Sensitivity of tropical woodland savannas to El Niño droughts

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Abstract

The 2015-2016 El Niño event led to one of the most intense and hottest droughts for many tropical forests, profoundly impacting forest productivity. However, we know little about how this event affected the Cerrado, the largest savanna in South America. Here we report 5 years of productivity of the dominant vegetation types in Cerrado, savanna (*cerrado*) and transitional forest-savanna (*cerradão*), continuously tracked before, during, and after the El Niño. We carried out intensive monitoring between 2014 and 2019 of the productivity of key vegetation components (stems, leaves, roots). *Cerradão* productivity declined strongly by 29% during the El Niño event. The most impacted component was stem productivity, reducing by 58%. By contrast, *cerrado* productivity varied little over the years, and while the most affected component was fine roots, declining by 38% during the event, fine root productivity recovered soon after the El Niño. The two vegetation types also showed contrasting patterns in the allocation of productivity to canopy, wood, and fine-root production. Our findings demonstrate that *cerradão* can show low resistance and resilience to climatic disturbances due to the slow recovery of productivity. This suggests that the transitional Amazon-Cerrado ecosystems between South America's largest biomes may be particularly vulnerable to drought enhanced by climate change.

Keywords: 2015-2016 El Niño, productivity, productivity allocation, climate events, *cerradão*, *cerrado*.

1 Introduction

The 2015-2016 El Niño event led to some of the most intense tropical droughts in a hundred years as well as record maximum temperatures, coming on top of decades of long-term warming (Jiménez-Muñoz et al., 2016; Liu et al., 2017). While the 2015-16 climate anomaly affected most of the tropics it was especially strong in South and Central America (Gloor et al., 2018, Powers et al., 2020). Intense droughts can increase tree mortality and affect the carbon sequestration capacity of forests as shown by long-term ground-based monitoring (e.g., Phillips et al., 2009; Feldpausch et al., 2016; Rifai et al., 2018; Bennett et al., 2023). Satellite-based analyses also reveal the impacts of climate anomalies on carbon dynamics (Palmer et al., 2018; Fan et al., 2019), providing a synoptic view of ecosystem productivity. However, we still lack ground-based, tree-level measurements of net primary productivity (NPP) through extreme tropical climate events, hindering our understanding of key aspects of the vegetation carbon cycle response, such as recovery following drought events, and NPP allocation. Measuring these ecosystem responses directly is helped by tracking long-term forest dynamics in permanent plots but especially requires high-fidelity process-based measurements sustained over time. These are exceptionally challenging to make and require long-term dedication to measurements before, during, and after major climate events like the 2015-16 El Nino.

We know especially little about how El Niño events affect the productivity of savanna ecosystems in the extensive Amazonia-Cerrado transition in South America. This contains a mixture of Amazon and Cerrado species, making the species composition of this region unique and diverse (Ratter et al., 1973; Marimon et al., 2006; Morandi et al., 2016). Despite its ecological importance, the region has been greatly impacted by deforestation (~41% between 1984 and 2014) so that today only fragments of native vegetation remain (e.g., Marques et al., 2020). In recent decades, the remaining vegetation has been affected by increasing temperatures, frequent wildfires, extreme drought events, and a long-term trend to longer dry seasons (e.g., Reis et al., 2018; Silvério et al., 2019; Nogueira et al., 2019; Matricardi et al., 2020; Araújo et al., 2021a). Deforestation, together with increases in temperature and reduction in precipitation during El Niño events, increases wildfire occurrence and carbon emissions, reducing the capacity of the vegetation to act as a carbon sink (Covey et al., 2021; Gatti et al., 2021). As the Amazonia-Cerrado transition is the driest, warmest, and most fragmented region in the Amazon basin (e.g., Matricardi et al., 2020; Marques et al., 2020; Covey et al., 2021; Reis et al., 2022) it is especially vital to understand better how climate change and extreme climate events impact productivity dynamics here.

The transition is composed naturally of a mosaic of vegetation, being the typical cerrado (referred to as *cerrado* hereafter) and woodland savanna (i.e., *cerradão*) the most common in the regions (Ratter et al., 1973; Marimon et al., 2006, Oliveras & Malhi, 2016). Despite co-existing in the same space, *cerrado* and *cerradão* vegetation formations show contrasting characteristics (Marimon-Junior & Haridasan, 2005; Marimon et al., 2006). The *cerradão* is a transitional forest-savanna characterized by closed canopy, understory formed by small shrubs and herbs, with few grasses, and average height of the tree stratum varying from 8 to 15 m, tree cover of 50 to 90%

(Ribeiro & Walter, 2008, Oliveras & Malhi 2016), while *cerrado* is a savanna vegetation type with a discontinuous canopy, trees, and shrubs with grass understorey, and a low average height of just 3 to 6 m, with tree cover of 20 to 50% (Marimon-Junior & Haridasan, 2005; Ribeiro & Walter, 2008).

In the *cerrado,* most species are deciduous, shedding their leaves during the dry season, whereas in the *cerradão,* brevi-deciduous and/or evergreen species predominate (Ribeiro & Walter, 2008). This phenological difference has direct implications for tolerance to water and thermal stress. *Cerrado* species exhibit conservative water-use strategies, characterized by smaller stomata and higher trichome density, which reduce water loss and protect the leaves from overheating (Araújo et al., 2021b; Araújo et al., 2023). In contrast, trees in the *cerradão* have larger stomata and a lower density of trichomes, which may result in higher stomatal conductance and, consequently, greater water demand (Araújo et al., 2021b).

Among species that co-occur in both vegetation types*,* individuals in *cerrado* shed their leaves earlier in the dry season than those in the *cerradão*, a strategy that prevents damage to photosynthetic apparatus during the driest and hottest period of the year (Araújo et al., 2021a). In the *cerradão*, later leaf senescence prolongs tree activity under water deficit, making them more vulnerable to rising temperatures, both under current conditions and in future projections (Araújo et al., 2021a). Trees in the *cerradão* are also taller than those in the *cerrado*, a trait that may increase their sensitivity to drought. Taller trees tend to have wider xylem vessels, making them more susceptible to embolism risk under severe water stress (Olson et al., 2018; Araújo et al., 2024). These contrasting strategies suggest that the responses of these two vegetation types to climatic disturbances such as El Niño events may differ substantially, and in particular that the physiological and anatomical characteristics of *cerradão* vegetation may make it more susceptible to marked temperature increases and prolonged water deficits.

