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Impact of the extreme 2015-16 El Niño climate event on forest and savanna tree species of the Amazonia-Cerrado transition

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Abstract

Extreme drought events, driven by the El Niño Southern Oscillation (ENSO), are linked to increased tree mortality and alterations in vegetation structure, dynamics, and floristic composition in tropical forests. Existing analyses, primarily focusing on Africa, Central America, and Amazonia, overlook the floristic impacts on biome transitions. This study evaluates the profound effects of the severe 2015/2016 ENSO event on tree density and floristic composition in the critical transition zone between Amazonia and Cerrado, South America's largest biomes. Our findings not only document significant biodiversity loss but also offer insights into species resilience, guiding conservation strategies under changing climate conditions. We inventoried long-term plots before and after the extreme drought event, sampling 12,465 individuals from 526 species, 224 genera, and 65 families, in Open Ombrophilous Forest (OF), Seasonal Forest (SF), Cerradão (CD), and Typical Cerrado (TC). We document the disappearance from our plots of 97 species after the ENSO, with only 61 new species being recorded. The total loss of individuals across the transition zone was almost 10%. The SF and CD forest plots showed the greatest replacements, species losses, and reductions in tree density. Their markedly seasonal baseline climate probably drove these changes. In most phytophysiognomies, there was an increase in pioneer species and drier environment habitat specialist species, indicating that although many species are vulnerable to extreme climate events, others benefit, especially those with a short life cycle. We found that the vegetation of the Amazonia-Cerrado transition overall is vulnerable to climate anomalies, with widespread loss of tree density and change in floristic composition. Our study also provides a species-by-species list of the most vulnerable and resistant trees which helps point to overall climate change vulnerabilities and assist with initiatives to recover degraded areas.

Keywords: drought, species replacement, species losses, drought resistant species, climate change.

1. Introduction

Climate change, manifested by escalating air temperatures and shifting precipitation patterns, poses significant risks to the floristic composition and structural integrity of tropical forests (Esquivel-Muelbert et al., 2019a; Hubau et al., 2020). Central to recent climate variability is the increased frequency and intensity of drought events tied to the El Niño Southern Oscillation (ENSO). The 2015/2016 episode stands out as one of the most severe warming phenomena affecting the southern Amazon, impacting hydrological cycles and thermal conditions. This study examines how these alterations influence the ecophysiological processes of trees, potentially escalating mortality rates and reshaping forest landscapes (Schiermeier, 2015; Jimenez et al., 2018; Esquivel-Muelbert et al., 2019b). Extended drought coupled with elevated temperatures leads to soil water deficits, impacting the photosynthetic efficiency of plants (Tiwari et al., 2020), and diminishing or even halting the accumulation of biomass in vegetation (Bennett et al., 2023). While the ecological ramifications of rising temperatures and diminished precipitation remain uncertain, it is noteworthy that the southern Amazonia forests recorded their highest temperatures during ENSO 2015/2016 (Jiménez-Muñoz et al., 2016; Jimenez et al., 2018). This event, in conjunction with extensive long-term monitoring now in place across the southern Amazonia region, presented a unique opportunity for a large-scale natural experiment to explore the impacts of drought on the vulnerability and dynamics of tree species composition across different ecosystems.

Most studies before the 2015-2016 ENSO have documented an increase in tree mortality in response to drought events in the Amazonia forest, including in 1997-1998 (Williamson et al., 2000), 2005 (Phillips et al., 2009), 2007 (Brando et al., 2014), and 2010 (Doughty et al., 2015; Meira Junior et al., 2020). However, concerning the Cerrado biome, the literature still lacks a significant number of specific studies on the effects of drought events on tree mortality. While some studies have addressed issues related to the response of Cerrado vegetation to extreme climatic events, such as drought, there is a substantial gap in understanding the underlying mechanisms and consequences for the dynamics of this vegetation (Bustamante et al., 2012). In the context of the transition region between the Amazonia and the Cerrado, there is growing awareness of the importance of investigating the effects of climate change in this area. Although there is some preliminary research addressing this topic, a more comprehensive effort is still needed to fully understand how drought events affect vegetation dynamics in this transition region and what the implications are for conservation and natural resource management (Marimon et al., 2014; Cunha et al., 2019). Nonetheless, not all investigations into the impacts of drought events in tropical regions have unequivocally demonstrated negative consequences. For instance, Zuleta et al. (2017) and Sousa et al. (2022) reported net biomass gains in some wet Amazonian forests, whilst Bennett et al. (2021) reported a diminished bit still positive carbon sink in African forests during the 2015-16 ENSO.

Experimental studies that induce severe and prolonged water deficits in vegetation, leading to cumulative hydrical stress, have demonstrated pronounced mortality rates ranging from 1.5% to 9% (e.g., Nepstad et al., 2007). Furthermore, the consequences of droughts in Neotropical regions often encompass diminished tree growth and declines in net primary productivity (Doughty et al., 2015; Feldpausch et al., 2016; Bennett et al., 2023). While these studies have predominantly centered on responses in ecosystem carbon stocks, and Esquivel-Muelbert et al. (2019a) documented biodiversity responses over three decades, we are unaware of any investigation into the impact of specific extreme drought events on the composition of tree species in the transition zones between biomes. What happens here may be especially critical in determining the long-term survival, extinction, or migration of thousands of species in response to climate change in Amazonia and the transition with Cerrado.

In South America, the two largest biomes are the Amazonia forest and the Brazilian savanna (Cerrado). These two biomes are of utmost significance, not solely due to their rich species diversity but also owing to their substantial carbon reservoirs and their pivotal role in regulating global climate dynamics (Morandi et al., 2018; Esquivel-Muelbert et al., 2019b; Klink et al., 2020; Zimbres et al., 2021; Hofmann et al., 2021). The transitional zone between Amazonia and Cerrado represents a naturally dynamic region, distinguished by pronounced floristic and phytophysiognomic heterogeneity, encompassing a variety of forests and savanna types (Ratter et al., 1973; Marimon et al., 2006, 2014; Morandi et al., 2016). However, in recent decades, human activities have led to the removal of nearly half of the forest cover in this transitional area (Marques et al., 2020), contributing to localized reductions in rainfall (Bonini et al., 2014), along with escalating temperatures and extended drought periods (Marengo et al., 2012; Jiménez-Muñoz et al., 2016). These changes, in addition to the extreme loss of habitat itself, have rendered the region's forests potentially vulnerable to multiple impacts (Brando et al., 2014; Esquivel-Muelbert et al., 2019a; Nogueira et al., 2019; Reis et al., 2018, 2022).

In the transitional zone between Amazonia and Cerrado, the co-occurrence of species assumes a pivotal role in shaping landscape dynamics, primarily driven by floristic connections bridging these two biomes (Ratter et al., 1973; Pinto and Oliveira-Filho, 1999; Oliveira-Filho and Ratter, 1995; Marimon et al., 2006; Morandi et al., 2016). These connections emerge from intricate interactions among biotic and abiotic factors, resulting in hyperdynamic vegetation (Marimon et al., 2014). Given the ongoing forest degradation, the occurrence of extreme drought events, and escalating temperatures, tree species in the Amazonia-Cerrado transition may be approaching their adaptability limits (Tiwari et al., 2020; Marimon et al., 2020; Araújo et al., 2021). The naturally high tree mortality rates in southern Amazonia have increased in recent years, likely attributable to landscape fragmentation triggering a cascade of adverse feedbacks within the deforestation × drought × fire nexus, and so impacting regional vegetation integrity and carbon sequestration capacity (Brando et al., 2014; Morandi et al., 2018; Nogueira et al., 2019; Prestes et al., 2020; Marimon et al., 2020; Reis et al., 2022; Bennett et al., 2023). While there has been a focus on structural and dynamic change, the extent to which floristic composition and individual species are being impacted remains unclear.

This research aims to contribute insight into understanding the resilience and adaptability of transitional vegetation to climate change. To achieve this, we set out to address the following questions: a) What were the repercussions of the ENSO event on vegetation types in the Amazonia-Cerrado transition in terms of floristic composition and individual tree densities? b) Which species, genera, and families experienced the greatest losses and gains in tree density as a result of the ENSO event? Our specific objective was to quantify change in the floristic composition and tree species richness of forest and savanna formations in the Amazonia-Cerrado transition following the ENSO event in 2015/2016. We employed a unique, standardized regional network of long-term monitoring plots, assessing multiple plots both before and after the ENSO event. Based on our research objectives, our hypothesis was formulated as follows: tree species in ecosystems typically not subject to prolonged drought, especially evergreen rainforests, would be most susceptible to extreme drought (see Fig. 1).

2. Materials and methods

2.1 Study area

The study was conducted across 27 permanent 1-hectare (100 × 100m) plots (see Table S1) situated within the transition zone connecting South America's two largest biomes, Amazonia and the Cerrado (Fig. 2). The region's climate falls within Köppen classification types of Aw (tropical with dry winters) and Am (tropical monsoons) (Alvares et al., 2013). Mean annual precipitation and temperature range from 1,511 to 2,353 mm and 24.1 to 27.3°C, respectively (Table S1) (Hijmans et al., 2005). Our sampling plots are strategically placed within distinct vegetation types of the Amazonia-Cerrado transition, including Open Ombrophilous Forest (OF), Seasonal Forest (SF), encompassing semi-deciduous and evergreen forests, Cerradão (CD), and Typical Cerrado (TC).

