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Slow Recovery and Loss of Species Richness in a Semi-Deciduous Seasonal Atlantic Forest After Selective Logging and Drought Events

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ABSTRACT

Questions: The structure and dynamics of tropical forests face increasing pressures from historical land use and climate change. We asked: (1) Is there a significant difference in forest structure and species composition over 23 years? (2) Which tree species increase or decrease in stem density and/or basal area during this period? (3) Does drought exert a more pronounced effect on the tree community in a more recently disturbed site?

Location: Guaxindiba State Ecological Station in São Francisco do Itabapoana (21°24'S, 41°04'W), Rio de Janeiro, Brazil.

Methods: Over 23 years, we monitored all trees with ≥ 10 cm diameter at breast height (DBH) in four permanent 0.25-ha plots established in 1995 at each of two sites: one with signs of selective logging until 1960 (US60) and another selectively logged until 1990 (LS90). We assessed changes in basal area, stem density, species richness, evenness and turnover, and calculated recruitment, mortality and relative growth. Climate variability was assessed using precipitation and temperature anomalies and maximum cumulative water deficit.

Results: Both sites showed slow recovery, with small increases in stem density and basal area and declines in species richness and evenness. Dominant species, such as *Metrodorea nigra* and *Marlimorimia contorta*, gained prominence, indicating a possible inhibitory role in the successional process. Recruitment decreased and mortality increased over time at both sites, possibly related to drought events. LS90 experienced greater species loss and structural changes compared to US60. Highlighting persistent selective logging legacies, exacerbated by recurrent droughts.

Conclusions: Selective logging and recurrent droughts created long-lasting impacts on the semi-deciduous seasonal Atlantic Forest (SSAF), reducing resilience and slowing ecological recovery. Community trajectories converged towards floristic simplification, with *drought-tolerant dominants displacing less resilient species*. These findings underscore the vulnerability of seasonal tropical forests to compound disturbance and climate stress, emphasizing the need for targeted conservation to enhance resilience, sustain biodiversity and preserve ecosystem services.

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1 | Introduction

Among the various terrestrial biomes in Tropical Americas, the Atlantic Forest stands out for its megadiversity and plant endemism, as well as for its ecological importance and priority for conservation, while simultaneously ranking among the most threatened global hotspots (Mittermeier et al. 1998; Antonelli and Sanmartín 2011; BFG 2022). Once covering more than 130 million hectares, this biome has been reduced to approximately 12.5% of its original extent, largely as a result of deforestation, forest degradation and fragmentation (Metzger 2009; Rodrigues et al. 2009; SOS Mata Atlântica Foundation and INPE 2022). In the Atlantic Forest, the semi-deciduous and deciduous forest phytophysognomies (IBGE 2012) exhibit marked seasonality, with distinct rainy and dry periods. The degree of deciduousness increases with decreasing rainfall (Mooney et al. 1995; Pennington et al. 2000, 2009).

Forest dynamics in seasonal forests are strongly influenced by both climatic variability and disturbance history, which jointly regulate tree growth, mortality, recruitment and long-term successional trajectories (Felfili 1995; Rolim et al. 1999; Vilella et al. 2006; Nascimento et al. 2014; Brien et al. 2015; Rowland et al. 2015; Corlett 2016; Browne et al. 2021; Tng et al. 2022). Drought events have emerged as a major driver of demographic change in tropical forests, altering water and nutrient availability, physiological performance and competitive interactions, often leading to elevated mortality and reduced growth among drought-sensitive species or tree species that cannot cope with these disturbances and stresses (Condit et al. 2013; Allen et al. 2017; Bretfeld et al. 2018; Browne et al. 2021). Increasing frequency and intensity of droughts under climate change scenarios raise concerns about forest resilience, especially in ecosystems already exposed to anthropogenic disturbances (IPCC 2022).

Selective logging represents one of the most widespread anthropogenic disturbances in tropical forests and can generate long-lasting legacies in forest structure, composition and functioning (Okuda et al. 2003; Gourlet-Fleury et al. 2013; Condé et al. 2019). Even when applied at low intensity or during a single extraction cycle, selective logging can change forest structure, reduce basal area and above-ground biomass, reduce carbon stocks, increase tree mortality and modify competitive hierarchies among species, with effects persisting for decades (Okuda et al. 2003; Vilella et al. 2006; Osazuwa-Peters et al. 2015; Ding et al. 2017; Watson et al. 2018; Condé et al. 2019; Arcanjo et al. 2023). In the Semi-deciduous Seasonal Atlantic Forest (SSAF), logged stands may retain substantially lower basal area, biomass and altered species dominance even four decades after disturbance, indicating slow recovery and reduced structural resilience compared to unlogged fragments (Arcanjo et al. 2023).

The impacts of drought and selective logging are unlikely to act independently. Logging-induced changes in forest structure, species composition and functional trait distributions may amplify forest vulnerability to subsequent climatic extremes, acting as complementary environmental filters that shape demographic responses and successional pathways (Nepstad et al. 2007; Brando et al. 2014; Anderegg et al. 2015). Forests with a legacy of disturbance often exhibit reduced resistance and resilience to drought due to shifts towards species with

lower hydraulic safety margins, simplified stand structure and diminished buffering capacity against water stress (McDowell et al. 2008; Rowland et al. 2015; Greenwood et al. 2017).

These interacting stressors may also promote floristic and functional homogenization, characterized by declines in species diversity and the increasing dominance of a limited subset of drought-tolerant or disturbance-adapted species (Ter Steege et al. 2013; Enquist et al. 2019; Esquivel-Muelbert et al. 2019). Such processes have raised concerns about the emergence of hyperdominance and reduced functional redundancy in tropical forests, potentially compromising ecosystem resilience and long-term carbon storage (Bastin et al. 2019; McDowell et al. 2020).

Long-term monitoring is crucial for disentangling the relative and interactive effects of disturbance history and climate variability on forest dynamics (Lewis et al. 2004; Brien et al. 2015). Continuous monitoring of forest plots allows us to assess forest dynamics, ecological resilience and ecosystem functions that change over time, especially in ecosystems exposed to multiple stressors (Moonlight et al. 2021). However, long-term datasets remain scarce for many Atlantic Forest formations, particularly for *Tabuleiro* forests, despite their ecological relevance and high conservation value. Studies in this forest type are limited in number and temporal extent, restricting our understanding of how these ecosystems respond to multiple, interacting stressors over decadal timescales (Rolim et al. 1999; Jesus and Rolim 2005; Vilella et al. 2006; de Paula and Soares 2011; de Abreu et al. 2014).

In this context, the present study provides an opportunity to evaluate forest dynamics over a 23-year period (1996–2019) in an SSAF, combining long-term monitoring with different logging disturbance histories. We compared two forest sites within the same landscape that experienced contrasting selective logging histories, one logged until the 1960s and another until the early 1990s (more disturbed), thereby allowing us to assess how legacy effects of disturbance mediate forest responses to subsequent drought events.

Specifically, we addressed the following research questions: (1) How have forest structure and species composition changed over the 23-year monitoring period? (2) Which tree species contributed most to changes in stem density and basal area through time? (3) Does drought exert stronger effects on forest dynamics in the more recently disturbed site? We hypothesized that forests with more disturbance history would exhibit lower resilience to drought, expressed as higher mortality, reduced basal area recovery and increased dominance of drought-tolerant species, reflecting the combined effects of disturbance legacies and climatic stress on successional trajectories.