Here, by setting up and sustaining intensive, long-term monitoring plots that experience a similar climate at *cerradão* and *cerrado*, we aimed to quantify and compare the effect of the 2015/2016 El Niño on the carbon cycle (productivity and allocation) of the two vegetation types. Our guiding questions and hypotheses are: **1) Did the 2015-2016 El Niño affect total productivity, productivity and partitioning of different compartments (canopy, stem and fine root) in the *cerradão* and *cerrado*?** We hypothesize that: (H1) *Cerrado* and *cerradão* NPP respond differently to El Niño events due to their distinct structural, anatomical, and eco-physiological strategies. We predict that the 2015–2016 El Niño reduced total productivity in both environments, but more severely in the *cerradão*, where traits such as taller trees, larger stomata, greater maximum stomatal pore opening, and reduced water loss control increase vulnerability to drought (e.g., Araújo et al., 2021a, b; 2023; 2024; Jancoski et al., 2022); (H2) The productivity decline should be more pronounced in the canopy and stem of the *cerradão*, whereas in the *cerrado*, the reduction may have been less significant due to its higher water-use resilience (Ball, 2010). During drought, *cerrado* plants are expected to reallocate resources from the aboveground compartments (canopy and stem) to fine roots, enhancing deep water access, whereas *cerradão* trees, with greater investment in vertical growth, experience increased water stress and reduced productivity (Comas et al., 2013; Pérez-Ramos et al., 2013; Scalon et al., 2022). **2) Did the *cerradão* and *cerrado* regain productivity after the El Niño?** (H3) The *cerrado* is expected to recover its productivity more quickly than the *cerradão*. In the *cerradão*, recovery may be slower due to greater structural damage and impairment of the trees' hydraulic system, such as xylem vessel embolism (Jancoski, 2019). The *cerrado* is expected to exhibit greater resilience due to its conservative water-use strategy and capacity for resprouting after extreme drought periods (Jancoski et al., 2022). In the *cerradão*, prolonged stress may have reduced the recovery rate, especially in trees that suffered embolism or partial canopy mortality (Reis et al., 2022; Araújo et al., 2024).

2 Materials and Methods

2.1 Study sites

We conducted this study in two long-term plots: one in *cerradão* (a transitional forest-savanna) and another in *cerrado* (*typical cerrado*; savanna), both located in Bacaba Municipal Park, Nova Xavantina, Mato Grosso State, Central Brazil. The park covers approximately 500 ha in the transition zone between the Cerrado (Brazilian savanna) and the Amazonia. Since the two plots are only ~300m apart, they experience similar climatic conditions, classified as *Aw* (tropical with dry winters) in Köppen's system (Alvares et al., 2013). The region has two well-defined seasons: a cooler dry season (April to September) and a hot rainy season (October to March). According to Brazilian National Institute of Meteorology (INMET) station #83319, the mean monthly temperature is 24.8 °C, the total annual precipitation is 1440 mm (Peixoto et al., 2017). The park's average altitude is ~ 250 m. There is no evidence of a shallow water table which might buffer the impact of climate extremes on vegetation (Marimon Junior & Haridasan, 2005).

Each plot covers 1 hectare and was established in 2002 (Marimon Junior & Haridasan, 2005), with multiple re-censuses conducted since then. Since 2010, these plots have been part of the PELD project (Cerrado-Amazonia Forest Transition: ecological and socio-environmental bases for Conservation), the RAINFOR network (Amazonia Forest Inventory Network; ForestPlots.net et al., 2021) and the ForestPlots.net database. Since 2014, they have also been integrated into the GEM network (Global Ecosystems Monitoring network; Malhi et al., 2021). These plots have supported numerous studies on topics including soil properties, species composition and diversity, biomass, nutrient allocation, and tree dynamics (e.g., Marimon Junior & Haridasan, 2005; Marimon et al., 2014; Scalon et al., 2022). Partial carbon cycle for the *cerradão* plot, including litterfall, soil CO_2 efflux and carbon stocks in fine roots, litter layer, and stems, have been published previously (Peixoto et al., 2017; Peixoto et al., 2018). Here we provide the first comprehensive description of net primary productivity in both plots, along with an extended time series that sheds light on the aftermath of the 2015/2016 El Niño event.

The plots have remained fire-free since 2008. The *cerradão* plot is a transitional forest-savanna ecosystem with overlapping savanna and forest species, a closed canopy, and dominant species such as *Hirtella glandulosa* Spreng. and *Tachigali vulgaris* L.G. Silva & H.C. Lima. Ratter et al. (1973) classified this vegetation type as *Hirtella glandulosa cerradão*. In contrast, the *cerrado* plot is characterized by an open canopy with trees and shrubs, a grass understorey, and two dominant tree species: *Qualea parviflora* Mart. and *Davilla elliptica* A.St.-Hil. (Marimon Junior & Haridasan, 2005; Marimon et al., 2014). However, the *cerrado* vegetation has been densifying, with reduced grass cover, possibly due to fire exclusion (Morandi et al., 2015).

Soil properties are similar across the plots, consisting of sandy loams classified as yellow latosol, which are acidic (pH < 5.0) and dystrophic (Ca^{2+} ~ 0.4 $cmol_c$ kg^{-1}), with high levels of exchangeable aluminium (Al^{3+} > 1.3 $cmol_c$ kg^{-1}). However, the *cerradão* soil has a higher clay content and greater water-holding capacity than the *cerrado* soil, potentially explaining the contrasting vegetation types at these adjacent sites (Marimon Junior & Haridasan, 2005). In the *cerrado* plot, the average tree height is 3.7 m, with a basal area of ~14.9 m^2 ha^{-1}, while in the *cerradão*, trees are taller on average (6.4 m) with a higher basal area (~ 21.4 m^2 ha^{-1}) (Marimon Junior & Haridasan, 2005). Both plots contain 77 tree species and similar tree densities (*cerrado* = 1890 trees, *cerradão* = 1884 trees) (Marimon Junior & Haridasan, 2005).

2.2 Site climate and the El Niño 2015/2016 event

We used climate variables—air temperature, relative air humidity, and precipitation—from a time series recorded at a meteorological station (World Weather Station 83319), located approximately 800 m from the plots. We calculated the maximum climatological water deficit (MCWD), a key measure of tropical forest water stress (see Aragão et al., 2007). For this calculation, we assumed a standardized evapotranspiration (ET) rate of 100 mm $month^{-1}$ for wet-season tropical forests (Aragão et al., 2007).

We used the hydrological year to define the period from May 2015 to April 2016 as representative of the climate conditions during the 2015-2016 El Niño Southern Oscillation event, based on Aragão et al. (2007) and Liu et al. (2017). During the event, the site experienced record-high mean annual and mean monthly maximum temperatures (26.0 °C and 35.4 °C, respectively) and record-low total annual precipitation (790.2 mm). Additionally, in September 2016, the annual MCWD reached a record low of -883.7 mm (Fig. 1; Table S1).

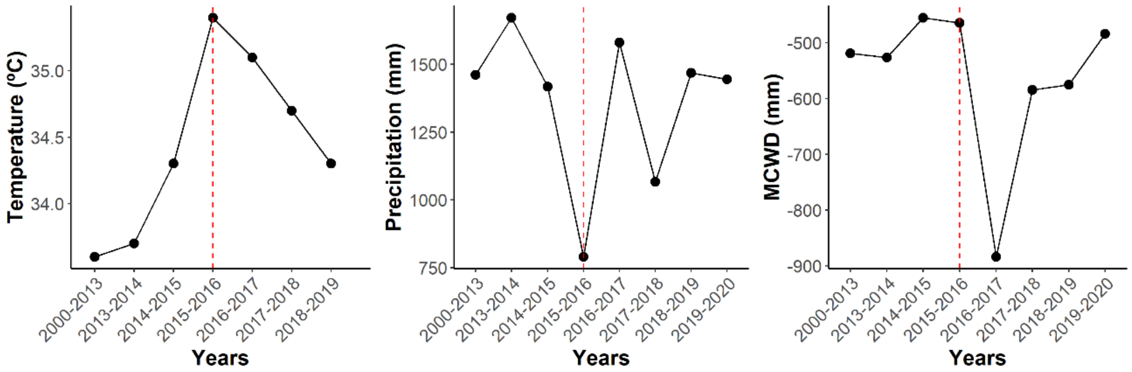

Fig. 1. Climate variables between 2000 and 2020 for *cerrado* and *cerradão*. We show (a) temperature (°C), (b) precipitation (mm/year) and (c) maximum climatological water deficit (MCWD, mm in a rolling year) with the 1st month of the dry season (May) representing the beginning of each year's climatic calendar. The temperature indicates the average maximum monthly temperatures. The dashed red line indicates the El Niño periods. Climatic data are from

meteorological station #83319 of the Brazilian National Institute of Meteorology (INMET). See Table S1 for data.