The evaluated phytophysiognomies represent a vegetation gradient. At one end is the Cerrado, a tropical savanna biome with a mixture of arboreal-shrub vegetation and grasses, coverage ranging from 20% to 50%, and heights between 3 and 6 m (Ribeiro and Walter, 2008). Within this biome, the TC is a specific phytophysiognomy characterized by an open canopy with sparse, low trees and a dense understory of shrubs and grasses. The TC is among the most threatened phytophysiognomies in the Cerrado due to deforestation from agriculture, livestock, and urbanization (Klink and Machado, 2005). This expansion has led to significant native vegetation loss, habitat fragmentation, and degradation (Strassburg et al., 2017). The soils in the Cerrado, including those in the TC, are predominantly acidic, alic, and dystrophic, classified as Red Yellow Latosol (Marimon-Junior and Haridasan, 2005). At the other extreme, the OF has evergreen vegetation with a closed canopy, trees that reach 50 m in height, and Oxisol soils (IBGE, 2009). Agriculture, livestock, and logging pose threats to this type of vegetation (Fearnside, 2017). Intermediate between these extremes are the FS, characterized by closed canopy trees and Oxisol soils, and the CD, a forest formation of a transitional nature between the FS and the savanna formations of the Cerrado biome (Marimon et al., 2006; 2014). SF are often subject to deforestation for agricultural expansion, livestock farming, and urbanization (Vieira et al., 2018). This pressure is exacerbated by the seasonality of rainfall, which can influence the vulnerability of these forests to fires during periods of drought (Marimon et al., 2014). The CD has a continuous canopy and tree cover ranging from 50% to 90%, with higher values in the rainy season and lower values in the dry season (Marimon et al., 2006; 2014). The trees here are between 8 and 15 m tall, and the soils have variable texture and fertility (Ratter et al., 1973). The Cerradão faces similar threats to the typical cerrado, including deforestation for pasture and agriculture, as well as frequent fires (Durigan, 2020). It is important to note that the specific conservation situation and tree density may vary depending on the exact location and specific human pressures in each area. For more details and descriptions of plots and phytophysiognomies, refer to Marimon-Junior and Haridasan (2005), Marimon et al. (2006; 2014), Morandi et al. (2016; 2018), Reis et al. (2018), and Nogueira et al. (2019).

2.2 Vegetation inventory

We conducted vegetation sampling following the protocols established by the RAINFOR network (http://www.rainfor.org/) (Phillips et al., 2002). Additionally, we utilized data collected by the Plant Ecology Laboratory team (UNEMAT, Nova Xavantina Campus), curated on the ForestPlots.net platform (Lopez-Gonzalez et al., 2011; ForestPlots.net et al., 2021). For our analysis, we utilized inventory data collected between 2013 and 2015, to represent the period preceding the ENSO, and inventory data spanning 2017 to 2020 to capture the post-ENSO period, with an average interval of three years between consecutive inventories. Data collection protocols were consistent across all inventories, including measuring and identifying all trees and palms with diameter at 1.3 m ≥ 10 cm in forested areas and at 0.3 m in TC plots. Taxonomic nomenclature adhered to APG IV (2016), and species names and synonyms were cross-referenced with Flora do Brasil (https://floradobrasil.jbrj.gov.br/consulta/#CondicaoTaxonCP).

2.3 Description of predictors

The climate component was represented by the Maximum Climatological Water Deficit (MCWD), based on the annual calendar (January to December) (as described by Aragão et al., 2007 and Malhi et al., 2008). We classified water stress for each plot during two intervals (before and during ENSO 2015/2016), following the modified model by Aragão et al. (2007). MCWD is defined as the most negative accumulated value of the climatological water deficit within a year (Aragão et al., 2007). Its calculation involves subtracting monthly rainfall from evapotranspiration and the water deficit from the previous month, utilizing a standardized evapotranspiration value of -100 mm per month for tropical forests (Malhi et al., 2008). Therefore, if the monthly precipitation in a given area (pixel) is less than 100 mm, it is considered a state of water deficit; otherwise, MCWD is set to zero. For average precipitation, we utilized TerraClimate data, based on the latitude and longitude coordinates of each plot (Abatzoglou et al., 2018). We further assessed the average maximum air temperature values for recent years (2013-2020) and compared them with values from the ENSO period (Fig. S4), using temperature data from the Climate Research Unit (CRU) repository (Harris et al., 2014).

2.4 Analyses

All comparisons were conducted between intervals (before and after ENSO), separately for each plot, and compared across different vegetation types. We examined which species, genera, and families were present in at least 50% of the plots, each with a minimum of 10 individuals per species within each vegetation type before ENSO. Subsequently, we computed the relative phytosociological parameters, including frequency, density, dominance, and the Importance Value Index (VI) (Mueller-Dombois and Ellenberg, 1974), for all species, genus, and family within each vegetation type. Following data processing, we selected the 20 species with the highest VI to assess how their population densities responded to the ENSO.

We computed, for each species, the average annual mortality ($M= \{1-[(N_0-N_m) /N_0]^{1/t}\} \times 100$) and annual recruitment ($R= [1-(1-N_r/N_t)^{1/t}] \times 100$) rates, based on the number of sampled individuals (Sheil et al., 1995; 2000), both before and after ENSO. To correct any bias associated with variation between intervals, we applied the correction method of Lewis et al. (2004): [$\lambda_{corr} = \lambda \times t^{0,08}$], where λ represents the rate and t the interval in years.

To assess the response of plant communities to extreme climatic events, we analyzed two primary response variables: species richness and tree density. These variables were evaluated before and after the ENSO event of 2015/16. Variations in species richness were used to identify potential changes in the floristic structure and composition over time, providing insights into the resilience and vulnerability of plant communities. Tree density, on the other hand, reflects the relative abundance of individuals within a community, allowing us to assess the presence or absence of specific species and the response of populations to altered environmental conditions. Monitoring these variables in response to ENSO events is crucial, as both are highly sensitive to changes in environmental conditions, including fluctuations in water availability and temperature variations associated with ENSO.

We calculated the tree density and the richness of species, genera, and families per plot. These values were subsequently compared based on vegetation type, both before and after ENSO, using the paired t-test, with assumptions required to conduct the paired t-test all evaluated and met (Zar, 2010). The paired t-test was favoured due to the longitudinal nature of the study, enabling assessment of changes at each site before and after the ENSO event. After comparing tree density and species richness, we conducted a paired t-test using MCWD and maximum temperature as predictor variables. The test compared these variables at two distinct time points: before and after the ENSO event. MCWD and maximum temperature were selected as they are relevant indicators of climate stress, directly impacting tree populations. These variables were examined over time to identify significant changes after ENSO.

We explored the dissimilarity in species composition before and after the ENSO event within each vegetation type using PERMANOVA analysis. Time represents the periods before and after the ENSO event. This multivariate approach enabled us to ascertain whether there were noteworthy alterations in species composition attributable to the climatic event. Additionally, we examined changes in species composition between intervals through PERMANOVA analysis, utilizing the Bray-Curtis difference matrix (Anderson, 2001). For this, we employed the *adonis* function from the 'vegan' package (Dixon, 2003), configured for 999 permutations, in conjunction with the *pairwise.adonis* function and package (Martinez Arbizu, 2020).

To assess sampling efficiency, we employed the rarefaction method for species, based on the number of individuals, enabling a comparison of richness among different sampling areas. Additionally, we evaluated the performance of species richness estimators ($q = 0$) by estimating and assessing sample sufficiency using interpolations and Hill extrapolations with the iNext function and package (Hsieh et al., 2016). This analysis considered the density of individuals within each vegetation type. All statistical analyses were conducted at a 5% significance level, and we processed both the data and the graphical representations using the R *software*.

3. Results

3.1 Climate parameters, tree density, and species richness

The extreme drought caused by ENSO event resulted in significant alterations in climate conditions within the Amazonia-Cerrado transition region, particularly evidenced by pronounced changes in mean consecutive wet-day (MCWD) duration (paired t-test, $p<0.03$, Fig. S1) and maximum temperature (paired t-test, $p<0.001$, Fig. S2). Throughout the 2015-2016 ENSO episode, the peak warmth occurred in late 2015 and early 2016, with variations in MCWD duration observed across specific geographical locations during this period. In general, it was observed that variations in species richness and tree density among different vegetation types may be related to the average temperature increase of 2°C recorded in most plots. Upon analyzing tree density and species richness before and after the event, it was found that plots subjected to maximum temperatures exceeding the annual average of the preceding years exhibited significant reductions in both tree density and species richness (Figs. 3 and 4). However, due to limitations in our dataset and sampling bias in each phytophysiognomy, it was not feasible to perform analyses beyond basic t-tests to directly correlate predictor variables with observed responses.

3.2 Changes in population structure and richness of species, genera, and families

In our diverse sampled plots, we documented a total of 526 species across 224 genera and 65 families. Before the ENSO event, the tree count stood at 12,465. After the event, it significantly dropped to 11,353—a net loss of 1,112 trees or about 8.82% of the original population. This decline varied across the vegetation types, with Seasonal Forests (SF) and Cerradão (CD) experiencing the most pronounced losses. On average, each plot recorded the loss of 41 trees (Table 1). The net decrease can be attributed to a significant disparity between mortality, with 1,934 trees, and recruitment, with 822 trees. In all vegetation formations studied, the number of dead trees exceeded that of newly recruited individuals. However, the disparities were more pronounced in the SF (1,094 deaths; 461 recruits) and CD (462 deaths; 65 recruits) formations. Additionally, we observed significant differences in species richness and tree density exclusively for these SF and CD formations, encompassing changes in families, genera, and species (Table 1). On the other hand, in the OF (128 deaths; 107 recruits) and TC (250 deaths; 189 recruits) formations, the differences between tree mortality and recruitment were less pronounced.

