nigra* (Vell.) Allemão ex Benth. | x | | |
| Rutaceae | *Dictyoloma vandellianum* A.Juss. | | x | x |
| Fabaceae | *Enterolobium contortisiliquum* (Vell.) Morong | x | | |
| Erythroxylaceae | *Erythroxylum citrifolium* A.St.-Hil. | x | x | |
| Erythroxylaceae | *Erythroxylum pelleterianum* A.St.-Hil. | x | x | x |
| Myrtaceae | *Eugenia* sp. | x | | |
| Myrtaceae | *Eugenia subundulata* Kiaersk. | x | x | x |
| Arecaceae | *Geonoma schottiana* Mart. | | x | |
| Nyctaginaceae | *Guapira graciliflora* (Mart. ex Schmidt) Lundell | x | | |
| Nyctaginaceae | *Guapira opposita* (Vell.) Reitz | x | | |
| Meliaceae | *Guarea macrophylla* Vahl | x | x | |
| Annonaceae | *Guatteria odontopetala* Mart. | x | x | x |
| Annonaceae | *Guatteria sellowiana* Schltdl. | x | x | |
| Annonaceae | *Guatteria villosissima* A.St.-Hil. | x | x | |
| Bignoniaceae | *Handroanthus chrysotrichus* (Mart. ex DC.) Mattos | | | |
| Aquifoliaceae | *Ilex dumosa* Reissek | x | | |
| Fabaceae | *Inga cylindrica* (Vell.) Mart. | | x | |
| Bignoniaceae | *Jacaranda micrantha* Cham. | x | | x |
| Lacistemataceae | *Lacistema pubescens* Mart. | x | x | x |
| Melastomataceae | *Leandra* sp. | x | | |
| Lecythidaceae | *Lecythis lanceolata* Poir. | x | | |

Continue...

**Suplementary material 1:** Continuation.

| Family | Species | Closed Forest | Perturbed Forest | Burned Forest |
|---|---|---|---|---|
| Verbenaceae | *Lippia brasiliensis* (Link) T.R.S.Silva | x | x | x |
| Fabaceae | *Lonchocarpus muehlbergianus* Hassl. | | x | |
| Malvaceae | *Luehea grandiflora* Mart. | x | | |
| Fabaceae | *Machaerium acutifolium* Vogel | | x | |
| Fabaceae | *Machaerium hirtum* (Vell.) Stellfeld | x | | |
| Fabaceae | *Machaerium nyctitans* (Vell.) Benth. | x | | |
| Euphorbiaceae | *Maprounea guianensis* Aubl. | | x | x |
| Celastraceae | *Maytenus salicifolia* Reissek | | x | |
| Melastomataceae | *Miconia cinnamomifolia* (DC.) Naudin | x | | |
| Melastomataceae | *Miconia discolor* DC. | x | | |
| Melastomataceae | *Miconia latecrenata* (DC.) Naudin | x | x | |
| Melastomataceae | *Miconia robustissima* Cogn. | | x | |
| Monimiaceae | *Mollinedia widgrenii* A.DC. | | x | |
| Melastomataceae | *Mouriri myrtilloides* (Sw.) Poir. | x | | |
| Myrtaceae | *Myrcia splendens* (Sw.) DC. | x | x | x |
| Myrtaceae | *Myrciaria floribunda* (H.West ex Willd.) O.Berg | | x | |
| Lauraceae | *Nectandra oppositifolia* Nees & Mart. | x | | |
| Lauraceae | *Nectandra reticulata* (Ruiz & Pav.) Mez | x | x | |
| Lauraceae | *Ocotea aciphylla* (Nees & Mart.) Mez | | x | |
| Lauraceae | *Ocotea silvestris* Vattimo-Gil | x | | |
| Lauraceae | *Ocotea corymbosa* (Meisn.) Mez | x | x | |
| Lauraceae | *Ocotea odorifera* (Vell.) Rohwer | x | x | x |
| Peraceae | *Pera barbinervis* (Mart. ex Klotzsch) Pax & K.Hoffm. | | x | |
| Peraceae | *Pera glabrata* (Schott) Baill. | x | | |
| Piperaceae | *Piper aduncum* L. | x | | |
| Piperaceae | *Piper tectoniifolium* Kunth | x | | |
| Piperaceae | *Piper vicosanum* Yunck. | x | | |
| Fabaceae | *Piptadenia gonoacantha* (Mart.) J.F.Macbr. | x | x | |
| Fabaceae | *Piptadenia paniculata* Benth. | x | | |
| Fabaceae | *Platypodium elegans* Vogel | | x | |
| Sapotaceae | *Pouteria guianensis* Aubl. | | x | |
| Burseraceae | *Protium heptaphyllum* (Aubl.) Marchand | x | x | |
| Rosaceae | *Prunus myrtifolia* (L.) Urb. | x | | |
| Myrtaceae | *Psidium cupreum* DC. | | x | x |
| Rubiaceae | *Psychotria cephalantha* (Müll.Arg.) Standl. | x | x | x |
| Rubiaceae | *Psychotria* sp. | x | | |
| Rubiaceae | *Psychotria vellosiana* Benth. | x | x | |
| Celastraceae | *Salacia elliptica* (Mart.) G. Don | | x | |
| Araliaceae | *Schefflera longipetiolata* (Pohl ex DC.) Frodin & Fiaschi | x | | |
| Fabaceae | *Schizolobium parahyba* (Vell.) Blake | | | x |
| Fabaceae | *Sclerolobium rugosum* Mart. | | x | |
| Siparunaceae | *Siparuna guianensis* Aubl. | x | x | x |
| Elaeocarpaceae | *Sloanea guianensis* (Aubl.) Benth. | | x | |
| Elaeocarpaceae | *Sloanea guianensis* (Aubl.) Benth. | x | | |
| Elaeocarpaceae | *Sloanea monosperma* Vell. | | x | |
| Solanaceae | *Solanum graveolens* Bunbury | | | x |
| Solanaceae | *Solanum velleum* Sw. ex Roem & Schult. | | x | x |
| Anacardiaceae | *Tapirira guianensis* Aubl. | | | x |
| Clusiaceae | *Tovomita brasiliensis* (Mart.) Walp. | | x | |
| Asteraceae | *Vernonanthura divaricata* (Spreng.) H.Rob. | | x | |
| Annonaceae | *Xylopia brasiliensis* Spreng. | | x | |
| Rutaceae | *Zanthoxylum rhoifolium* Lam. | x | | |