2.3 Field methods and measurement uncertainties

We followed the GEM protocol manual (Marthews et al., 2014; Malhi et al., 2021) to collect data for this study. We measured the main components of NPP, including canopy (leaves, twigs, reproductive parts, and others), wood (stems and branches), and fine roots. Additionally, we estimated other NPP components, such as canopy (leaf herbivory) and wood (coarse root). The field methods measurement and uncertainties are described below.

Litterfall net primary productivity ($NPP_{litterfall}$): We collected litterfall—dead organic material production (< 2 cm diameter)—every 14 days from January 2014 to December 2019. We used 0.2827 m2 circular collectors placed 1 m above the ground at the center of each of the 25 subplots in each plot (*cerradão* and *cerrado*). We separated litter into leaves, twigs, reproductive parts (flowers, fruits, and seeds), and unidentifiable material. We calculated $NPP_{litterfall}$ as: $NPP_{litterfall}$ = NPP_{canopy} – Loss to Leaf Herbivory. We oven-dried at 65°C to a constant mass, weighed it and then separated it into leaves, twigs, reproductive parts, and others. We estimated litter to contain 49.2% carbon, based on mean values from Amazonia (Patiño et al., 2012). We calculated errors as the standard error associated with variation among the litter traps (collectors).

Loss to leaf herbivory ($NPP_{herbivory}$): We estimated leaf herbivory loss based on Neyret et al. (2016), which observed that herbivory loss was 3.11% in NXV-01 and 4.43% in NXV-02. Data collection was conducted between March and May 2014. Each leaf's fractional herbivory (H) was calculated as H = (Anh – Ah) / Anh, where Ah is the area of each leaf, including the damage caused by herbivory, and Anh is the leaf area prior to herbivory (Neyret et al., 2016). We derived the average H value for all leaves collected per litterfall trap and then calculated plot-level means A systematic uncertainty of +50% was assigned to the values for error propagation.

Aboveground coarse wood net primary productivity (NPP_{stem}): To estimate stem NPP, we used the data measured every 2-3 years, collected between 2013 and 2020, in *cerradão* and *cerrado* plots. All trees ≥ 5 cm in diameter were surveyed to determine growth rate of surviving trees and rate of recruitment of new trees. The default measurement point was set at 30cm (DAS30cm) above soil surface, instead of a typical forest diameter at breast height at 1.3m. Biomass of each stem was calculated using Rezende et al. (2006) specific allometric equation for the Cerrado: C = 0.24564+0.01456*(D/10)2*H where C is aboveground Carbon stocks (kg), D is the diameter (30 cm above the soil), and H is the height (m). We measured the total height using a Leica DISTO laser measurement device. The authors assumed that dry stem biomass consists of 50% carbon. Systematic uncertainty of +25% was assigned to recognize systematic error in the use of allometry.

Branch turnover net primary productivity ($NPP_{branch\ turnover}$): Every three months, between 2014 and 2019, we collected branchfall > 2 cm diameter (excluding that associated with dead trees) within four 1 m x 100 m transects in each plot (*cerrado* and *cerradão*). Small branches were cut to include only the transect-crossing component, then removed and weighed. Larger branches had their dimensions taken (diameter at three points) and were assigned a wood density value according to decomposition class (Harmon et al., 1995). See RAINFOR-GEM manual (Marthews et al., 2014; p. 74) for a description of decomposition status and surface area formulas. Errors were calculated as the standard error associated with variation among transects.

Coarse root net primary productivity ($NPP_{coarse\ root}$): Root biomass was estimated based on Miranda et al. (2014) which is specific to the vegetation types of Cerrado. Based on this study, the Root(belowground) to shoot ratio (aboveground) biomass is 1.37 for *cerrado* and 0.22 for *cerradão*. A recent study using 144 plots found a similar relationship, with a root (belowground) to shoot (aboveground) biomass ratio of 1.58 in Brazilian savannas (Terra et al., 2023). Systematic uncertainty of +20% was assigned to values for error propagation. Although we did not measure this component, we find it useful to include this information given the scarcity of such estimates for savannas.

Fine root net primary productivity ($NPP_{fine\ root}$): Every three months, from September 2014 to February 2020, we collected fine roots in each plot (*cerradão* and *cerrado*) using sixteen ingrowth cores (mesh cages, 12 cm diameter, to 30 cm depth). Fine roots were manually removed from soil samples in four 10-minute time steps, following a method that corrects for the underestimation of hard-to-extract root biomass (Metcalfe et al., 2007). This method was used to predict root extraction beyond 40 minutes (up to 120 min); typically, an additional 33% correction factor was applied for fine roots not collected within 40 minutes. A correction for fine root productivity below 30 cm depth (Galbraith et al., 2013) increased the value by 39%. Errors were calculated as the standard error associated with variation among sampling points. Root-free soil was then reinserted into the ingrowth core. Collected roots were thoroughly rinsed, oven-dried at 65◦C to a constant mass, and weighed. This process was repeated for each subsequent measurement.

For total NPP (calculated as the sum of several components, see Equation 1 below), the uncertainty value is calculated by combining uncertainty of each component by error propagation (Hughes & Hase, 2010; Malhi et al., 2015). The uncertainty of each component is explained above.

2.4 NPP calculation

We measured the NPP in the two plots between 2014 and 2020, as described above. We calculated all major components of NPP using the following equations:

$NPP_{total} = NPP_{coarse\ root} + NPP_{fine\ root} + NPP_{stem} + NPP_{branch} + NPP_{litter\ fall} + NPP_{herbivory}$ (1)

$NPP_{canopy} = NPP_{litter\ fall} + NPP_{herbivory}$ (2)

$NPP_{woody} = NPP_{coarse\ root} + NPP_{stem} + NPP_{branch\ turnover}$ (3)

$NPP_{ACW} = NPP_{stem}$ (4)

NPPfine $_{root}$ = $NPP_{fine\ root}$ (5)

Our calculations above neglect several small NPP components, such as NPP lost through volatile organic compound emissions (NPP_{VOC}), unmeasured litter trapped in the canopy, or litter dropped from understorey flora below the litter traps (1 m). However, in central Amazonia, Malhi et al. (2009) found that NPP_{VOC} represents a relatively minor fraction of total NPP (0.13 + 0.06 Mg C ha^{-1} $year^{-1}$). For belowground NPP, we do not include root exudates and mycorrhizae, which contribute less than 2 Mg C ha^{-1} $year^{-1}$ and represent a modest portion of carbon fluxes (Malhi et al., 2017). Therefore, we focus on canopy, wood, and fine root productivity, which together account for over 85% of NPP (See Riutta et al., 2018 and their references).