We observed significant time-dependent changes in rarefied taxon richness, both at the level of individual plots and across different vegetation types, as depicted in Figures S3 and S4. Particularly, these changes were strikingly evident in the SF and CD habitats, where we observed a substantial reduction in the species richness and population density (paired t-test, $p<0.05$ for SF, and $p<0.02$ for CD; see Table 1). Additionally, despite the observed time-dependent changes in rarefied taxon richness, particularly pronounced in SF and CD, the subsequent PERMANOVA analysis did not yield significant results in floristic composition (Table S2). Notably, 97 species were lost and 61 new species were recorded in the plots, resulting in a net loss of 36 species after ENSO. Again, this change was most pronounced in SF and CD (Table S3).

We also documented the loss of 16 genera after ENSO: three in OF (*Bertholletia*, *Cariniana*, and *Sarcaulus*), five in SF (*Annona*, *Chomelia*, *Dalbergia*, *Heisteria*, and *Triplaris*), six in CD (*Anacardium*, *Antonia*, *Cardiopetalum*, *Caryocar*, *Miconia*, and *Plenckia*), and two in TC (*Styrax* and *Zeyheria*). Eleven new genera were recruited to the plots: three in OF (*Eriotheca*, *Senegalia*, and *Styrax*), four in SF (*Acacia*, *Andira*, *Callichlamys*, and *Perebea*), one in CD (*Cecropia*), and three in TC (*Antonia*, *Dulacia*, and *Maprounea*). The plots also lost four families: Caryocaraceae, and Celastraceae (CD), Polygonaceae (SF), and Styracaceae (TC), and added three: Styracaceae (OF), Urticaceae (CD), and Euphorbiaceae (TC).

3.3 Which species, genera, and families lost or gained the most individuals after ENSO?

Tree species from SF and CD experienced the greatest reductions in population density following ENSO, with notable declines to *Miconia pyrifolia* (-45%), *Tapirira guianensis* (-40%; -71%), and *Xylopia aromatica* (-89%) (Table 2A). Among the 20 species with the highest VI in SF before ENSO, *Nectandra cuspidata* experienced the greatest drop in ranking, from 16th to 25th position. In CD, *Xylopia aromatica* declined from 6th to 27th (Tables S4B and C). Also in CD, species lost the most individuals, with 29 losing at least 10% of all trees.

Among the species experiencing a decline in individuals within the OF, those belonging to the genus *Inga* (-39%) exhibited the most pronounced losses, notably *Inga grandiflora*, *I. marginata*, *I. alba*, and *I. edulis* (Table S3). The reduction in tree density of these species suggests their classification within the initial or intermediate stage of ecological succession. Within the top 20 most important species, *Celtis schippii* experienced the most substantial decline in classification, transitioning from the 9th to the 13th position.

In the OF, species such as *Pseudolmedia macrophylla* and *Rinoreocarpus ulei* exhibited gains in individuals (Table 2A). In the TC, the most substantial losses were recorded for *Qualea multiflora* (-21%), which descended from the 15th to the 21st position in the VI ranking before and after the ENSO event (Tables 2A and S4D). Conversely, *Tachigali vulgaris* in the TC witnessed a remarkable 125% increase in tree density (Table 2A). Among the genera experiencing the most notable losses in individuals in the CD were *Terminalia* (-79%) and *Tapirira* (-71%) (Table 2B).

At the family level, the most substantial declines in the number individuals occurred in CD and SF, with 24 and 20 families, respectively, losing at least 10% (Table 2C). In CD, noteworthy families with significant reductions include Anacardiaceae (-65%), Sapindaceae (-51%), and Combretaceae (-49%), while in SF, the most affected families were Sapindaceae (-36%) and Simaroubaceae (-23%). The TC exhibited notable decreases in individuals for Ochnaceae (-26%), Celastraceae (-25%), and Dilleniaceae (-20%), as well as increases in Icacinaceae (+22%) and Annonaceae (+18%) (Table 2C).

When considering all vegetation types and accounting for changes in floristic composition, certain species were representative and persistent. In OF, *Protium altissimum* and *P. sagotianum* maintained prominent VI positions after the ENSO (Table S4A). All 20 species with the highest VI before the ENSO also remained among the 20 most significant afterwards, with nine of them retaining the same level of importance (Table S4A). However, among all species surveyed in OF, noteworthy shifts in VI positions include the rise of *Crepidospermum goudotianum* by 50 or more positions and the decline of *Bertholletia excelsa* and *Trattinnickia rhoifolia* by around 100 positions.

In SF, *Amaioua guianensis* and *Brosimum rubescens* held the first and second VI positions before ENSO but these positions reversed after the event (Table S4B). Of the 20 species with the highest VI, nine retained their positions, five decreased, and six improved their positions after ENSO (Table S4B). When considering all the sampled species in SF, notable changes in VI positions after the ENSO include the ascent of *Acacia polyphylla* by 50 or more positions and the decline of *Terminalia lucida* by approximately 100 positions.

In CD floristic change was also more evident. The species with the highest VI values initially were *Hirtella glandulosa* and *Tachigali vulgaris*, but after the event *T. vulgaris* dropped to third, and *Emmotum nitens* rose to second (Table S4C). Among the top 10 species with the highest VI, only two retained their positions, four declined, and four ascended one or two positions in the inventories conducted after ENSO. Of the 20 species with the highest VI recorded before ENSO, 18 remained among the 20 most significant after the event, with *Xylopia aromatica* and *Terminalia argentea* in lower positions, and only three maintaining their original positions (Table S4C). When considering all the sampled species in CD after ENSO, the species with the greatest increase in IV position was *Schoepfia brasiliensis* (+19), while that which experienced the largest decline was *Byrsonima basiloba* (-23).

In TC, the species with the highest IV were *Qualea parviflora* and *Emmotum nitens* both before and after ENSO (Table S4D). All 20 species with the highest IV values before ENSO remained among the 20 most significant after the event, with twelve maintaining the same level of importance (Table S4D). When considering all species sampled, those showing the greatest increase in VI positions were *Dulacia candida* (+31) and *Maprounea guianensis* (+26), while those declining most were *Erythroxylum tortuosum* and *Zeyheria montana*, both dropping by 22 positions.

Among genera, *Aspidosperma* was the only genus recorded with a top 20 VI in at least three of the vegetation types evaluated (SF, CD, TC). In OF, the two most representative genera were *Protium* and *Pseudolmedia,* both before and after ENSO (Table S5A). However, among the top 10 genera with the highest VI recorded in OF before ENSO, three dropped, with *Trattinnickia* notably declining from 9th to 16th (Table S5A). In SF, the top three genera (*Ocotea*, *Amaioua*, and *Brosimum*) changed their positions after ENSO, with only *Dacryodes* maintaining their position (9th) (Table S5B). In CD, the most representative genus during both periods was *Hirtella*, but *Tachigali*, in second place before ENSO, dropped to third after the event, replaced by *Emmotum* (Table S5C). Among the top 10 genera with the highest VI in CD, four moved down with *Tapirira* experiencing the greatest decline (from 10th to 20th) (Table S5C). In TC there were fewer changes, with *Qualea* and *Emmotum* the most important genera before and after ENSO, and seven genera maintaining their positions and others only moving one position (Table S5D).

In terms of families, composition was more stable. In OF, the dominant families in terms of VI were Burseraceae, Moraceae, and Fabaceae, both before and after ENSO. Among the top 10 families, only Malvaceae dropped (to 11th) after the event (Table S6A). In SF plots, Burseraceae again stood out, maintaining first position, followed by Fabaceae and Moraceae (Table S6B). In CD, Fabaceae, Chrysobalanaceae, and Icacinaceae were prominent both before and after ENSO. Only two of the top 10 families with the highest VI changed their positions after the event (Table S6C). In TC, the families that stood out both before and after ENSO were Vochysiaceae and Fabaceae. The third (Proteaceae) and fourth (Icacinaceae) positions before the event were reversed, while the others remained unchanged (Table S6D).

4. Discussion

The 2015/2016 ENSO event triggered significant ecological changes in the Amazonia-Cerrado transition, marked primarily by substantial reductions in tree numbers and species diversity. These changes highlight the vulnerability of certain species to climate alterations, particularly during extreme weather events. Additionally, an average temperature increase of 2°C across most plots imposed further stress on these ecosystems. Although initial observations suggested stability in floristic composition, our detailed analyses reveal significant declines in species richness and tree density, particularly in the Seasonal Forests and Cerradão. These observations indicate that the current changes may herald even more severe alterations in floristic composition, potentially increasing the risk of local and regional extinctions among climate-sensitive species, as discussed by Esquivel-Muelbert et al. (2019). Our descriptive approach aimed to illustrate how to decrease precipitation and increase in temperature might have influenced the observed reductions in tree density and species richness. This pattern aligns with findings from other studies that have documented similar impacts on response variables, such as carbon storage and biomass (e.g., Meira Junior et al., 2020; Bennett et al., 2023). Unfortunately, our dataset did not allow for more robust analyses due to the sampling bias across different physiognomies. Therefore, we recommend that future research establish additional monitoring plots in the Amazonia-Cerrado transition to more accurately understand the ecological changes in climate variables.

The observed reduction in tree density and species richness following the ENSO event led to notable changes in the floristic composition of the four most common and widely distributed vegetation types in the region. This outcome suggests that, despite the observed reductions, other factors or potential methodological limitations may have influenced the results. It is crucial to emphasize that the lack of significance in the PERMANOVA analysis does not necessarily dismiss the possibility of ENSO impacting floristic composition. Instead, it underscores the need for further investigation into potential confounding variables or methodological considerations that could have affected the findings. The increased mortality of certain species, despite recruitment efforts, indicates that many species could not compensate for these losses. Similar trends of increased tree mortality have been documented in core Amazonia forests following previous drought events, such as in 2005 (Phillips et al., 2009) and 2010 (Feldpausch et al., 2016; Meira Junior et al., 2020), alongside changes in floristic composition (Esquivel-Muelbert et al., 2019a).