2 | Methods

2.1 | Study Site

This study was conducted at the *Estação Ecológica Estadual de Guaxindiba* (Guaxindiba State Ecological Station—EEEG), located in the municipality of São Francisco de Itabapoana, Rio de Janeiro, Southeast Brazil (21°24'06.03"S and 41°05'26.81"W)

(Appendix S1). Our studied forest is a type of SSAF called *Tabuleiro* Forest, covering approximately 1200 ha and considered one of the last and most significant forest remnants of the *Tabuleiro* Forest of the State of Rio de Janeiro (Silva and Nascimento 2001). *Tabuleiro* Forest is a lowland Atlantic Forest associated with the *Barreiras* Group that differs from other formations of the Atlantic Forest as it occupies a large coastal plain on Tertiary deposits (Veloso et al. 1991; Rizzini 1997; Nascimento and Lima 2008).

The original forest cover was severely reduced throughout the 20th century due to charcoal production, establishment of sugarcane and pineapple plantations, pasture expansion and selective logging of commercially valuable timber species, such as *Aspidosperma* spp., *Machaerium* spp., *Paratecoma peroba* and *Melicoccus oliviformis* subsp. *intermedius* (Villela et al. 2006). The flora is highly diverse, with Leguminosae, Myrtaceae and Euphorbiaceae standing out as the most species-rich families, and structurally important species such as *Metrodorea nigra* (Rutaceae), *Paratecoma peroba* (Bignoniaceae) and *Marlimorimia contorta* (Leguminosae) (Silva and Nascimento 2001). The forest has no record of systematic management, and all logging can be considered illegal, with harvesting having occurred in a cycle of a single selective extraction involving about 20 species, mostly for local trade (Villela et al. 2006). Beyond its floristic relevance, the EEEG has strategic importance for the conservation of regional biodiversity, serving as a refuge for endemic species and providing essential ecosystem services in a landscape heavily affected by forest fragmentation (Santos et al. 2024).

Past degradation associated with deforestation, selective logging and edge effects resulting from forest fragmentation (Santos et al. 2024) has contributed to a forest structure characterized by high densities of small-diameter trees and reduced basal area compared with undisturbed SSAFs, as well as elevated mortality of large trees (Silva and Nascimento 2001; Villela et al. 2006; de Abreu et al. 2014).

According to Köppen's classification, the region is an Aw type (tropical wet with a dry winter) (Alvares et al. 2013), with high temperatures and marked seasonality, with a rainy summer (December to March) and drier autumn-winter (May to October) (< 100 mm/month) (Appendix S2a).

The climatological normal shows that the average annual rainfall has been decreasing with each series (30 years), with an average annual rainfall of 1084 mm for the years 1931 to 1960 (RADAMBRASIL 1983), 1055 mm between 1961 and 1990 (INMET 2023), and 982 mm between 1991 and 2020 (INMET 2023) and indicates that the area experienced periods of relative drought, specifically in 2000–2003, 2010–2012 and 2014–2017 (Appendix S2b). According to Tomasella et al. (2023), the climate in the northern region of Rio de Janeiro has undergone significant changes over the past 30 years, transitioning to a 'sub-úmido seco' (dry sub-humid) classification. This shift is supported by an aridity index of 0.65 (calculated as the ratio between accumulated precipitation and reference evapotranspiration for each period), which represents the lowest value recorded for the region between 1990 and 2020. These findings highlight an increasing climatic dryness that may have profound implications for ecosystem resilience and water availability.

According to Fidalgo et al. (2005), the region has deep and well-drained soils, primarily *Latossolo Amarelo* and *Latossolo Vermelho* (Ferralsol in WRB FAO classification), with elevations ranging from 15 to 40 m above sea level.

2.2 | Field Sampling

Four permanent plots of 50 m × 50 m (0.25 ha) were randomly installed in October 1995 in each of the two forest sites selected, one with signs of selective logging until 1960 (US60) and the other in an area selectively logged until 1990 (LS90) (see Villela et al. 2006 for more details about sites). No fire occurrence was reported in any of the evaluated permanent plots. The plots of each site are located at least 600 m from the edge of the forest fragment to minimize edge effects and are spaced an average of 25 m apart from each other, and they are believed to have been similar in floristic structure and composition before selective logging (Villela et al. 2006).

Measurements of vegetation structural parameters were carried out in 1996, 2003, 2008, 2014, and 2019. Species identification was based on herbarium material comparison and consultations with experts. The family names were classified according to the APG IV system (Angiosperm Phylogeny Group—IV 2016). Botanical vouchers from the collections for identification were incorporated into the Herbarium of the Centre for Biosciences and Biotechnology at *Universidade Estadual do Norte Fluminense Darcy Ribeiro* (HUENF), and duplicates were sent to the Herbarium of the *Jardim Botânico do Rio de Janeiro* (RB). Species and family names can be found in Appendix S3.

All trees with DBH ≥ 10 cm were censused in 1996, 2003, 2008, 2014, and 2019. The DBH of the trees was measured at 1.3 m above ground. For trees on hillsides, height above ground was measured on the upslope side of the tree. In the case of trees broken at 1.3 m from the ground but with regrowth, the DBH was measured 20 cm below the breakage. Trees not found in the current census were considered missing.

2.3 | Data Collection

2.3.1 | Forest Structure and Dynamics

Phytosociological parameters, including number of individuals (*N*), total basal area (BA_T), relative density (RD), relative dominance (RDo) and importance value index (IVI), were calculated for the trees using the Fito.R function (Dalagnol et al. 2018). For the species diversity analysis, we used the effective number of species (ENS_p) and Pielou's evenness (*J'*) (Jost 2006; Moro and Martins 2011). Comparative assessments of species richness between the years sampled and between the areas studied were conducted through the analysis of rarefaction and extrapolation curves (Gotelli and Graves 1996; Roswell et al. 2021) (Appendix S4).

For dynamic rates, we calculated the annual rates of mortality and recruitment (Sheil 1995; Sheil et al. 2000). We also calculated turnover, defined as the average between recruitment and mortality rates, which represents the time required for the total

renewal of the forest's tree component (Hartshorn 1990; Phillips et al. 2004). Additionally, we calculated the annual RGR of trees (Bischoff et al. 2005). To assess overall stand dynamics, the annual rate of net change was calculated for the number of trees (ΔN) and basal area (ΔBA) (Korning and Balslev 1994). The formulas used can be found in Appendix S5.

2.3.2 | Climate

We calculated climatic variation (e.g., air temperature, precipitation and evapotranspiration) using data from the INMET (National Institute of Meteorology of Brazil) meteorological station in Campos dos Goytacazes, 45 km from the EEEG (<https://portal.inmet.gov.br/>—Meteorological Station: 83698—Campos). We used a time series of 27 years (1992–2019), covering 4 years before the first vegetation census (1996) to the end of this study's census (2019). This station was chosen for its proximity to the study area and its robust, continuous time series with minimal data gaps.

Precipitation indices such as CDD (Consecutive Dry Days), CWED (Consecutive Wet Days) were calculated for the dry (May to October) and rainy (November to April) seasons to understand rainfall behaviour and support discussions of the relationship between forest resilience and climate based on INMET data (Marengo et al. 2020; Soldini and Darvini 2025).

In addition, daily reanalysis data of 2-m air temperature and precipitation were used for the same time series, obtained from the ERA5 Reanalysis (which represents the fifth Generation of Atmospheric Reanalysis produced by the European Centre for Medium-Range Weather Forecasts—ECMWF; Hersbach et al. 2020).