We calculated the relative allocation to the main NPP components (woody, canopy, and fine roots NPP) for leaves, fine roots, and stems using the following equations:

$Allocation_x = (NPP_x * 100)/NPP_{total}$ (6)

2.5 Data analyses

Our analyses focused on comparing NPP across years (2014 to 2019), comprising the periods before, during, and after the El Niño 2015/2016 event, in both *cerrado* and *cerradão*. To compare total canopy NPP across years in each vegetation type (*cerradão* and *cerrado)*, we performed a repeated -measures ANOVA. The statistical model considered year as a fixed factor, while litter traps were included as a random effect to account for the hierarchical structure of the data over time. When significant differences were detected, we used Tukey's post hoc test to compare total canopy NPP between years. We applied the same analysis to compare stem and fine root NPP across different years in each plot. For stem NPP, we used subplots as random effects, and for fine roots NPP, we used ingrowth cores as random effects. In cases where residuals violated ANOVA assumptions, we applied Friedman's non-parametric test. We performed all analyses in the R environment, with a significance level of 0.05.

3 Results

3.1 Total NPP and its allocation

During the El Niño event, total NPP in *cerradão* decreased by 29% (6.6±0.6 Mg C ha^{-1} $year^{-1}$) and reaching a level similar to that of *cerrado* (6.6±1.3 Mg C ha^{-1} $year^{-1}$; Fig. 2; Table S2). By 2018, it remained 13% lower than pre-El Niño conditions (Fig. 2). In contrast, total NPP in the *cerrado* showed little variation before, during, and after the El Niño.

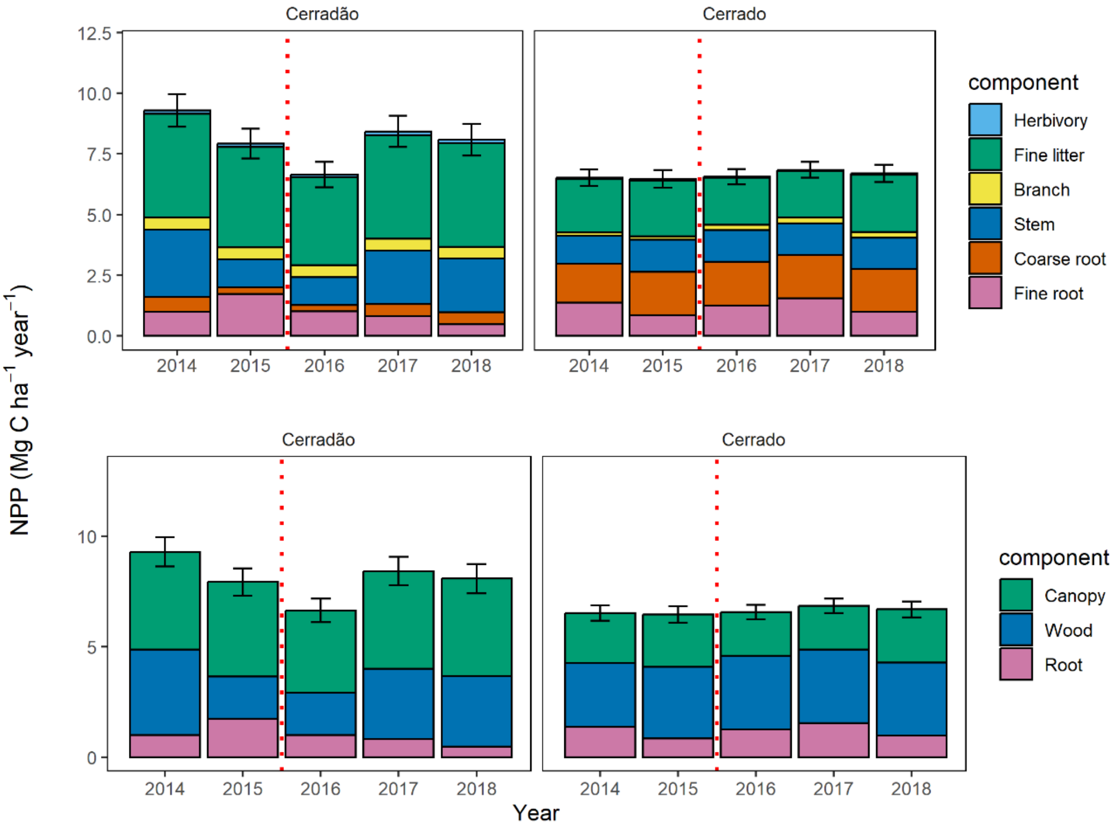

Fig. 2. Mean total annual net primary productivity (NPP) between 2014 and 2018 split into its components (a) and annual NPP allocation into the canopy, wood, and root components (b) at *cerradão* and *cerrado*. The branch data from *cerradão* was collected in 2014 and repeated in other years. The error bars represent the standard error for total NPP. The dashed red line indicates the El Niño periods.

Throughout the study period, NPP allocation in *cerrado* exhibited little interannual variation and showed no clear drought signal. The primary axis of interannual variation was between canopy investment and root allocation, while woody allocation remained constant (Figs. 2 and 3). However, in *cerradão*, a clear drought signal was observed, with increased investment in fine roots during the drought and reduced investment in woody growth. Canopy allocation remained relatively constant.

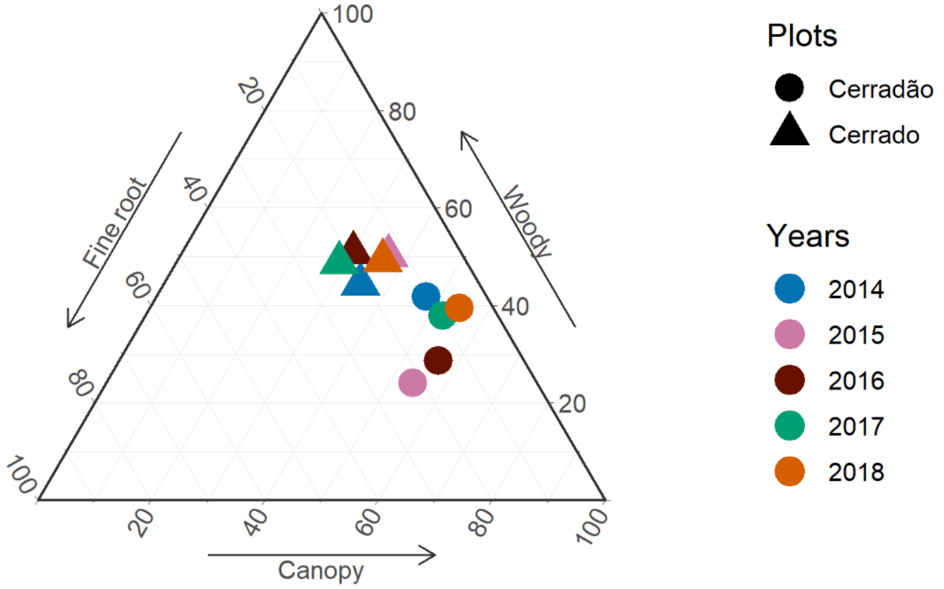

Fig. 3. Relative allocation (% of total) of net primary productivity (NPP) to canopy, woody, and fine root NPP in *cerrado* and *cerradão*. Woody components include stem, coarse root and branch turnover; Fine root includes fine root NPP only (no roots exudates); Canopy includes litterfall and herbivory.