Our study shows that climate factors, including water deficit and temperature increases, drive altered dynamics and floristic composition of tree communities in the large transitional region at the edge of the Amazonia biome and into the Cerrado. Specifically, the Seasonal Forest and Cerradão were the most affected vegetation types in this transition zone. These areas experienced significant changes in species composition and tree community dynamics, highlighting their sensitivity to climatic stressors such as increased temperature and water scarcity. These impacts show that even where ecosystems are known to be very dynamic already (Marimon et al., 2014; Esquivel-Muelbert et al., 2020; Reis et al., 2018, 2022), still greater increases in mortality can be caused by climate extremes.

Our expectation was that the forests in the Open Ombrophilous Forests on the southern edge of Amazonia would be most negatively impacted by the ENSO event (see Figure 1). This was based on the fact that these forests host species adapted to normally humid environments, with consistent and abundant precipitation (Esquivel-Muelbert et al., 2017a, b). Therefore, when these trees are exposed to prolonged periods of drought and elevated temperatures, they are more likely to experience hydraulic failure and have greater susceptibility to mortality (Choat et al., 2012; 2018; McDowell, 2018). Hydraulic failure refers to the inability of trees to transport water from their roots to their leaves, resulting in cavitation or embolism within the conducting vessels. This phenomenon occurs under high water stress, such as during extreme droughts, and can lead to severe water stress and potentially the death of the plant. Recent studies indicate that hydraulic failure is a crucial factor in tree mortality during extreme drought events, as observed in various regions of the Amazonia. For example, Phillips et al. (2009) and Esquivel-Muelbert et al. (2019) highlight that increased mortality rates are associated with the trees' inability to maintain water transport under intense drought conditions. Similarly, research by Cochard and Delzon (2013) and Brodribb et al. (2020) demonstrates that hydraulic failure can occur under severe drought conditions, despite the fact that hydraulic repair mechanisms are not routinely observed in trees.

However, contrary to our expectations, it was the forests in drier environments (Seasonal Forest and Cerradão) which were most impacted by the ENSO, losing both tree density and species richness (see Table 1). This unexpected finding may be attributed to these vegetation types being situated in more seasonal climates characterized by consistent ecophysiological stress, including high temperatures and seasonal moisture deficits (Araújo et al., 2021). Consequently, their species may already be operating near their adaptive limits, which refers to the point at which a species or a community of organisms reaches the extent of its capacity to adapt to environmental changes (Tiwari et al., 2020; Reis et al., 2018, 2022; Bennett et al., 2023), making them more vulnerable to extreme weather events. Further, given that drier tropical forests often are less functionally diverse than wetter forests (Aguirre-Gutiérrez et al., 2022), they may have less functional redundancy when subjected to more significant water deficits. In all, our findings reveal the climate vulnerability of transitional forest communities in drier Amazonian locations, both in terms of vegetation structure and floristic composition.

Conversely, species inhabiting the Open Ombrophilous Forest, the wettest community we assessed and characterized by the lowest water deficit through the year, were the most resistant to water stress induced by ENSO. Our observations indicate that baseline precipitation plays a pivotal role in predicting the impacts of droughts on tropical vegetation (Phillips et al., 2009). One likely mechanism underlying this is that forests located in regions with higher year-round precipitation have greater access to groundwater resources, enabling them to use this reserve during prolonged water stress periods, as was the case during the 2015/2016 ENSO (Giardina et al., 2018).

While we did not observe the highest levels of individuals and species loss in the Open Ombrophilous Forest plots after the ENSO, when compared to Seasonal Forest, the long-term prospects for these forests are uncertain. Several studies have already suggested an increase in tree mortality in response to climate change (Nepstad et al., 2007; McDowell, 2018; Choat et al., 2018; Bennett et al., 2023). Thus, we postulate that the impacts of the 2015/2016 drought on the Open Ombrophilous Forest (e.g., reduced productivity and increasing mortality) might manifest more gradually compared to the other vegetation types within the Amazonia-Cerrado transition (Meira Junior et al., 2020). For all other vegetation types, already subjected to persistent water stress, their detrimental effects were apparent in the short term (Marimon et al., 2020; Esquivel-Muelbert et al., 2020; Reis et al., 2022).

The resilience of Cerrado species to extreme drought events like ENSO raises critical questions about the potential transformation of the Amazonia rainforest into Cerrado-like landscapes (Stark et al., 2020). While Seasonal Forests and Cerradão are highly sensitive, demonstrating substantial declines in tree density and species richness, species in the Typical Cerrado showed remarkable resistance, with minimal impacts observed during the ENSO event. This contrasting resilience underscores the need for targeted conservation strategies to mitigate the risk of biome shift under changing climate conditions (Hoffman et al., 2021; 2023). This resilience is attributed to structural and ecophysiological adaptations such as deep root systems, thick cuticles, water conservation, and stress tolerance, which equip Cerrado species to cope with periods of water deficit (Oliveira et al., 2005; Araújo et al., 2021). While recurrent and severe droughts could theoretically lead to a transition of Amazonia vegetation towards a Cerrado-like state, this process is influenced by a complex interplay of factors including climate variables such as precipitation and temperature, as well as fire regimes, soil characteristics, and human activities (Marimon et al., 2014; Morandi et al., 2016). The resilience observed in Cerrado species does not necessarily predict an immediate or irreversible shift to a Cerrado ecosystem but highlights the need to understand the adaptive capacities of diverse vegetation types under changing environmental conditions.

Consequently, in a scenario where extreme drought events become more frequent, our findings suggest that forests within the Amazonia-Cerrado transition, particularly seasonal forests, will become increasingly vulnerable. This vulnerability may lead to the replacement of forest species by those better adapted to drought conditions, typically found in savanna formations (Esquivel-Muelbert et al., 2019a; Araújo et al., 2021). Thus, our study underscores that in environments characterized by persistent water stress, like the Amazonia-Cerrado transition, more frequent and intense droughts could significantly alter floristic composition and ecosystem dynamics.

To address our second research question regarding the species, genera, and families experiencing the most significant changes in tree density due to the ENSO event, we reference findings from Baker et al. (2014). Their study, which used ecological factors to enhance species richness estimations through models based on diversification rates, indicated that specific environmental conditions and increased mortality rates often favour species with high turnover rates. This trait is prevalent among species-rich Amazonia genera such as *Inga*, suggesting a substantial demographic influence on the diversity observed in certain Amazonia lineages. The notable decline in *Inga* species within our Open Ombrophilous Forest plots may reflect this genus's intrinsic characteristics and its capacity for in situ diversification in response to historical extreme events or climate change (Hoorn et al., 2010).

The species with the highest VI in the Open Ombrophilous Forest plots, *Protium altissimum* and *P. sagotianum*, retained their positions after ENSO, while *Crepidospermum goudotianum* saw the largest increase. All three belong to the Burseraceae family, predominant in southeastern Amazonia (ter Steege et al., 2006). Conversely, the Brazil nut tree (*Bertholletia excelsa*), crucial for indigenous sustenance and global consumption, vanished from the Open Ombrophilous Forest plots. Post the 2015/2016 ENSO event, Brazil nut production plummeted by nearly two-thirds, exacerbating concerns about the impact of climate change on this culturally significant species (Thomas et al., 2014; Cooper, 2019).

While some species, including those with the highest VI in the Seasonal Forest plots, maintained their positions throughout our study—such as *Hymenaea courbaril* and *Trattinnickia glaziovii*, key to the regional timber trade (Ivanauskas, 2002; Cipriano et al., 2014)—others, including *Nectandra cuspidata*, *Ocotea guianensis*, *Miconia pyrifolia*, and *Jacaranda copaia*, declined notably. This decline may be attributed to their rapid growth and shorter life cycles, which typically increase mortality among pioneer species (Swaine and Lieberman, 1987; Swaine and Whitmore, 1988; Wright et al., 2010). These species tend to produce lighter wood and less mechanically robust trunks, lacking in drought resistance and long-term defense, characteristics that are disadvantageous in the seasonal climates of the southern periphery of Amazonia (Hietz et al., 2017). Consequently, they are more vulnerable than species in rainforests.

Conversely, in both Cerradão and Typical Cerrado plots, *Emmotum nitens* showed an increase in the number of individuals after the ENSO event. Notably, in the Cerradão plots, *Hirtella glandulosa*, recognized as an indicator of dystrophic Cerradão within the Amazonia-Cerrado transition (Ratter et al., 1973; Marimon et al., 2006), retained its top position in terms of VI. This species is characterized by high leaf water potential and a high hydraulic safety margin, which may confer ecophysiological advantages following extreme climate events (Jancoski et al., 2022). A hydraulic safety margin refers to the difference between the water potential at which hydraulic failure occurs (cavitation or embolism) and the operational water potential of the plant (Cochard and Delzon, 2013). A high hydraulic safety margin indicates that the plant operates within a safer range, far from the point of hydraulic failure, thus reducing the risk of severe water stress (Brodribb et al., 2020). Conversely, a low hydraulic safety margin would mean the plant operates close to this critical point, making it more vulnerable to drought conditions. Additionally, Oliveira-Filho and Ratter (1995) identified both *Emmotum nitens* and

Hirtella glandulosa as keystone species linking Riparian Forests, Typical Cerrado, and transitional vegetation along the southern Amazonian border, highlighting their potential role in restoration efforts in the Amazonia-Cerrado transition.