The Maximum Cumulative Water Deficit (MCWD) method proposed by Aragão et al. (2007, 2018) was employed to understand the impacts and intensity of drought periods on forest dynamics. To calculate the MCWD, first, we calculate the monthly water deficit (WD) for each year, using evapotranspiration (E) and monthly precipitation (P) (Aragão et al. 2007). The rationale for this calculation is that when monthly rainfall is lower than evapotranspiration, the forest system loses water, entering into a water deficit status. The following rule was applied to calculate the WD for each month (n). Therefore:

$$\begin{aligned} \text{If } WD_{n-1} - E + P_n < 0; \\ \text{then } WD_n &= WD_{n-1} - E + P_n \\ \text{else } WD_n &= 0 \end{aligned}$$

The variables precipitation (P) and evapotranspiration (E) for calculating WD and MCWD were obtained from the time series of 27 years (1992–2019) of the climatic survey.

2.4 | Data Analysis

To identify differences in forest structure and composition between sites over time, we analysed BA_{t} , stem density, $ENSP$ and J' . Given that the four plots within each site share the same

fragmentation history and environmental conditions, they do not represent independent spatial units. Therefore, we avoided multivariate models that would assume spatial independence. Instead, we examined bivariate associations using Analysis of Covariance (ANCOVA) to compare the two sites (US60 and LS90) as the primary units of analysis. This approach prioritizes the comparison of disturbance legacies, assuming original floristic similarity between sites (Villela et al. 2006), by testing whether the relationship between forest dynamics metrics and time differs between the two areas.

Associations between variables were tested using linear and polynomial regression models, and their multiple coefficients of determination (R^2) were reported (functions `lm` and `poly`, BASE package, R Core Team 2025). The confidence intervals of each regression model were presented graphically (function `predict`, BASE package, R Core Team 2025). A type I error rate of $\alpha = 0.05$ was assumed a priori in all cases. The significance of the interaction term in an ANCOVA was used to test whether parameter variation differed between sites. When the interaction term was not significant, it was removed from the model, and a common slope coefficient was assumed to perform mean comparisons adjusted by this shared slope. When necessary, the data were adjusted using a maximum likelihood function (boxcox function, MASS package, Venables and Ripley 2002) to meet the assumptions of regression models (linearity, normality and homoscedasticity of residuals). For the species richness in the areas, the rarefaction and extrapolation curves (Hsieh et al. 2016; Roswell et al. 2021) were compiled using the `iNEXT` function (`iNEXT` R package, Hsieh et al. 2016), and estimates were calculated as the mean of 1000 bootstrap replications with 95% confidence interval.

The 20 main species for each census were ranked by IVI for both sites. Community-level and species-specific RGR were calculated using only the largest stem for multiple-stemmed trees. For the latter, we selected species that met the following criteria: highest IVI, $N > 10$ and presence among the top 20 species in the IVI rank across all censuses. Based on these criteria, RGR was calculated for the following six species: *Marlimorimia contorta*, *Metrodorea nigra*, *Metternichia princeps*, *Pachystroma longifolium*, *Senegalia polyphylla* and *Trigoniodendron spiritusancense*.

We calculated tree community dynamics (recruitment, mortality, ΔN , ΔBA and turnover rates) using the `forest.din` function (Higuchi 2018; Réjou-Méchain et al. 2017). Mortality, recruitment and turnover rates were standardized using the equation: $\lambda_{\text{corr}} = \lambda \times t^{0.08}$, where λ is the rate and t is the time between censuses in years (Lewis et al. 2004).

To characterize drought intensity and duration, we calculated the MCWD anomaly (MCWDa) based on the Z-score used by Aragão et al. (2007). If the deficit is greater (more negative values of MCWDa), plants are more susceptible to suffering the effects of droughts. For the 2-m air temperature and precipitation, we applied anomalies to these Reanalysis data to understand the behaviour of climate variables in different intervals relative to the climatological average of the time series (1996–2019). Four periods were defined for calculating the anomalies, corresponding to the alternation of forest census interval that goes from 1996 to 2003, 2004 to 2008, 2009 to 2014, and finally, from 2015 to 2019.

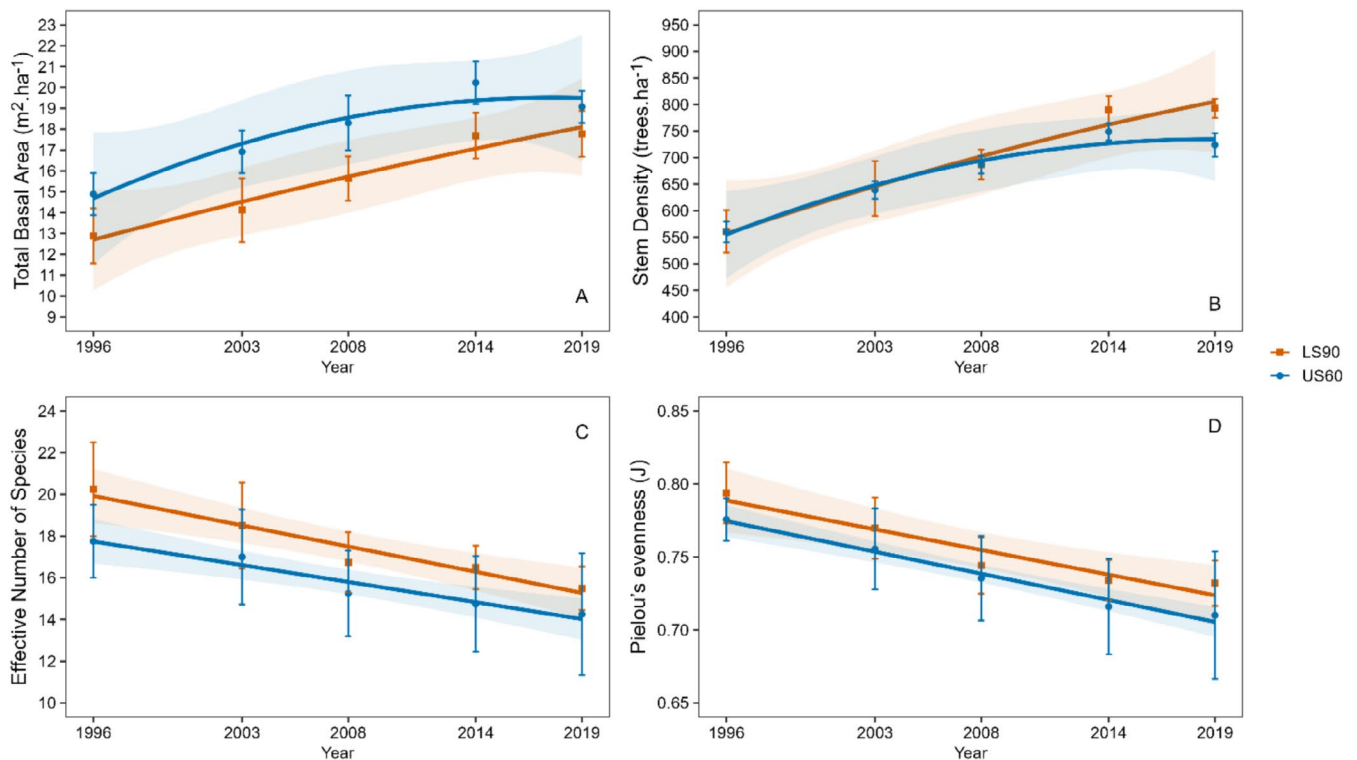


FIGURE 1 | Quadratic regressions for the variables of Total Basal Area (A) and Stem Density (B); and linear regressions for the Effective Number of Species (C) and Pielou's Evenness (D) per plot of the tree community in US60 and LS90 sites. The model equations and tests are reported in Appendix S6. The error bars represent the standard error of the mean, and the shaded area is the 95% confidence interval of the model.