3.2 Canopy NPP

Canopy productivity was affected after the El Niño event in both *cerradão* (F= 2.8, p= 0.01; -16.7%) and *cerrado* (F= 6.7, p< 0.001; -16.2%) (Fig. 4). However, NPP of this component had fully recovered within two years after the event. When analyzing leaf NPP, the primary component of NPP litterfall, the *cerrado* exhibited a pattern similar to total NPP litterfall, with a 13.2% decline in 2016, followed by recovery. In contrast, the *cerradão* showed a 12% increase in the year El Niño began, followed by a 28% decline in 2016 and subsequent fluctuations in the following years. Notably, in the *cerradão*, branch (twig) production increased following the event, and by 2018, its production had doubled compared to previous years.

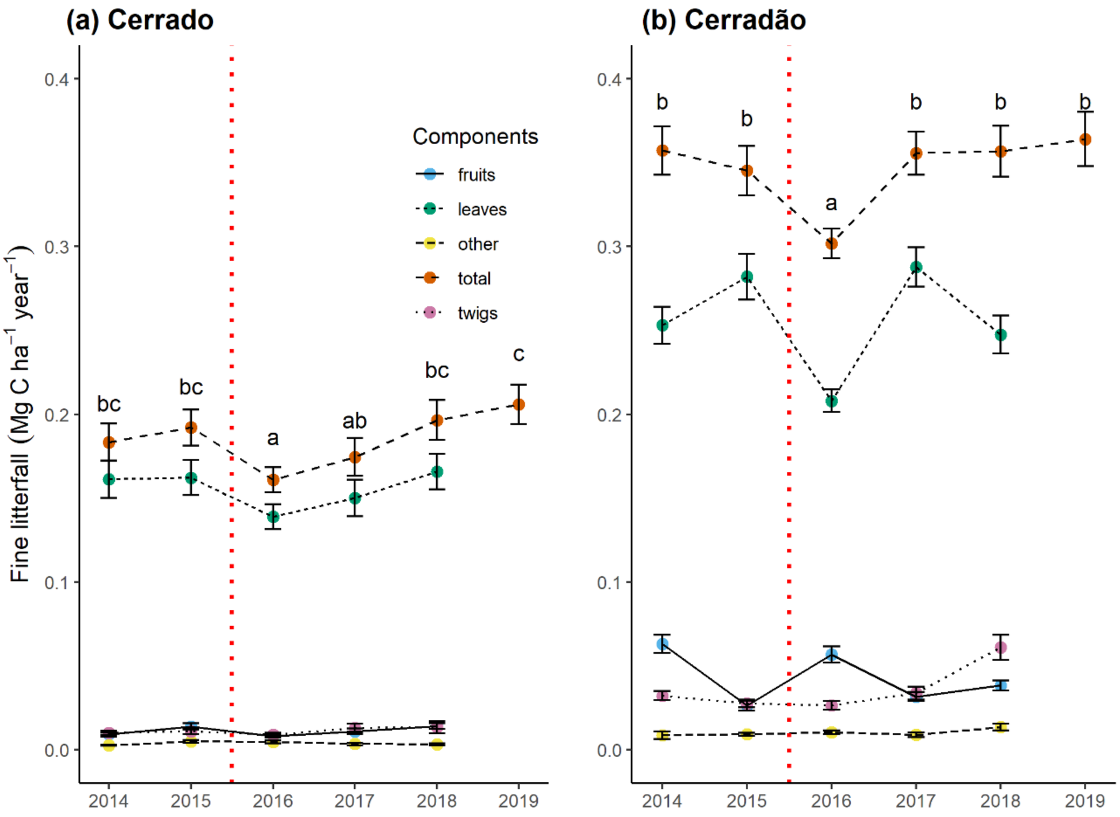

Fig. 4. Mean monthly productivity in canopy litterfall and its components for *cerrado* (a) and *cerradão* (b) between 2014 and 2019: (fruits) flower, fruit, and seed fall; (leaves) leaf fall; (other) not identified and (total) total canopy fine litterfall (as measured in litter traps); (twigs) twig fall (< 2 cm). The error bars represent the standard error. The dashed red line indicates the El Niño periods. Different letters denote significant differences between years in total canopy fine litterfall (Tukey post hoc test).

3.3 Stem NPP

In *cerradão*, the most affected component was stem net primary productivity (NPPs), which declined by 58% during and after El Niño (F= 15.6, p< 0.001; Fig. 5). By 2019, it remained 21% lower than pre-El Niño conditions. This decline was primarily driven by two key species in this transitional forest, *Hirtella glandulosa* Spreng. and *Tachigali vulgaris* L.G.Silva & H.C.Lima, which contributed 22% and 17% to NPPs after El Niño, respectively. Before the event, *T. vulgaris* was the dominant contributor to NPPs (26%). In *cerrado*, stem productivity was unaffected by the El Niño event (Fig. 5).

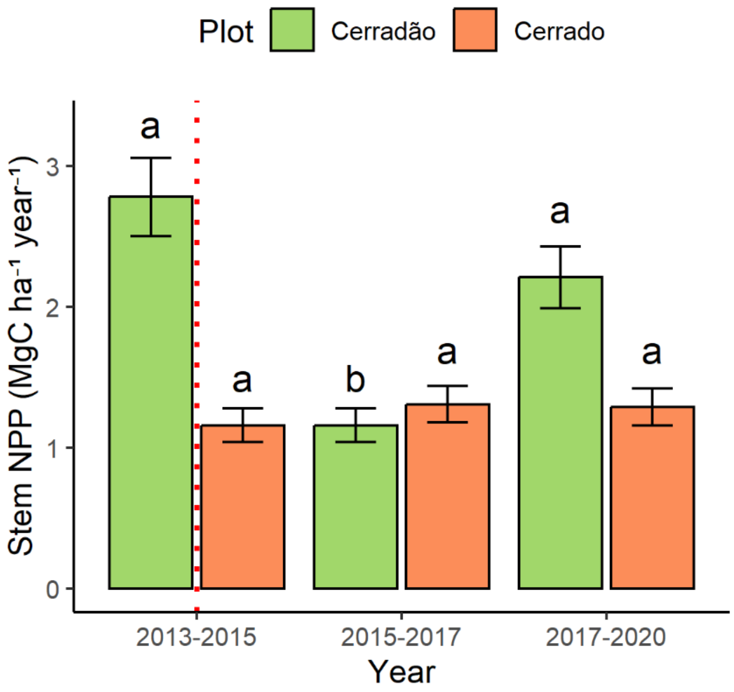

Fig. 5. Stem net primary productivity (NPP$_{stem}$, MgC ha^{-1} year^{-1}) for stems larger than 5cm diameter in *cerradão* and *cerrado*. The dashed red line indicates the El Niño periods. Different letters denote significant differences between years in each plot (Tukey post hoc test).