In the Typical Cerrado plots, most species maintained their VI positions between before and after ENSO inventories. *Qualea parviflora* consistently held the top position, underscoring its widespread distribution across 80% of 376 assessed areas in the Cerrado biome, including disjunct and peripheral regions, showcasing its adaptation to varied soil and climate conditions (Ratter et al., 2003; Buzatti et al., 2017). Additionally, Jancoski et al. (2022) highlighted its ecophysiological traits, such as high potential hydraulic conductivity and large xylem vessel diameter, coupled with significant drought resistance, evidenced by a high hydraulic safety margin. These characteristics likely contribute to its sustained prominence in the Typical Cerrado plots, even after the ENSO event.

The genera and families with the highest tree density and VI have shown notable stability over time, suggesting resilience at higher taxonomic levels. *Protium* and *Trattinnickia*, in particular, have maintained their relevance in both open and seasonal forest ecosystems throughout ENSO events. These genera are crucial to the Amazonia-Cerrado transition forests and should be prioritized in reforestation efforts aimed at restoring degraded areas, given their demonstrated resilience to extreme climate events and their significant role in the local flora (Ratter et al., 1973; Oliveira-Filho and Ratter, 1995; Ivanauskas, 2002; Marimon et al., 2014, 2020; Morandi et al., 2016). Additionally, about 70% of the genera newly recorded in plots after ENSO are characteristic pioneer species, highlighting dynamic ecological responses to climate disturbances (Morandi et al., 2016).

Aspidosperma is prominent in the Open Ombrophilous Forest, Cerradão, and Typical Cerrado, acting as a vital element of these transitional ecosystems (Ratter et al., 1973; 2003; Oliveira-Filho and Ratter, 1995; Marimon et al., 2006). Research indicates that *Aspidosperma* species excel under water stress, likely contributing to their resilience across various vegetation types, even following the 2015/2016 ENSO event (Freitas and Silva, 2018; Pájaro-Esquivia et al., 2021). After ENSO, the Cerradão plots experienced the complete disappearance of the Caryocaraceae family, known for its crucial fruit that sustains both humans and wildlife (Prance and Silva, 1973). The loss of an entire botanical family due to an extreme weather event highlights serious concerns about ecosystem regeneration and stability.

The increase in mortality among vulnerable species has led to decreased productivity, particularly in those most susceptible. This decline in tree density and floristic diversity has potentially facilitated the establishment of more resilient species (Esquivel-Muelbert et al., 2017a, b; 2019a; Bennett et al., 2023). Although our study does not include seedling monitoring, it suggests an after-ENSO trend of species replacement favoring pioneers and those adapted to drier conditions. For example, *Zanthoxylum ekmanii* saw a 50% increase in individuals in the Open Ombrophilous Forest (Ruschel et al., 2015), and *Tachigali vulgaris*, known for its climate resilience, expanded by 125% in the Typical Cerrado plots (Farias et al., 2016).

Our investigation revealed that the expected changes in floristic composition within the forest and savanna formations due to an extreme climate event associated with intense drought were not supported by our findings. However, we did observe significant losses in tree density and species richness in the typical transitional forest types, the Seasonal Forests and Cerradão. These results underscore the particular vulnerability of vegetation in the Amazonia-Cerrado transition to temperature and precipitation anomalies linked to the ENSO phenomenon, leading to substantial declines in tree density and shifts in floristic composition. By analyzing specific species and monitoring population gains and losses during the 2015/2016 ENSO event, our study identified species that are most susceptible, including *Dialium guianense* in Open Ombrophilous Forest, *Miconia pyrifolia* in the Seasonal Forest, *Xylopia aromatica* in Cerradão, and *Guapira noxia* in Typical Cerrado. Conversely, we pinpointed species demonstrating resilience, such as *Rinoreocarpus ulei* in Open Ombrophilous Forest, *Tapirira obtusa* in Seasonal Forest, *Emmotum nitens* in Cerradão, and *Tachigali vulgaris* in Typical Cerrado. This vital information can guide strategic decisions for managing and restoring degraded areas by either avoiding the use of vulnerable species or promoting more resistant species in restoration efforts. The insights gained from this study highlight the need for targeted conservation strategies that can mitigate the impacts of climate extremes on these crucial transitional ecosystems, thereby preserving their biodiversity and ecological functions.

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Figure Legends

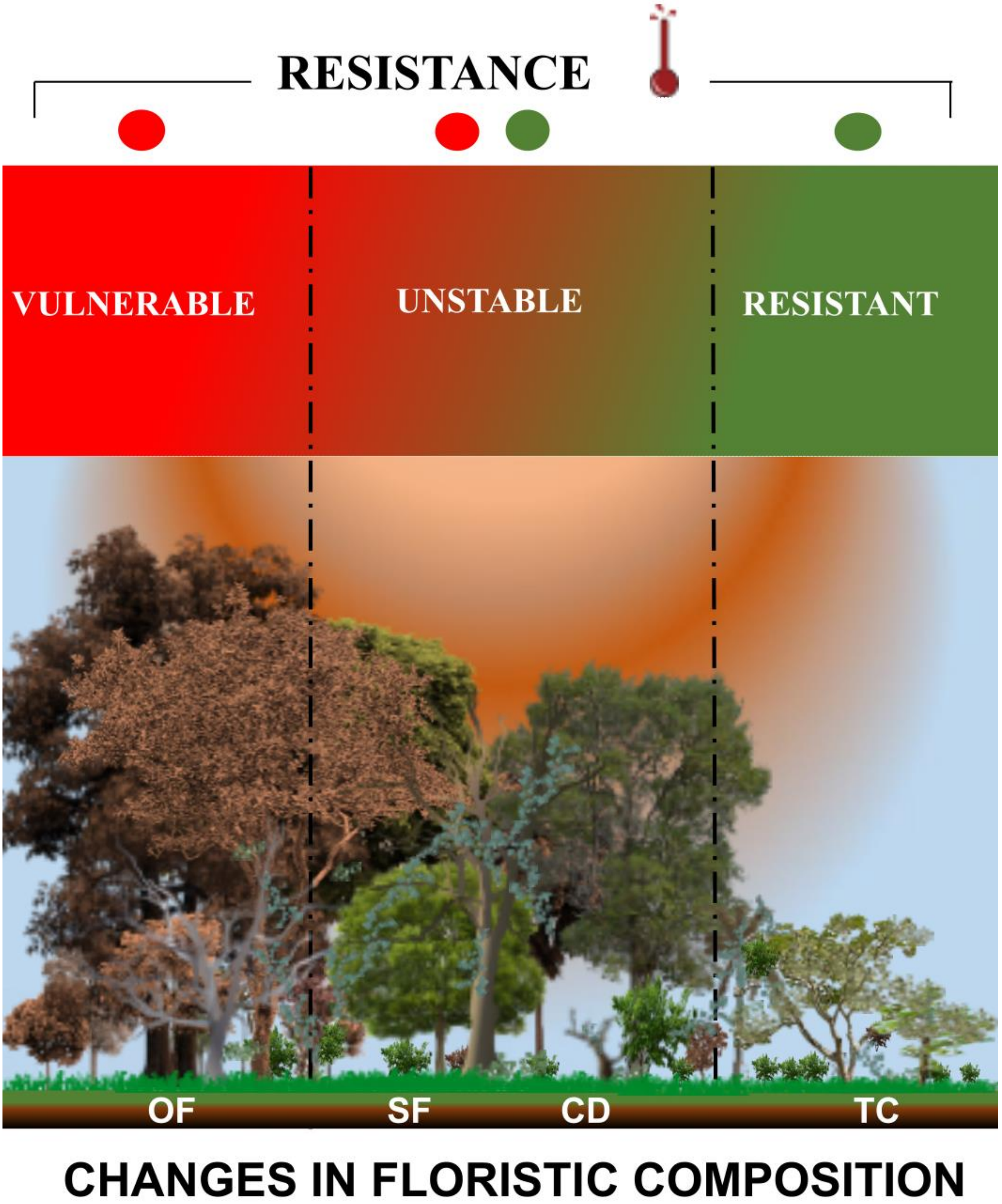

Figure 1. Illustrative hypothesis of changes in arboreal floristic composition in the phytophysiognomies of Open Ombrophilous Forest (OF), Seasonal Forest (SF), Cerradão (CD), and Typical Cerrado (TC) as a result of the 2015/2016 El Niño Southern Oscillation (ENSO) event, sampled in the Amazonia-Cerrado transition, Brazil. Floristic resistance is indicated by circles, showing systems dominated by vulnerable species (red), an unstable mixture of responses (red and green), and resistant species (green).