These anomalies were calculated as follows: $\text{Anomaly} = P_2 - P_1$, with period 1 (P_1) corresponding to the climatological average (1996–2019) and period 2 (P_2) corresponding to the average of each census interval, so that we can understand the intensity of the census periods, both for the dry and rainy seasons.

All statistical analyses were performed using the R program (R Core Team 2025).

3 | Results

3.1 | Floristic Structure and Composition Over 23 Years (1996–2019)

Dynamics of structural parameters such as BAt, stem density, ENSp and J' did not differ between sites (Figure 1), but showed strong trends over time across censuses. Correlations with the census interval ranged from 0.86 to 0.98 (Appendix S6).

BAt increased steadily from census 1 (1996) to census 5 (2019) in both sites, rising from $14.89 \pm 2.01 \text{ m}^2 \cdot \text{ha}^{-1}$ to $19.08 \pm 1.55 \text{ m}^2 \cdot \text{ha}^{-1}$ in US60 and from $12.88 \pm 2.64 \text{ m}^2 \cdot \text{ha}^{-1}$ to $17.78 \pm 2.18 \text{ m}^2 \cdot \text{ha}^{-1}$ in LS90 (Figure 1a). Stem density followed a similar trend, increasing from $560 \pm 39 \text{ trees} \cdot \text{ha}^{-1}$ to $724 \pm 44 \text{ trees} \cdot \text{ha}^{-1}$ in US60 and from $561 \pm 80 \text{ trees} \cdot \text{ha}^{-1}$ to $793 \pm 36 \text{ trees} \cdot \text{ha}^{-1}$ in LS90 (Figure 1b). In contrast, species diversity (ENSp and J') decreased in both sites (Figure 1c,d), with higher values in LS90 and more pronounced species dominance. This decline in richness, particularly after 2014, was corroborated by rarefaction curves (Appendix S4).

The diameter distribution of trees and the basal area showed a reverse J-shaped distribution in all censuses, with most individuals concentrated in the initial diameter class ($10 < 20 \text{ cm}$) (Figure 2), consistent with a regenerating forest. In US60, the $>40 \text{ cm}$ diameter class contains more trees and contributes more than twice the basal area compared to LS90 (Figure 2).

In 2019, resprouting individuals accounted for 2.2% ($n=33$) of all sampled trees, with 67% occurring in LS90. Resprouting was observed in 8% of species in US60 and 19% in LS90.

3.2 | Temporal Changes in Species and Basal Area Over 23 Years

An assessment of the top 20 dominant species, ranked by IVI over the 23-year period (Appendix S7), revealed shifts in community composition and dominance. While the most abundant species generally maintained their ranking, turnover occurred within the top 20 species between censuses. In US60, 17 of the initial top 20 species remained in this dominant group by 2019, whereas in LS90, only 14 persisted. Among these top 20 dominants, species such as *Melicoccus oliviformis* and *Metternichia princeps* increased in both IVI and abundance, particularly in LS90. Conversely, other dominant species, such as *Trichilia pseudostipularis* (in US60) and *Copaifera lucens* (in LS90), exhibited strong declines in stem density and basal area.

It is worth noting that at both sites, *Metrodorea nigra* and *Marlimorimia contorta* consistently ranked among the top positions in the IVI throughout the 23-year period, together

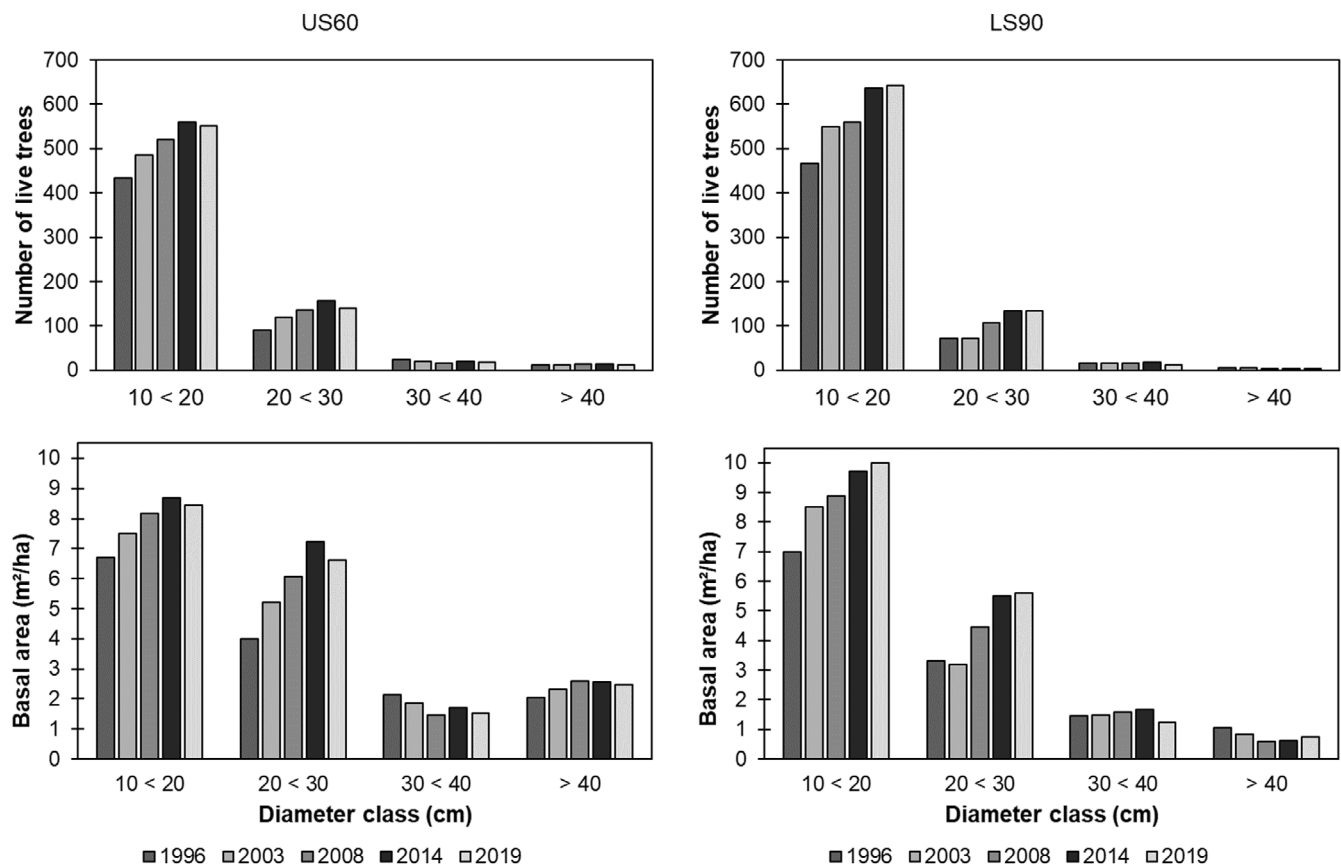


FIGURE 2 | Diameter class distribution and basal area of the tree community in the US60 and LS90 sites.

accounting for more than one-third of the BA_T. An analysis of changes in stem density and basal area between 1996 and 2019 indicates that both species experienced significant increases in these metrics, representing approximately 50% of the stem density and BA_T at both sites during the last two censuses (2014 and 2019) (Appendices S7, S8).