3.4 Fine root NPP

In *cerradão*, fine root net primary productivity (NPP$_{fr}$) increased significantly (+42%) during the El Niño event (F= 17.3, p< 0.001), but declined in the following years (Fig. 6). In contrast, *cerrado exhibited* the opposite pattern. NPP$_{fr}$ decreased by 38% during the event (F= 5.6, p= 0.001; Figs. 2 and 6). However, this component re-established itself shortly after the El Niño, but experienced another decline of approximately 38% in 2018.

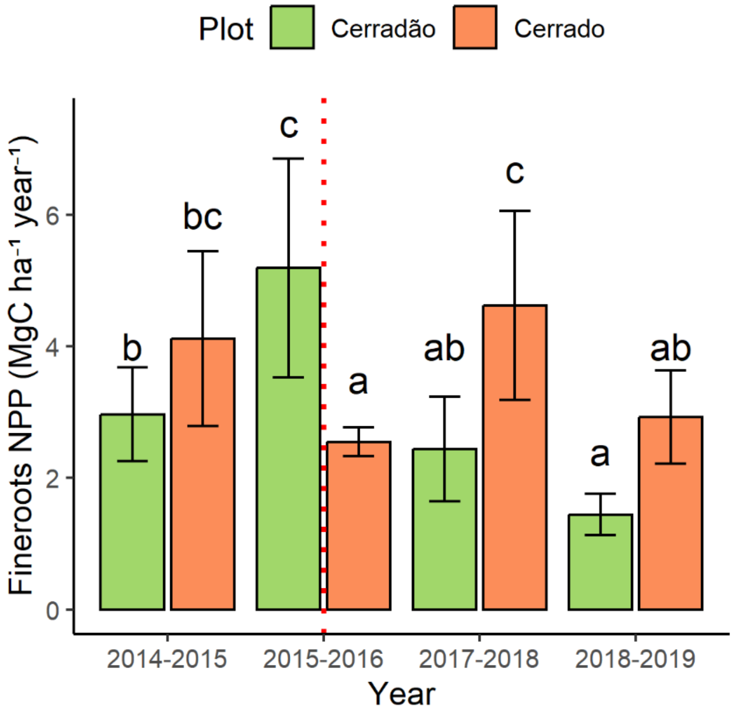

Fig. 6. Fine root net primary productivity (NPP$_{fr}$) for *cerrado* (light green) and *cerradão* (orange) between September 2014 and August 2019. The error bars represent the standard error. The dashed red line indicates the El Niño periods. Different letters denote significant differences between years in each plot (Tukey post hoc test).

4 Discussion

Cerradão and *cerrado* showed contrasting responses to the 2015/2016 El Niño-associated drought event. The *cerrado* appears to be more resistant, as total NPP and stem NPP were not impacted by the El Niño event, and the components that experienced a reduction (e.g., production of fine roots and canopy productivity) soon re-established themselves. In contrast, the *cerradão* exhibited lower resistance, as all NPP components were affected during the El Niño event, including total NPP and stem NPP. Furthermore, although most components recovered, fine root production remained significantly lower than pre-event levels (-51%), and stem production, while not statistically significant, was still 20% lower. Our findings demonstrate the high sensitivity of the *cerradão* to extreme drought events.

4.1 Total NPP and its allocation

The decline in total NPP during El Niño in the *cerradão* was primarily driven by reduced stem growth (-58%), followed by a decrease in fine litter production (-16%). Each of these parameters will be discussed in detail later. Total productivity of *cerradão* was more affected (-29%) than the Amazonian rainforest (-7.6% to -8.5%) during the El Niño drought of 2015/2016 (Machado-Silva et al., 2021). Moreover, the reduction in stem productivity was much larger (-58%; -1.62 Mg C ha^{-1}) than that estimated for tropical forests as a whole (-8.3% in 1997/1998, and -9% in 2015/2016; Rifai et al., 2018) and (-0.40 Mg C ha^{-1}; Bennet et al., 2023). This demonstrates the high sensitivity of this vegetation to climate anomalies.

NPP partitioning between canopy, wood and fine roots varies substantially within tropical ecosystems (Zhang-Zheng et al., 2024). Reports on NPP partitioning change under drought were very scarce. Doughty et al. (2014) found that NPP portioning to roots decreases while partitioning to leaves increases during drought. Whereas, we see such a pattern, only very slightly in *cerrado* in 2015. Our *cerradã*o site, however, shows a marked decrease in NPP partitioning to wood, which was not observed in Amazonia forests. One possibility is that these shifting strategies reflect points on an aridity continuum from sub-humid Amazonian forest through transitional or seasonally dry forests through to savanna. Alternatively, the differences in soil fertility may play a role, changing the costs and advantages of investment in fine-root production.

4.2 Canopy NPP

The *cerradão* adopted the strategy of shedding more leaves at the onset of El Niño. However, both cerradão and *cerrado* showed a significant reduction in leaf litter production toward the end of the event (Fig. 4). The observed patterns in leaf litter production suggest that both *cerradão* and *cerrado* responded to the extreme drought conditions induced by the 2015–2016 El Niño, but with distinct temporal dynamics. The early onset of leaf shedding in the *cerradão* indicates a shift in its typical phenological strategy, likely as an adaptive response to water stress, since full or partial deciduousness, along with strong stomatal regulation, appears to be a common water regulation strategy during the dry season for *cerrado* species but not for *cerradão* species (Araújo et al., 2021a; Jancoski et al., 2022). The accelerated leaf abscission at the beginning of El Niño may have functioned as a short-term mechanism to reduce transpiration and prevent excessive hydraulic stress.

Despite these initial adjustments, both vegetation types exhibited a marked decline in leaf litter production toward the end of the event, suggesting that prolonged drought imposed significant physiological constraints on canopy maintenance. This reduced litterfall could be attributed to a combination of factors, including lower overall canopy productivity, leaf damage resulting from extended drought stress, or a decrease in new leaf formation. During periods of soil water stress, it is well known that plants often shed their leaves as a strategy to minimize water loss and avoid potential mortality (e.g., Brando et al., 2008). This leaf loss likely contributed to the observed decline in litterfall, as the plants prioritize conserving water over maintaining canopy coverage. Interestingly, this leaf loss strategy can also have benefits for nutrient cycling; when leaves drop, the nutrients they contain are released into litter layer and soil, where they can be reabsorbed by the plants as they re-establish leaf growth after the high-stress period (e.g., Oliveira et al., 2017). Thus, while the reduction in litterfall may initially appear detrimental, it can also facilitate nutrient availability for future growth, highlighting the complex interactions between water stress, leaf dynamics, and ecosystem productivity. This response aligns with findings from other tropical and subtropical ecosystems, where extreme drought events disrupt typical phenological cycles and lead to declines in aboveground productivity (Sippel et al., 2018; Duan et al., 2018). The convergence in response at the end of El Niño highlights the widespread impact of severe climatic anomalies on carbon allocation strategies in the Cerrado biome. While *cerradão* species initially adjusted by shedding more leaves, the prolonged water deficit ultimately constrained their ability to maintain productivity, leading to reductions in leaf turnover similar to those observed in the *cerrado*. This suggests that, despite differences in initial strategies, extreme drought events may override ecosystem-specific adaptations, emphasizing the vulnerability of both vegetation types to future increases in climate variability.