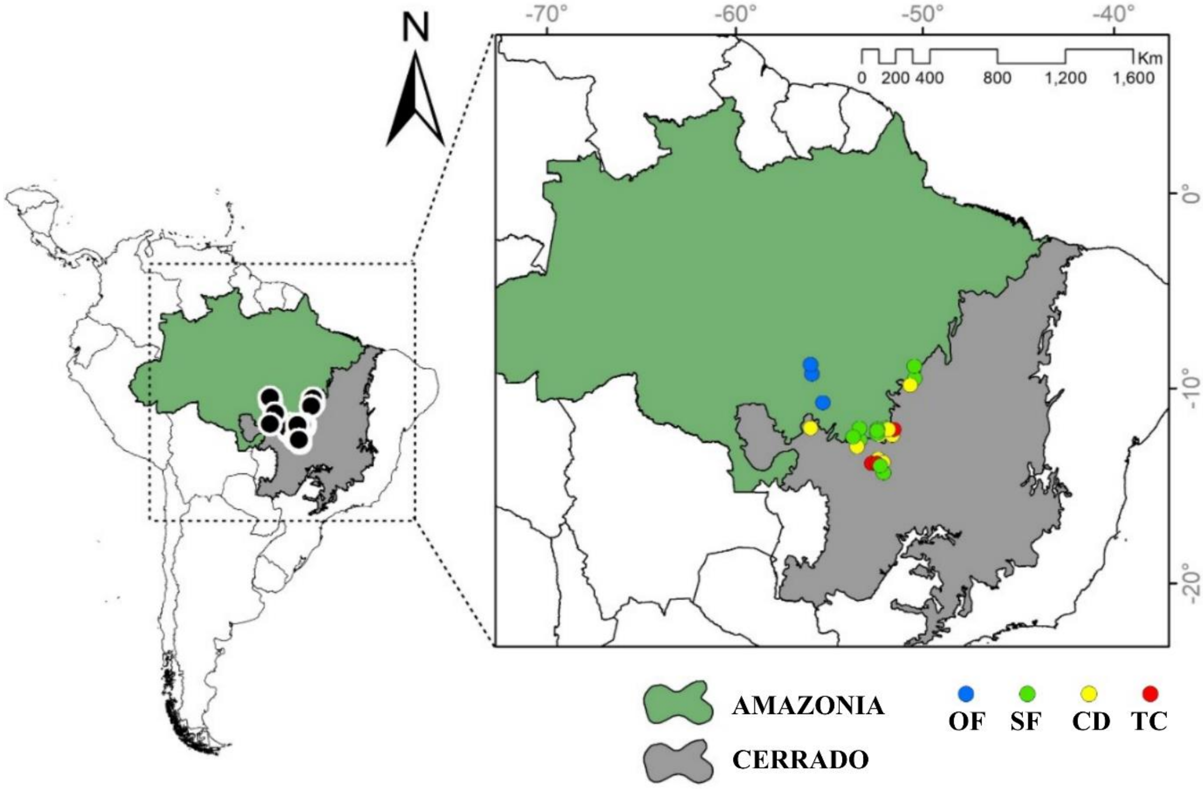

Figure 2. Location of permanent plots of Open Ombrophilous Forest (OF), Seasonal Forest (SF), Cerradão (CD), and Typical Cerrado (TC) sampled in the Amazonia-Cerrado transition, Brazil.

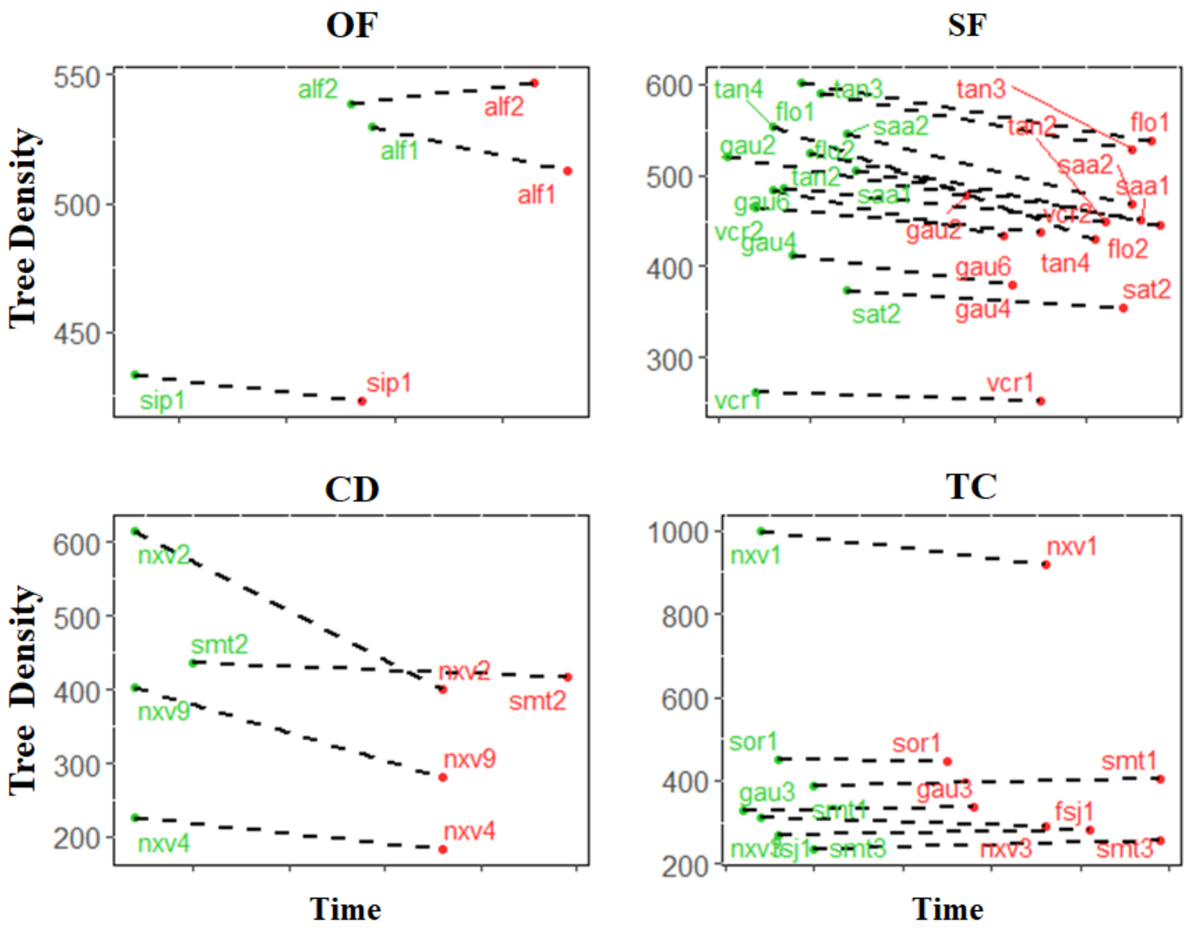

Figure 3. Change in the tree density about time (before and after) in Open Ombrophilous Forest (OF, top left), Seasonal Forest (SF, top right), Cerradão (CD, lower left), and Typical Cerrado (TC, lower right) plots, sampled in the Amazonia-Cerrado transition, Brazil. Each panel shows stand-level values before (green) and after (red) the 2015/2016 El Niño Southern Oscillation (ENSO) event. Time represents the periods before and after the ENSO event. The dashed line connecting the points represents indicates the variation in tree density in each area over time. In the figures, plots are identified by abbreviated plot names.

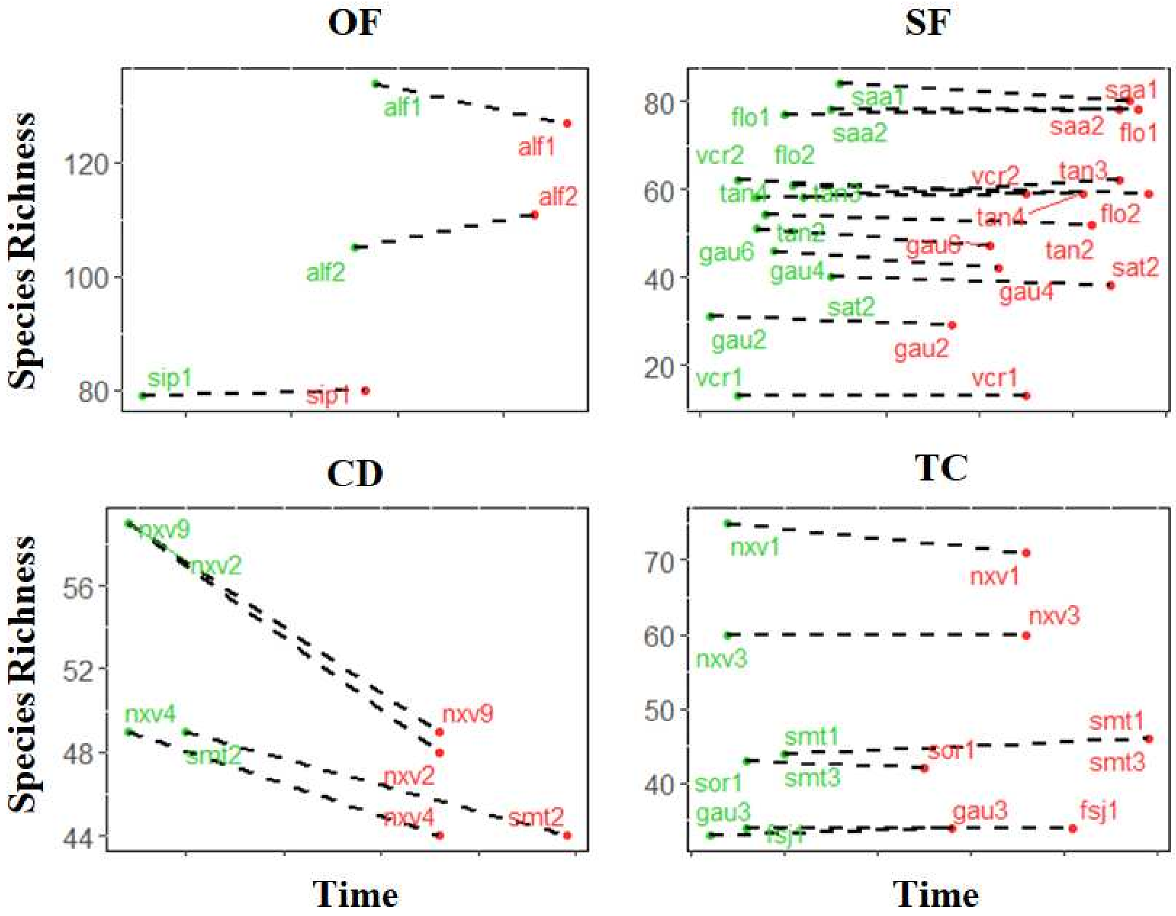

Figure 4. Change in species richness about time (before and after) in Open Ombrophilous Forest (OF), Seasonal Forest (SF), Cerradão (CD), and Typical Cerrado (TC), sampled in the Amazonia-Cerrado transition, Brazil. Each panel shows stand-level values before (green) and after (red) the 2015/2016 El Niño Southern Oscillation (ENSO) event. Time represents the periods before and after the ENSO event. The dashed line connecting the points represents indicates the variation in species richness in each area over time. In the figures, plots are identified by abbreviated plot names.