The ΔN among the top 20 species revealed distinct differences in population trends between sites (Figure 3). The primary contrast was the broader population expansion in LS90, where 14 species showed positive ΔN (with one stable and five declining), compared to only 10 growing species in US60 (three stable and seven declining). Furthermore, some species exhibited entirely opposite trends depending on the site; notably, *Trichilia pseudostipularis* experienced the steepest decline in US60 but showed positive ΔN in LS90. Despite these contrasting dynamics, *Melicoccus oliviformis* consistently exhibited the highest gains across both sites, while the most severe decline in LS90 was observed for *Copaifera lucens*.

RGR analyses revealed a general decrease after the 2008–2014 census interval at both sites (Figure 4). While *Marlimorimia contorta* generally maintained the highest RGR values across most of the study period, *Metrodorea nigra* exhibited a distinct pattern in the final interval (2014–2019). During this last period, *Metrodorea nigra* deviated from the general declining trend, showing an increase in RGR in US60 and maintaining relatively high values in LS90.

3.3 | Drought Impacts in Disturbed (LS90) vs. Less Disturbed Sites (US60)

We identified two main periods of intensified drought conditions over the 23-year study: the first between 1996 and mid-2005, and the second occurring during the final census interval (2014–2019). The first drought was characterized by prolonged negative MCWDa (Figure 5) and reduced precipitation in both the rainy and drier seasons (Appendix S10b,c), representing the most severe water deficit in the study period. We observed an overall increasing trend in CDD over the years, with prominent peaks corresponding to the drought episodes, while CWeD showed a decreasing trend (Appendix S11). The identification of the second drought episode was strongly supported by combined climate trends; precipitation anomaly maps (Appendix S10) showed pronounced negative values, especially during 2014–2019, which coincided with a marked warming trend revealed by temperature anomalies (Appendix S12). Together, these records indicate an intensification of drought conditions in the latter years, driven by elevated 2-m air temperature anomalies and pronounced negative precipitation anomalies.

In the 2014–2019 census interval, we observed high values in CDD and a strong positive temperature anomaly (Appendix S12), mortality increased and recruitment declined, particularly in US60. US60 showed negative values of ΔN and ΔBA (Figure 6), indicating a decline in population. LS90 also showed reduced ΔN and ΔBA , maintaining a positive balance.

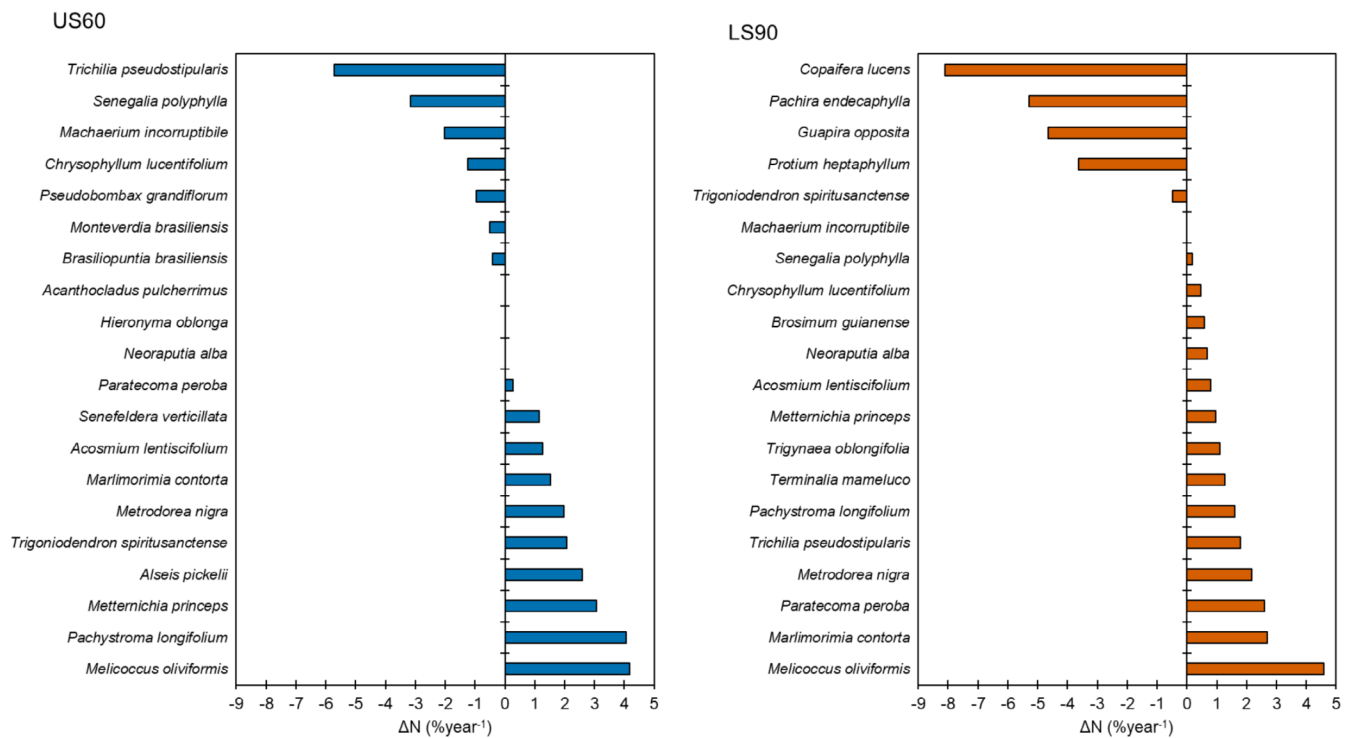


FIGURE 3 | Variation of the net change in number of individuals (ΔN) for the 20 most important species for the 23-year interval (1996–2019), ranked by IVI for the tree community in US60 and LS90 sites.