4.3 Stem NPP

The results indicating a significant decline in stem net primary productivity (NPPs) in the cerradão during and after the El Niño event highlight the vulnerability of this ecosystem to extreme climatic conditions. The 58% reduction in NPPs, along with the continued 21% decrease by 2019 compared to pre-El Niño conditions, suggests that the structural integrity and growth potential of the dominant species in this transitional forest were notably compromised. This decline can be attributed primarily to two dominant species, *Hirtella glandulosa* and *Tachigali vulgaris*, which play crucial roles in the ecological dynamics of the *cerradão* (Reis et al., 2015; 2017). The significant contribution of *H. glandulosa* to NPPs after the El Niño event (22%) indicates that while this species was able to maintain some level of productivity, it still suffered under the adverse conditions imposed by the drought. Meanwhile, *T. vulgaris*, which was the dominant contributor to NPPs prior to the event (26%), experienced a decline in its growth or survivorship, reflecting its sensitivity to prolonged drought stress (Prestes et al., 2024). This shift in species dominance and productivity highlights the intricate interdependencies among species within the *cerradão*, emphasizing the importance of specific species in maintaining overall forest productivity.

In contrast, the *cerrado* exhibited a resilience in stem productivity during the same climatic event, with no significant changes noted (F= 1.3, P=0.28). This resilience may be attributed to the inherent differences in water-use strategies between the two ecosystems. The *cerrado*, characterized by its conservative water-use strategies, may have been better adapted to cope with the drought conditions brought about by El Niño, allowing for sustained stem productivity (Jancoski et al., 2022; Araújo et al., 2023). The contrasting responses of stem NPPs between these ecosystems underscore the potential for differential impacts of climate extremes, driven by the distinct ecological strategies employed by their resident species. The decline in stem NPPs in the *cerradão* has implications for carbon storage and overall ecosystem health. As stem productivity is closely linked to biomass accumulation, the reduced NPPs could lead to long-term alterations in carbon dynamics within this forest type. Additionally, decreased stem growth may affect the structural complexity of the forest, with potential consequences for habitat provision and biodiversity. The persistent reduction in stem productivity even after the El Niño event suggests a lagged response in the ecosystem's recovery, possibly due to lingering effects of drought stress or nutrient limitations. This highlights the need for further monitoring of these ecosystems to understand recovery trajectories and to inform conservation strategies.

4.4 Fine root NPP

The observed changes in fine root net primary productivity (NPP_{fr}) during the El Niño event reveal significant differences in how the *cerradão* and *cerrado* ecosystems respond to extreme climatic conditions. In the *cerradão*, there was a notable increase in fine root NPP_{fr} of 42% during the El Niño event ($F = 17.3$, $P < 0.001$). This increase suggests that the *cerradão*, characterized by taller trees and greater leaf area (Araújo et al., 2023), may have adapted to drought conditions by investing more resources into fine root growth. This response could be a strategy to enhance water absorption capabilities during a period of soil elevated atmospheric demand and potential soil moisture deficits (Metcalfe et al., 2008). However, this strategy does not ameliorate drought risk, as tree mortality was high (Prestes et al., 2024) despite a high investment in fine roots. Yet, following the El Niño event, NPP_{fr} in the *cerradão* declined in subsequent years. This decline may indicate that the initial increase in root production could not be sustained in the long term due to prolonged drought stress or nutrient limitations, leading to a reduction in overall root biomass and productivity.

The *cerrado*, on the other hand, exhibited an opposite pattern, with a marked reduction in NPP_{fr} during the El Niño. This reduction in fine root productivity suggests that the *cerrado*, which typically employs a more conservative water-use strategy (Araújo et al., 2021b, 2023), experienced greater stress during the drought. The decrease in fine root NPP_{fr} may reflect the challenges these species faced in maintaining root function under extreme conditions, resulting in a lower investment in root growth. The strategy observed in the *cerrado* was similar to that of tropical dry forests, reflecting root phenological patterns linked to water availability (Kummerow et al., 1990; Kavanagh & Kellman, 1992). Interestingly, after the El Niño event, fine root productivity in the *cerrado* re-established itself, indicating some level of resilience and recovery. However, this recovery was short-lived, as NPP_{fr} experienced another decline of approximately 38% in 2018. This subsequent decline may be attributed to the residual effects of the El Niño event, including persistent water deficits or nutrient availability issues, which may have hindered the full recovery of fine root productivity.

5 Conclusions

Cerradão is an important transitional vegetation type within the Amazon-Cerrado ecotone, connecting two of Brazil's major biomes: the Cerrado and the Amazon. However, this vegetation type is highly vulnerable to climatic events (as shown in the present study), wildfires (Reis et al., 2015; 2017), and windstorms (Reis et al., 2022). One of its most dominant trees, *T. vulgaris*, which plays a key role in carbon uptake, showed strong sensitivity to El Niño events. Thus, if these extreme drought events continue to become more frequent and intense, the *cerradão* may release more carbon than it absorbs, consistent with a regional scale atmospheric result for south-east Amazonia (Gatti et al., 2021). Moreover, as a transitional zone between the Cerrado and the Amazon, the *cerradão* plays an important role in maintaining the ecological balance along this interface. Our results suggest that the increasing frequency of El Niño events could disrupt this transition, creating conditions for the progressive degradation of forests along the edges of the

Amazon. This highlights the urgent need for actions to mitigate the impacts of climate change in this sensitive region.

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Competing interests

The contact author has declared that none of the authors has any competing interests.

References

Alvares, C. A., Stape, J. L., Sentelhas, P. C., Gonçalves, J. D. M., & Sparovek, G. (2013). Köppen’s climate classification map for Brazil. Meteorologische Zeitschrift, 22(6), 711-728.

Aragão, L. E. O., Malhi, Y., Roman-Cuesta, R. M., Saatchi, S., Anderson, L. O., & Shimabukuro, Y. E. (2007). Spatial patterns and fire response of recent Amazonian droughts. Geophysical Research Letters, 34(7).

Araújo, I., Marimon, B. S., Scalon, M. C., Fauset, S., Junior, B. H. M., Tiwari, R., ... & Gloor, M. U. (2021a). Trees at the Amazonia-Cerrado transition are approaching high temperature thresholds. Environmental Research Letters, 16(3), 034047.

Araújo, I., Marimon, B. S., Scalon, M. C., Cruz, W. J., Fauset, S., Vieira, T. C., ... & Gloor, M. U. (2021b). Intraspecific variation in leaf traits facilitates the occurrence of trees at the Amazonia–Cerrado transition. Flora, 279, 151829.

Araújo, I., Scalon, M. C., Amorim, I., Menor, I. O., Cruz, W. J., Reis, S. M., ... & Marimon, B. S. (2023). Morpho-anatomical traits and leaf nutrient concentrations vary between plant communities in the Cerrado–Amazonia transition?. Flora, 306, 152366.

Araújo, I., Marimon, B. S., Junior, B. H. M., Oliveira, C. H., Silva, J. W., Beú, R. G., ... & Galbraith, D. R. (2024). Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests. Environmental and Experimental Botany, 226, 105905.