Table 1. Species richness (at species, genera, and families) and tree density (at species, genera and families) in different vegetation types of the Amazonia-Cerrado transition, Brazil. For each parameter values are given before and after the 2015/2016 El Niño Southern Oscillation (ENSO). OF = Ombrophilous Forest, SF = Seasonal Forest, CD = Cerradão, and TC = Typical Cerrado. P values ≤ 0.05 are highlighted in bold.

Taxon	**Parameters**	**interval**	**OF**	**ST**	**CD**	**TC**
Trees	Density	Before	1.498	5.945	1.677	3.345
		After	1.477	5.312	1.28	3.284
		p-value	t= 1.4, df=239 p>0.05	t= 3.9, df=255 **p<0.0001**	t= 3.6, df=99 **p<0.0004**	t= 1.1, df=129 p>0.05
Species	Richness	Before	231	242	99	124
		After	228	235	89	126
		p-value	t= 0, df=2 p>0.05	t=2.2, df=11 **p<0.04**	t=4.8, df=3 **p<0.01**	t=0, df=7 p>0.05
Genera	Richness	Before	127	117	77	77
		After	127	116	72	78
		p-value	t= -0.9, df=2 p>0.05	t= 3.2, df= 11 **p<0.008**	t= 3.6, df=3 **p<0.04**	t= -0.2, df=7 p>0.05
Families	Richness	Before	45	50	39	36
		After	46	49	38	36
		p-value	t=-1, df=2 p>0.05	t=3.1, df=11 **p<0.01**	t= 1.6, df=3 p>0.05	t=0, df=7 p>0.05

Table 2. All species (A), genera (B), and families (C) with at least 10 individuals recorded after 2015/2016 El Niño Southern Oscillation (ENSO) and present in at least 50% of plots in each vegetation type (OF = Open Ombrophilous Forest, SF = Seasonal Forest, CD = Cerradão, and TC = Typical Cerrado), sampled in the Amazonia-Cerrado transition, Brazil. In red are values of species that lost the most, and in green are those that gained the most individuals in each vegetation type. Colour intensity indicates strength of response (red - vulnerable, green - resistant), with darker shades representing more extreme values. Abbreviations: Losses (L) and gains of individuals (G) order the parameters (L/G%) of the mortality rate (M, % year^{-1}) and recruitment rate (R, % year^{-1}).

A) Species	**OF**			**SF**			**CD**			**TC**		
	L/G%	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**
Amaioua guianensis Aubl.				-15	5.3	0.9						
Andira cujabensis Benth.										-6	1.8	0
Aspidosperma macrocarpon Mart. & Zucc.										0	0	0
Aspidosperma multiflorum A.DC.							-17	5.1	0	0	0	0
Aspidosperma tomentosum Mart. & Zucc.										-6	1.6	0
Astrocaryum aculeatum G.Mey.	0	0	0									
Astronium fraxinifolium Schott							-33	10.9	0			
Bellucia grossularioides (L.) Triana				-31	12.6	2.7						
Bowdichia virgilioides Kunth							-16	4.9	0	-7	2.7	0.6
Brosimum lactescens (S.Moore) C.C.Berg	-3	2.0	1.0									
Byrsonima coccolobifolia Kunth										-5	2.5	1.1
Byrsonima pachyphylla A.Juss.										3	1.9	2.6
Caryocar brasiliense Cambess.										3	0	0.9
Celtis schippii Standl.	-3	3.1	2.1									
Chaetocarpus echinocarpus (Baill.) Ducke				-4	2.7	1.7	-5	1.5	0			
Cheiloclinium cognatum (Miers) A.C.Sm.	2	0.5	1.0	-10	3.4	0.4						
Chrysophyllum venezuelanense (Pierre) T.D.Penn.	0	0	0									
Copaifera langsdorffii Desf.				0	0	0						
Cordiera sessilis (Vell.) Kuntze							0	0	0			
Curatella americana L.							-19	5.9	0	-13	4.5	0.8
Dialium guianense (Aubl.) Sandwith	-15	4.5	0									

Didymopanax morototoni (Aubl.) Decne. & Planch.				0	2.0	2.0						
Dimorphandra mollis Benth.										-17	6.2	1.7
Diospyros lasiocalyx (Mart.) B.Walln.										-4	2.2	1.1
Dipteryx alata Vogel							0	0	0			
Emmotum nitens (Benth.) Miers							3	2.3	3.1	22	0.9	6.3
Eriotheca gracilipes (K.Schum.) A.Robyns							-22	7.0	0	-2	1.0	0.3
Euplassa inaequalis (Pohl) Engl.							-28	11.3	2.6			
Guapira graciliflora (Mart. ex Schmidt) Lundell							-14	7.0	2.5			
Guapira noxia (Netto) Lundell							-36	12.1	0	-47	16.0	0
Guarea kunthiana A.Juss.	0	1.4	1.1									
Handroanthus ochraceus (Cham.) Mattos										-4	1.3	0
Heisteria ovata Benth.							-20	6.2	0			
Himatanthus articulatus (Vahl) Woodson				-13	4.0	0						
Hirtella glandulosa Spreng.							-10	3.0	0			
Hymenaea courbaril L.				-3	1.4	0.5						
Hymenaea stigonocarpa Mart. ex Hayne										0	0	0
Inga thibaudiana DC.				10	4.5	7.1						
Iryanthera laevis Markgr.	0	0	0									
Jacaranda copaia (Aubl.) D.Don				-19	8.5	3.0						
Kielmeyera rubriflora Cambess.										-6	1.7	0
Lafoensia pacari A.St.-Hil.										-3	1.0	0
Leptobalanus apetalus (E.Mey.) Sothers & Prance				-5	3.0	1.5						
Leptobalanus humilis (Cham. & Schltdl.) Sothers & Prance										-2	1.1	0.6
Licania blackii Prance				0	1.0	1.0						
Luetzelburgia praecox (Harms) Harms							0	0	0			
Maprounea guianensis Aubl.							-17	8.0	3.0			
Maquira guianensis Aubl.	0	3.0	3.0									
Matayba guianensis Aubl.							-59	22.4	0			
Metrodorea flavida K.Krause	-9	3.0	0									

Mezilaurus crassiramea (Meisn.) Taub. ex Mez							-15	4.4	0	-9	2.6	0
Miconia punctata (Desr.) DC				-20	19.4	14.2						
Miconia pyrifolia Naudin				-45	20.7	5.8						
Micropholis venulosa (Mart. & Eichler) Pierre				-19	6.3	0.6						
Mouriri elliptica Mart.										-1	1.2	0.8
Myrcia splendens (Sw.) DC.							-38	17.6	5.4	-17	8.8	3.7
Myrciaria floribunda (H.West ex Willd.) O.Berg				-9	3.7	1.0						
Nectandra cuspidata Nees				-29	12.6	3.7						
Ocotea guianensis Aubl.				-33	12.4	1.7						
Ocotea leucoxylon (Sw.) Laness.				6	4.4	6.0						
Ormosia paraensis Ducke				-3	1.6	0.8						
Ouratea discophora Ducke				-4	4.13	3						
Ouratea hexasperma (A.St.-Hil.) Baill.										-12	3.6	0
Pouteria ramiflora (Mart.) Radlk.				4	2.4	3.4	0	0	0	-1	1.2	0.9
Protium altissimum (Aubl.) Marchand	0	3.0	2.7									
Protium heptaphyllum (Aubl.) Marchand							-3	0.7	0			
Protium pilosissimum Engl.				4	6.4	7.4						
Protium sagotianum Marchand	-3	1.4	0.6									
Protium tenuifolium (Engl.) Engl.	8	0	2.3									
Protium unifoliolatum Engl.				-21	9.2	2.7						
Pseudobombax longiflorum (Mart.) A.Robyns							-8	2.5	0	0	0	0
Pseudolmedia laevigata Trécul	-5	1.4	0									
Pseudolmedia laevis (Ruiz & Pav.) J.F.Macbr.	-3	3.6	2.8									
Pseudolmedia macrophylla Trécul	12	0	3.1	-4	3.0	2.0						
Pterodon pubescens Benth. (Benth.)							0	2.5	2.5	-5	2.1	0.7
Qualea grandiflora Mart.							-17	5.3	0	2	0.6	1.1
Qualea multiflora Mart.										-21	7.9	1.3
Qualea parviflora Mart.							-11	3.3	0	-1	1.4	1.2
Rinoreocarpus ulei (Melch.) Ducke	12	1.7	4.8									