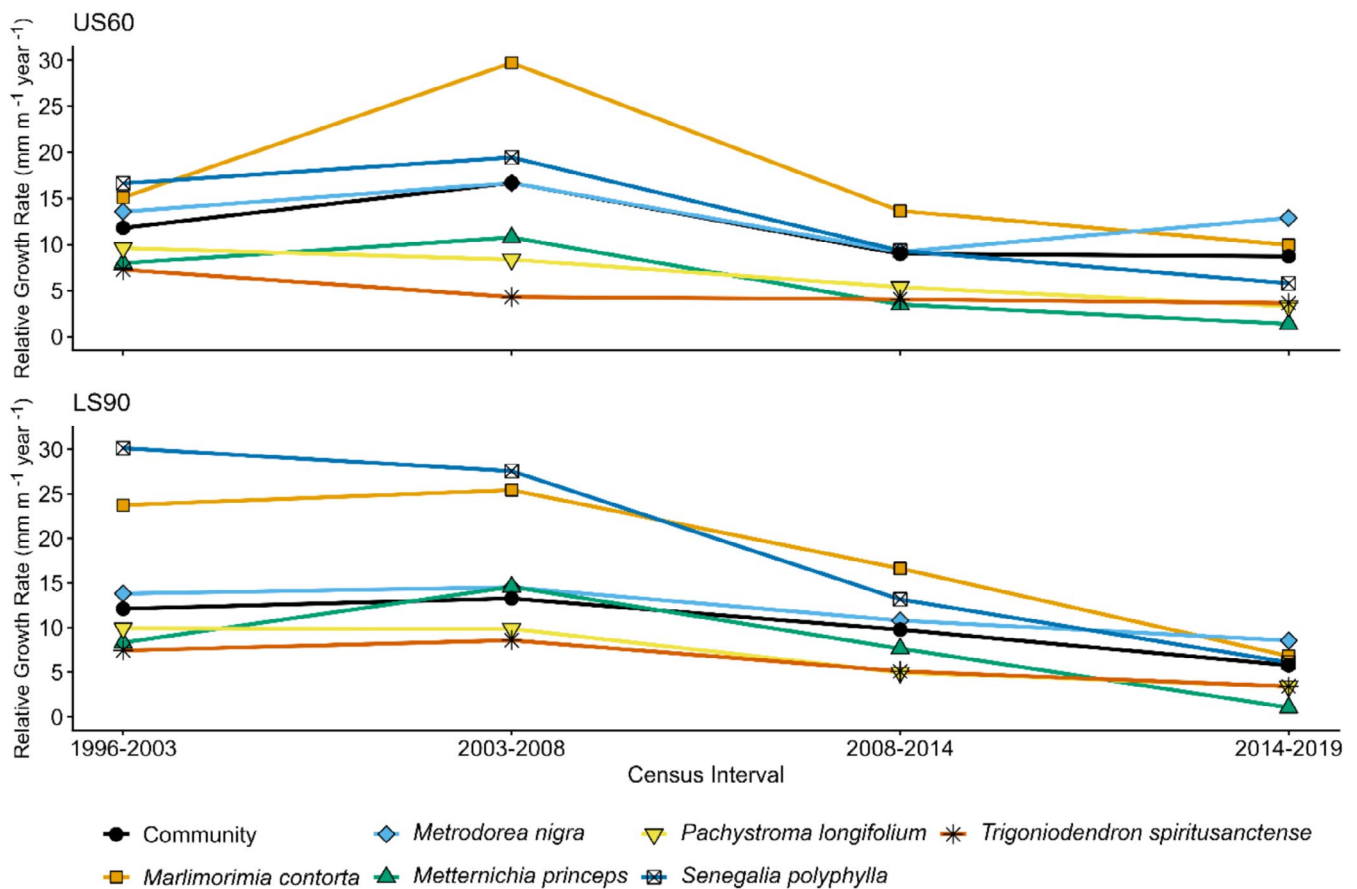


FIGURE 4 | Relative growth rate for species with $N > 10$ among the 20+ of the US60 and LS90 sites. Recruitment and mortality rates for those species can be found in Appendix S9.

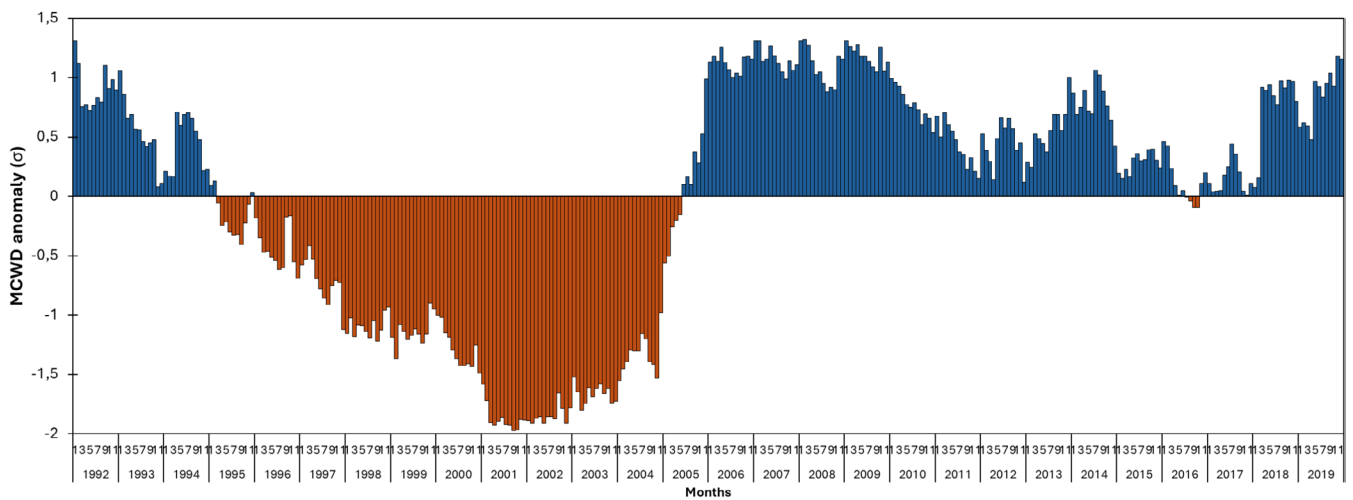


FIGURE 5 | Maximum accumulated water deficit (month of the year minus average of each month over the period in mm) referring to Campos dos Goytacazes, Rio de Janeiro, Brazil.

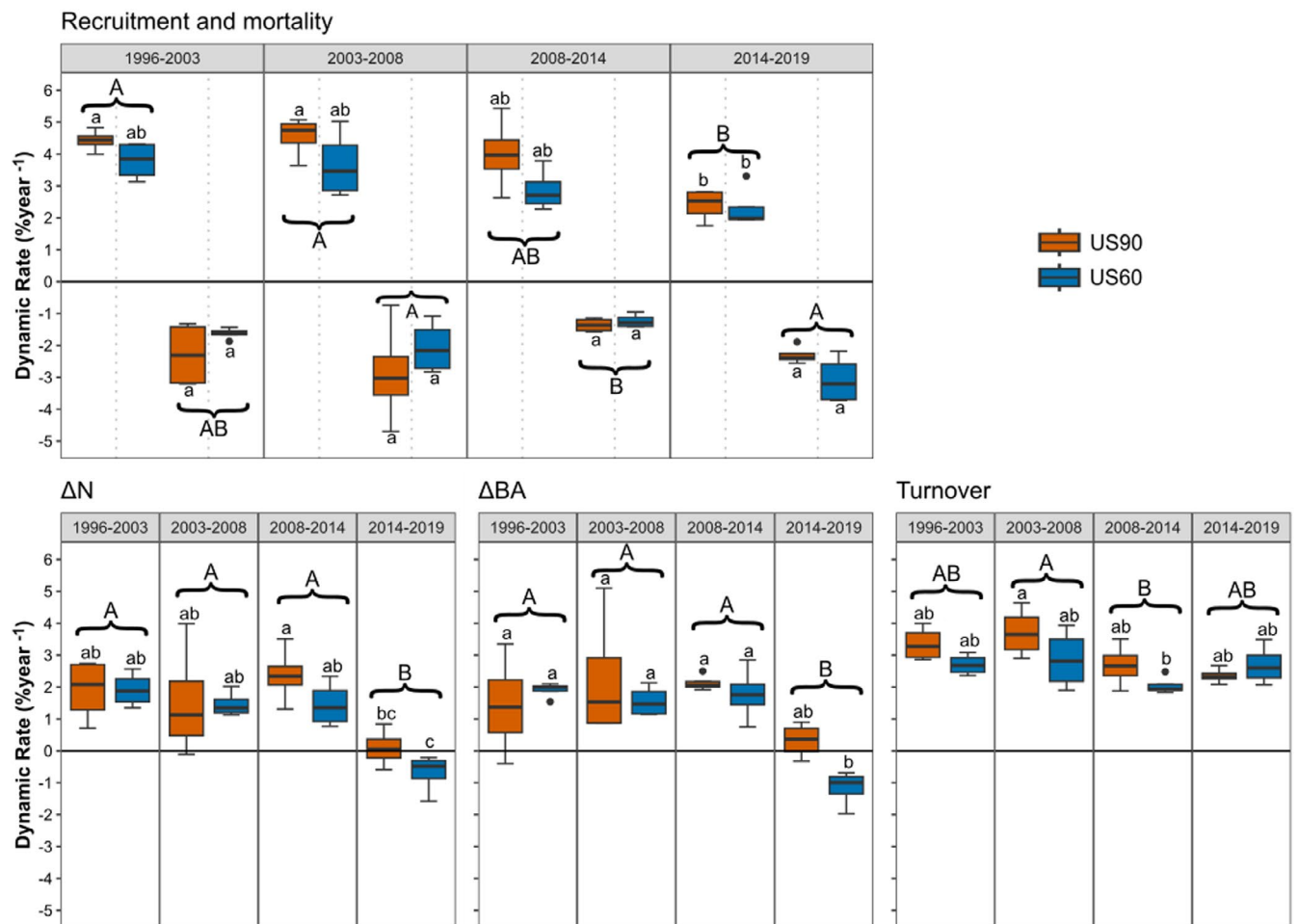


FIGURE 6 | Temporal variation of the recruitment (positive values), mortality (negative values), net change in number of individuals (ΔN), net change in basal area (ΔBA) and turnover rates for the four census intervals and the 23-year census interval of the tree community in US60 and LS90 sites. Positive values represent recruitment rate; negative values represent mortality rate. The letters above the boxes represent statistically different values according to the Tukey test ($p < 0.05$); capital letters indicate significant differences among the years, lowercase letters indicate the difference among the areas along the years together due to the occurrence of statistical interaction between predictor variables.

Regarding tree community dynamics over the 23-year period, mean mortality rates were similar between sites, while recruitment and turnover rates were generally higher in LS90 than in US60 (Appendix S13). The highest mortality values for both sites occurred during the 2003–2008 and 2014–2019 intervals, with turnover also peaking in 2003–2008 (Figure 6). For overall stand changes, ΔN and ΔBA showed little significant variation across the first three censuses until both declined significantly at both sites during the final 2014–2019 interval (Figure 6).

4 | Discussion

4.1 | Floristic Composition and Forest Structure Over Time Following Selective Logging and Climate Stress

Over the 23-year monitoring period, forest structure at both US60 and LS90 sites exhibited signs of gradual increases in stem density and BA_t which may indicate recovery from past logging. However, this structural recovery did not coincide with increases in biodiversity metrics such as species richness and evenness. At both sites, species richness (Appendix S4) and $ENSp$ declined, while evenness remained low ($J' < 0.8$) (Figure 1), suggesting that community structure became increasingly dominated by a few species. This pattern suggests a process of biotic homogenization driven by the synergistic effects of historical logging legacies and intensifying climatic stress. We argue that these two disturbances act as complementary environmental filters: logging initially simplified the community structure, and recurrent droughts are now further filtering out functionally vulnerable species, leading to a community dominated by a few resilient taxa (Tabarelli et al. 2012; Esquivel-Muelbert et al. 2019).

The observed floristic simplification indicates that the loss in species richness reflects genuine ecological changes rather than sampling bias. The low evenness values, atypical for mature *Tabuleiro* forests, which generally exceed $J' > 0.8$ (Jesus and Rolim 2005; Mariano et al. 2019), signal a reduction in functional redundancy. This loss of diversity may compromise the forest's capacity to buffer against future extremes (Fichtner et al. 2020), as the community becomes increasingly reliant on a small subset of previously present species (hyperdominance) to maintain ecosystem functions.

Despite the recovery trend, current BA_t values ($\sim 18 \text{ m}^2 \cdot \text{ha}^{-1}$) remain below the reference threshold reported for mature *Tabuleiro* forests ($\sim 30\text{--}35 \text{ m}^2 \cdot \text{ha}^{-1}$) (Jesus and Rolim 2005; de Paula and Soares 2011; Rolim et al. 2017). Although stem density has reached levels comparable to mature forests ($500\text{--}1000 \text{ trees} \cdot \text{ha}^{-1}$), the slow recovery of BA_t suggests that the forest is not following the typical recovery trajectory of tropical secondary forests, where stem density and basal area usually increase concurrently (Poorter et al. 2021). Instead, our findings align with evidence that logging legacies can constrain successional trajectories for decades (Arcanjo et al. 2023), likely creating a 'demographic bottleneck' where trees die from drought stress before reaching large size classes.

This limited resilience is further evidenced by the reproductive strategies observed. The low contribution of resprouting

individuals ($\sim 2.2\%$) suggests that vegetative regeneration is not a primary mechanism for these *Tabuleiro* forest species. Therefore, the recovery of trees following mortality events caused by selective logging and severe drought is unlikely to be supported by individual regrowth. However, our results indicate a better post-disturbance regeneration capacity in the most disturbed site (LS90).

Climatic trends, such as decreasing precipitation, rising temperatures and increasing in CDD, provide an abiotic context for these patterns. Under water stress, forests are subject to intensified environmental filtering that promotes drought-tolerant species but limits shade-tolerant or slow-recruiting taxa, gradually eroding community diversity (Allen et al. 2010; Corlett 2016; Gazol et al. 2020). This finding raises concern for the studied area, where a decrease in species richness and diversity was observed, alongside an increase in the frequency of drought events.

4.2 | Species Dynamics and Directional Change in Composition

Throughout the monitoring period, the tree community exhibited a directional shift characterized by the increasing dominance of *Metrodorea nigra* and *Marlimorimia contorta*. These species remained dominant throughout the study, together accounting for approximately 50% of the BA_t . Their continued prominence suggests competitive advantages under prevailing environmental conditions. Their continued persistence and expansion suggest that they possess specific functional traits conferring competitive advantages under the 'double filter' of logging legacies and recurrent drought.

For *Metrodorea nigra* (Rutaceae), its success is likely linked to high wood density and conservative water use, traits that enhance survival by preventing xylem embolism during moisture deficits (Hacke et al. 2001; Chave et al. 2009). In contrast, *Marlimorimia contorta* (Leguminosae) maintained high RGR even during drier intervals. This performance suggests an acquisitive strategy facilitated by deep-rooting systems, allowing access to subsurface water or nitrogen-fixing capabilities that support growth in nutrient-poor soils (Gei et al. 2018). This functional divergence allows these dominant species to monopolize resources, reinforcing the trajectory towards an oligarchic forest state.

Conversely, species such as *Copaifera lucens* (LS90) and *Trichilia pseudostipularis* (US60) declined or disappeared from the top ranks. These species' turnover was notably more dynamic in LS90. These declines likely reflect a lack of hydraulic safety margins, making these populations vulnerable to carbon starvation or hydraulic failure during intensified dry seasons. The species-level turnover was notably more dynamic in the recently disturbed site (LS90), where six new species entered the top 20 rank by 2019, compared to only three in US60. This confirms that LS90 retains a more flexible compositional structure (Seidl and Turner 2022), typical of earlier successional stages where space availability allows for the recruitment of opportunistic taxa like *Melicoccus oliviformis* (Maracahipes-Santos et al. 2023).

These patterns align with predictions from functional trait-based models, where species with acquisitive strategies (e.g.,

fast growth, low wood density) tend to gain advantage during early succession or following disturbances, while conservative strategists dominate later stages (Westoby et al. 1992; Wright et al. 2004). Future work could benefit from integrating trait data to better understand the mechanisms driving these shifts.