Roupala montana Aubl.							-15	4.4	0	-2	1.8	1.4
Sacoglottis guianensis Benth.				-5	2.6	1.1						
Salvertia convallariodora A.St.-Hil.							0	0	0	-1	0.6	0.3
Simarouba amara Aubl.				-23	13.0	6.2						
Strychnos pseudoquina A.St.-Hil.										-6	2.0	0
Tabebuia aurea (Silva Manso) Benth. & Hook.f.										-10	3.0	0
Tachigali vulgaris L.G.Silva & H.C.Lima							-48	22.5	6.8	125	11.0	29.4
Tapirira guianensis Aubl.				-40	15.3	2.0	-71	30.0	0			
Tapirira obtusa (Benth.) J.D.Mitch.				13	3.0	6.18						
Terminalia argentea Mart. & Zucc.							-64	25.5	0			
Terminalia corrugata (Ducke) Gere & Boatwr.							-15	4.7	0	4	0	1.1
Theobroma speciosum Willd. ex Spreng.	9	0.8	3.2									
Trattinnickia glaziovii Swart				-5	2.6	1.1						
Trichilia quadrijuga Kunth	5	2.7	3.9									
Vatairea macrocarpa (Benth.) Ducke							-18	6.2	0.7	-4	1.9	0.6
Virola sebifera Aubl.				0	0	0						
Vochysia haenkeana Mart.							-27	8.7	0			
Vochysia rufa Mart.										-12	6.2	3.0
Xylopia amazonica R.E.Fr.				2	7.0	7.4						
Xylopia aromatica (Lam.) Mart.							-89	46.2	0			
Xylopia frutescens Aubl.				-38	21.0	9.7						

B) Genera	**OF**			**SF**			**CD**			**TC**		
	L/G%	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**
Amaioua				-15	5.3	0.9						
Andira										-4	1.0	0
Annona										-17	7.9	3.0
Aspidosperma				1	1.4	1.7	-15	4.6	0	-3	1.0	0
Astrocaryum	0	0	0									
Astronium							-33	11.0	0			
Bellucia				-31	13.0	2.7						
Bowdichia							-16	4.9	0	-7	2.7	0.6
Brosimum	-3	1.8	0.9									
Byrsonima				-8	5.1	2.7				-3	2.6	1.9
Caryocar										3	0	1.0
Casearia				-15	7.9	3.5						
Celtis	-3	3.1	2.1									
Chaetocarpus				-4	2.7	1.7	-5	1.5	0			
Cheiloclinium	2	0.5	1.0	-10	3.4	0.4						
Chrysophyllum	0	0	0									
Copaifera				0	0	0						
Cordiera							0	0	0			
Curatella							-19	5.9	0	-13	4.5	0.8
Dialium	-15	4.5	0									
Didymopanax				0	2.0	2.0						
Dimorphandra										-17	6.2	1.2
Diospyros				7	0	2.0				-4	2.2	1.1
Dipteryx							0	0	0			
Duguetia				9	0	2.5						
Emmotum							3	2.3	3.0	22	0.9	6.3

Enterolobium				10	0	2.7						
Eriotheca							-22	7.0	0	-2	0.9	0.3
Eugenia										0	0.5	0.5
Euplassa							-28	11.0	2.6			
Ficus				-20	9.7	3.7						
Guapira							-28	9.9	1.1	-18	6.0	0.5
Guarea	-2	2.6	2.0									
Guatteria				13	17.0	20.0						
Handroanthus										-4	1.3	0
Heisteria							-20	6.2	0			
Himatanthus				-13	3.7	0						
Hirtella				-15	4.8	0.3	-10	2.8	0			
Hymenaea				-3	1.4	0.5				0	0	0
Inga	-39	15.9	3.0	-20	11.0	5.1						
Iryanthera	0	0	0									
Jacaranda				-19	8.5	2.9						
Kielmeyera										-11	3.6	0.4
Lafoensia										-3	1.0	0
Leptobalanus				-7	3.8	1.8				-2	1.1	0.6
Luetzelburgia							0	0	0			
Maprounea							-17	7.9	3.0			
Maquira	0	1.9	2.0									
Matayba							-59	22.0	0			
Metrodorea	-9	2.7	0									
Mezilaurus							-15	4.4	0	-9	2.6	0
Miconia				-29	18.0	9.9						
Micropholis				-15	5.6	1.0						
Mouriri				-6	2.8	1.1				-1	1.1	0.7
Myrcia				-36	14.0	2.1	-39	18.0	5.4	-1	3.7	3.3

Myrciaria				-9	3.7	1.0						
Nectandra				-29	13.0	3.7						
Ocotea	0	0	0	-17	7.9	2.8						
Ormosia				-3	1.6	0.8						
Ouratea				-4	4.1	3.0				-26	8.1	0
Pourouma	-6	7.9	6.2									
Pouteria	7	0	2.0	-5	3.8	2.3	0	0	0	-1	1.2	0.9
Protium	-2	4	3	2	6.6	7.2	-3	0.7	0			
Pseudobombax							-8	2.5	0	0	0	0
Pseudolmedia	5	1.8	3.1	-5	3.0	1.6						
Pterodon							0	2.5	2.5	-6	2.3	0.5
Qualea	-10	3.0	0				-15	4.9	0.5	-2	1.8	1.2
Rinoreocarpus	12	1.7	4.8									
Roupala							-15	4.4	0	-2	1.8	1.4
Sacoglottis				-5	2.6	1.1						
Salvertia							0	0	0	-1	0.6	0.3
Simarouba				-23	13.0	6.2						
Sloanea				-10	4.5	1.5						
Strychnos										-6	1.9	0
Tabebuia							-8	2.5	0	-7	1.9	0
Tachigali							-47	22.0	6.7	100	8.5	25
Talisia	0	2.1	2.1									
Tapirira				-8	7.2	5.1	-71	30.0	0			
Terminalia				6	1.6	3.1	-79	29.7	0	4	0	1.1
Theobroma	8	0.7	2.8									
Tovomita	0	0.6	0.6									
Trattinnickia	-13	3.7	0	-5	2.7	1.1						
Trichilia	8	3.7	5.9									
Vatairea							-18	6.2	0.7	-4	1.9	0.6

Virola				6	0	1.5						
Vochysia	11	1.5	4.3				-53	19.0	0	-4	3.8	2.7
Xylopia				-1	7.8	7.5	-45	20.0	5.3	38	9.2	17.0

C) Families	**OF**			**SF**			**CD**			**TC**		
	L/G%	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**	**L/G%**	**M**	**R**
Anacardiaceae	0	0	0	-5	6.1	4.6	-65	26.1	0	2	0	0.5
Annonaceae				-1	7.0	6.7	-45	20.0	5.2	18	8.7	13.0
Apocynaceae	-6	1.6	0	-1	1.8	1.5	-16	4.8	0	-3	0.9	0
Araliaceae				0	1.9	1.9						
Arecaceae	-6	3.9	2.2									
Bignoniaceae	-20	6.2	0	-16	7.6	2.8	-13	3.7	0	-7	2.1	0
Burseraceae	-1	2.4	2.1	-4	3.4	2.3	-3	0.7	0			
Calophyllaceae										-11	3.5	0.4
Cannabaceae	-3	3.1	2.1									
Caryocaraceae										3	0	1.0
Celastraceae	2	0.5	1.0	-10	3.4	0.4				-25	8.0	0
Chrysobalanaceae	0	0	0	-10	4.2	1.3	-9	2.8	0	-2	1.2	0.5
Clusiaceae	0	0.6	0.6									
Combretaceae				5	3.1	4.5	-49	17.4	0	-6	2.4	0.7
Dilleniaceae							-19	5.9	0	-20	6.4	0.3
Ebenaceae				7	0	1.9				-4	2.2	1.1
Elaeocarpaceae				-10	4.5	1.5						
Euphorbiaceae	11	0	2.8	-1	7.8	7.6	-13	5.8	2.1			
Fabaceae	-17	7.2	2.1	-9	4.4	1.9	-26	10.5	2.4	1	2.7	3.0
Humiriaceae				-5	2.6	1.1						
Icacinaceae							3	2.3	3.1	22	0.9	6.3
Lauraceae	6	2.8	4.4	-19	8.5	2.9	-15	4.4	0	-9	2.6	0

Lecythidaceae	-12	3.5	0									
Loganiaceae										-3	1.9	0.9
Lythraceae										-3	0.9	0
Malpighiaceae				-8	5.1	2.7	-30	13.6	4.31	-2	2.5	1.8
Malvaceae	4	1.9	3.1	-5	3.1	1.6	-20	6.2	0	-2	0.7	0.2
Melastomataceae				-23	13.2	6.5				1	1.0	1.3
Meliaceae	1	2.8	3.2									
Moraceae	0	1.9	1.9	-2	1.8	1.2						
Myristicaceae	-5	3.1	1.6	6	0	1.5						
Myrtaceae				-13	4.7	1.0	-36	16.1	4.6	-1	2.3	2.1
Nyctaginaceae							-28	10.0	1.1	-18	5.8	0.5
Ochnaceae				-3	4.2	3.2				-26	8.1	0
Olacaceae				-21	7.2	0.7	-18	5.6	0			
Peraceae				-4	2.9	1.8	-5	1.5	0			
Proteaceae							-21	7.6	1.1	-3	2.4	1.5
Rubiaceae				-16	5.7	0.9	0	1.3	1.3			
Rutaceae	0	2.3	2.0									
Salicaceae				-15	7.9	3.5						
Sapindaceae	-3	2.0	1.1	-36	12.8	0.7	-51	18.5	0			
Sapotaceae	7	0.7	2.6	-12	4.9	1.5	0	0	0	-1	1.1	0.9
Simaroubaceae				-23	12.9	6.2						
Urticaceae	0	8.4	8.0									
Violaceae	7	2.1	4.0									
Vochysiaceae	3	2.0	2.6				-19	6.2	0.4	-2	1.8	1.2