The analysis of RGR showed a strong dependency on precipitation pulses. The highest community-level RGR values were recorded during the 2003–2008 interval, a period marked by high rainfall (Appendix S10d) following a water deficit. Water availability acts as a limiting factor for growth patterns in many forests (Linares and Camarero 2012; Mendivelso et al. 2014; Tng et al. 2022), with SSAF being more affected than rainforests (Baker et al. 2003; Souza et al. 2014; Corlett 2016; Allen et al. 2017). Mendivelso et al. (2014) observed that although tree species in dry forests tolerate short drought periods, their growth declines during prolonged droughts. However, species in dry forests have a good response (growth) to short periods of high rainfall. This fact seems to have contributed to the greater recovery of the RGR in the 2003–2008 period, since a clear recovery response in the growth of some species was found in the period of greater rainfall.

The RGR slowed across most dominant species after 2008, coinciding with the onset of drought signals (Appendices S10–S12). The exception was *Metrodorea nigra*, whose sustained growth in the last census interval was only in US60, suggesting physiological traits (e.g., deep rooting, high water-use efficiency) that confer resilience to water stress, further consolidating its dominance.

The pattern of increasing dominance by a few drought-resilient species, coupled with floristic simplification, indicates functional homogenization, an ecological outcome associated with reduced ecosystem resilience and stability under climatic disturbances (Swenson et al. 2012; Fichtner et al. 2020). This limits the range of responses available to the community in the face of future climatic disturbances, potentially reducing ecosystem stability.

4.3 | Interactive Effects of Selective Logging and Drought on Forest Dynamics

The demographic dynamics of the tree community (mortality, recruitment, ΔN and ΔBA) responded sensitively to variations in drought intensity and frequency, with clear differences between the two sites potentially reflecting their distinct disturbance histories.

The response to this climatic filter diverged significantly between the two sites, driven by their distinct successional stages and disturbance legacies. LS90 displayed greater demographic flexibility, characterized by higher turnover and recruitment rates. This dynamic response is typical of early-to-mid successional communities dominated by species with acquisitive resource-use strategies (Wright et al. 2010; Lohbeck et al. 2013). These species prioritize rapid growth and high reproductive output, allowing them to quickly colonize canopy gaps created by drought-induced mortality. The higher recruitment rate in LS90 is plausibly related to increased light penetration resulting

from canopy opening caused by selective logging, as reported by Villela et al. (2006). Other authors have also observed a positive relationship between canopy opening, increased light penetration and recruitment (Alvarez-Buylla 1994; Baker et al. 2003; Souza et al. 2014). Thus, in LS90, the drought acted as a disturbance that maintained the system in a high-turnover loop, favouring opportunistic species that sustain stem density even as BA_t fluctuates.

In contrast, US60 exhibited signs of demographic inertia, inertia caused by long lifespans and slow community turnover (Malhi et al. 2009), and chronic stress (Jara-Guerrero et al. 2021). The forest structure at this site, characterized by larger and older trees, presents a different hydraulic vulnerability profile. Large canopy trees are often more susceptible to drought due to greater path lengths for water transport and higher exposure to vapour pressure deficit (Rowland et al. 2015; McDowell and Allen 2015). This site presents an inability to effectively recruit and recover BA_t during 2014–2019, suggesting that the ‘legacy effect’ of the past droughts was compounded by more recent changes in precipitation and temperature (Appendices S10, S12). Consequently, the recent drought accelerated senescence in the older stand while limiting the recruitment of late-successional species, which typically require moister understory conditions to establish.

Although our study has some limitations (e.g., number of plots, pseudoreplication, spatial scale and edge effects), we consider that, despite these restrictions, our results provide a solid basis for understanding how disturbance legacies shape the responses of an SSAF to climate change. Thus, our results indicate that the recovery trajectory of selectively logged SSAF may be strongly constrained by increasing climatic variability, an interpretation consistent with observed patterns. The compounded effects of past disturbance and recent droughts have led to species loss, reduced evenness and increased dominance, all of which are early warning signs of functional simplification and reduced ecosystem resilience. The observed decline in species richness and increase in dominance by a few species may reduce ecosystem stability and functional diversity, with consequences for carbon storage, nutrient cycling and habitat provision (Eisenlohr and Oliveira-Filho 2015; Méndez-Toribio et al. 2020; Arcanjo et al. 2023).

The interaction between past disturbance and climate stress underscores the need for nuanced management strategies. Forests recovering from logging may require tailored interventions, such as assisted regeneration or enrichment planting, to enhance diversity and promote resilience under increasingly variable climates.

5 | Conclusion

This 23-year study demonstrates that structural recovery in post-logging tropical forests does not guarantee the recovery of biodiversity. Our central conceptual contribution highlights how historical disturbance legacies and contemporary extreme droughts act as compounded environmental filters. These dual stressors drive divergent successional pathways, demographic inertia and hydraulic vulnerability in the older stand (US60)

versus acquisitive plasticity and high turnover in the younger stand (LS90). Despite these divergent demographic responses, both pathways ultimately converge towards biotic simplification and functional homogenization, marked by the increasing hyperdominance of a few drought-resistant species, such as *Metrodorea nigra* and *Marlimorimia contorta*.

The observed decline in species richness and evenness serves as an early warning sign of eroding ecological resilience. From a conservation and management perspective, these findings underscore that passive regeneration may be insufficient to maintain ecosystem stability under intensifying climate change. Forest management in seasonal tropical ecosystems must move beyond stem density and basal metrics. Active restoration strategies, such as the enrichment planting of functionally diverse, late-successional and drought-sensitive species, are urgently needed to restore functional redundancy and buffer these fragmented forests against future climatic tipping points.

Finally, we acknowledge that our sampling design, which relies on the comparison of two distinct sites with internal plots, limits broad spatial replication and regional inference. However, the rarity of a 23-year dataset provides critical insights into the slow-moving successional dynamics and demographic bottlenecks that short-term studies often miss. Overall, our findings warn that the synergistic impacts of past land-use pressures and modern climatic extremes are fundamentally reshaping *Tabuleiro* forests, demanding proactive conservation to prevent irreversible biodiversity loss.

Author Contributions

Nilson Berriel: conceptualization, formal analysis, investigation, writing – original draft, project administration. **Dora Maria Villela:** conceptualization, writing – review and editing. **Luiz Eduardo Oliveira e Cruz de Aragão:** methodology, writing – review and editing. **Matheus Gomes Tavares:** formal analysis, writing – review and editing. **Haroldo Cavalcante de Lima:** validation, writing – review and editing. **Marcelo Trindade Nascimento:** conceptualization, methodology, validation, resources, data curation, supervision, project administration, funding acquisition, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in at <https://zenodo.org/records/17308409>, reference number 10.5281/zenodo.17308408.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Location of the study area. **Appendix S2:** Monthly and annual variation in precipitation and temperature. **Appendix S3:** List of botanical families and species. **Appendix S4:** Species richness rarefaction and extrapolation curves. **Appendix S5:** Equations for forest dynamics. **Appendix S6:** Adjusted regression models for the tree community parameters. **Appendix S7:** Top 20 tree species ranked by Importance Value Index (IVI) in ascending order. **Appendix S8:** Relative dominance and relative density of six selected tree species in the US60 and LS90 sites. **Appendix S9:** Recruitment and mortality for species with $N > 10$ among the 20+. **Appendix S10:** Precipitation anomaly. **Appendix S11:** Extreme indices of Consecutive Dry Days (CDDs) and Consecutive Wet Days (CWED). **Appendix S12:** Temperature anomaly. **Appendix S13:** Dynamic rates for the 23 years.