Ball, R. A. (2010). Ecophysiological leaf traits of Cerrado woody plants. University of Alberta. 105p. https://era.library.ualberta.ca

Bennett, A. C., Rodrigues de Sousa, T., Monteagudo-Mendoza, A., Esquivel-Muelbert, A., Morandi, P. S., Coelho de Souza, F., ... & Phillips, O. L. (2023). Sensitivity of South American tropical forests to an extreme climate anomaly. Nature Climate Change, 13(9), 967-974.

Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., & Camargo, P. (2008). Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philosophical Transactions of the Royal Society B: Biological Sciences, 363, 1839-1848.

Chen, J. M., & Cihlar, J. (1995). Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. IEEE transactions on geoscience and remote sensing, 33(3), 777-787.

Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. Frontiers in plant science, 4, 442.

Covey, K., Soper, F., Pangala, S., Bernardino, A., Pagliaro, Z., Basso, L., ... & Elmore, A. (2021). Carbon and beyond: The biogeochemistry of climate in a rapidly changing Amazon. Frontiers in Forests and Global Change, 4, 11.

Doughty, C. E., Malhi, Y., Araujo-Murakami, A., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., ... & Ledezma, R. (2014). Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought. Ecology, 95(8), 2192-2201.

Duan, S., He, H. S., & Spetich, M. (2018). Effects of growing-season drought on phenology and productivity in the west region of central hardwood forests, USA. Forests, 9(7), 377.

Fan, L., Wigneron, J. P., Ciais, P., Chave, J., Brandt, M., Fensholt, R., ... & Peñuelas, J. (2019). Satellite-observed pantropical carbon dynamics. Nature plants, 5(9), 944-951.

Feldpausch, T. R., Phillips, O. L., Brienen, R. J. W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., ... & Vos, V. A. (2016). Amazon forest response to repeated droughts. Global Biogeochemical Cycles, 30(7), 964-982.

ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., ... & De Araujo, R. O. (2021). Taking the pulse of Earth's tropical forests using networks of highly distributed plots. Biological Conservation, 260, 108849. https://doi.org/10.1016/j.biocon.2020.108849

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D., Doughty, C. E., Fisher, R. A., ... & Lloyd, J. (2013). Residence times of woody biomass in tropical forests. Plant Ecology & Diversity, 6(1), 139-157.

Gatti, L. V., Basso, L. S., Miller, J. B., Gloor, M., Gatti Domingues, L., Cassol, H. L., ... & Neves, R. A. (2021). Amazonia as a carbon source linked to deforestation and climate change. Nature, 595(7867), 388-393.

Gloor, E., Wilson, C., Chipperfield, M. P., Chevallier, F., Buermann, W., Boesch, H., ... & Sullivan, M. J. (2018). Tropical land carbon cycle responses to 2015/16 El Niño as recorded by atmospheric greenhouse gas and remote sensing data. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1760), 20170302.

Harmon, M. E., Whigham, D. F., Sexton, J., & Olmsted, I. (1995). Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. Biotropica, 305-316.

Hughes, I. G., & Hase, T. P. A. (2010). Measurements and their uncertainties: A practical guide to modern error analysis. Oxford: Oxford University Press.

Jancoski, H. S. (2019). Características morfofuncionais de árvores em resposta à sazonalidade climática e herbivoria na transição Cerrado-Amazônia. Universidade do Estado de Mato Grosso. 89p. https://portal.unemat.br/media/files/halina-soares.pdf

Jancoski, H.S., Schwantes Marimon, B., C. Scalon, M., de V. Barros, F., Marimon-Junior, B. H., Carvalho, E., ... & Oliveras Menor, I. (2022). Distinct leaf water potential regulation of tree species and vegetation types across the Cerrado–Amazonia transition. Biotropica, 54(2), 431-443.

Jiménez-Muñoz, J. C., Mattar, C., Barichivich, J., Santamaría-Artigas, A., Takahashi, K., Malhi, Y., ... & Van Der Schrier, G. (2016). Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. Scientific reports, 6(1), 1-7.

Kavanagh, T., & Kellman M. (1992). Seasonal Pattern of Fine Root Proliferation in a Tropical Dry Forest. Biotropica, 24, 157.

Kummerow, J., Castillanos, J., Maas, M., & Larigauderie, A. (1990). Production of fine roots and the seasonality of their growth in a Mexican deciduous dry forest. Vegetatio, 90, 73-80.

Liu, J., Bowman, K. W., Schimel, D. S., Parazoo, N. C., Jiang, Z., Lee, M., ... & Eldering, A. (2017). Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. Science, 358(6360).

Machado-Silva, F., Peres, L. F., Gouveia, C. M., Enrich-Prast, A., Peixoto, R. B., Pereira, J. M., ... & Libonati, R. (2021). Drought resilience debt drives NPP decline in the Amazon Forest. Global Biogeochemical Cycles, 35(9), e2021GB007004.

Malhi, Y., Aragao, L. E. O., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., ... & Teixeira, L. M. (2009). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Global Change Biology, 15(5), 1255-1274.

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A., Marthews, T. R., ... & Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Global Change Biology, 21(6), 2283-2295.

Malhi, Y., Girardin, C. A., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., ... & Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. New Phytologist, 214(3), 1019-1032.

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E., Rifai, S. W., ... & Phillips, O. L. (2021). The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. Biological Conservation, 253, 108889.

Marimon Junior, B. H., & Haridasan, M. (2005). Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado sensu stricto em áreas adjacentes sobre solo distrófico no leste de Mato Grosso, Brasil. Acta Botanica Brasilica, 19, 913-926.

Marimon, B. S., Lima, E. S., Duarte, T. G., Chieregatto, L. C., & Ratter, J. A. (2006). Observations on the vegetation of Northeastern Mato Grosso, Brazil. IV. An analysis of the Cerrado-Amazonian Forest ecotone. Edinburgh Journal of Botany, 63, 323-341.

Marimon, B. S., Marimon-Junior, B. H., Feldpausch, T. R., Oliveira-Santos, C., Mews, H. A., Lopez-Gonzalez, G., ... & Phillips, O. L. (2014). Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. Plant Ecology & Diversity, 7(1-2), 281-292.

Marques, E. Q., Marimon-Junior, B. H., Marimon, B. S., Matricardi, E. A., Mews, H. A., & Colli, G. R. (2020). Redefining the Cerrado–Amazonia transition: implications for conservation. Biodiversity and conservation, 29(5), 1501-1517.

Marthews, T. R., Riutta, T., Oliveras-Menor, I., Urrutia, R., Moore, S., Metcalfe, D., … & Cain, R. (2014). Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v3.0). Global Ecosystems Monitoring Network, Oxford.

Matricardi, E. A. T., Skole, D. L., Costa, O. B., Pedlowski, M. A., Samek, J. H., & Miguel, E. P. (2020). Long-term forest degradation surpasses deforestation in the Brazilian Amazon. Science, 369(6509), 1378-1382.

Metcalfe, D. B., Meir, P., Aragao, L. E. O. C., Malhi, Y., Da Costa, A. C. L., Braga, A., ... & Williams, M. (2007). Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. Journal of Geophysical Research: Biogeosciences, 112(G4).

Metcalfe, D. B., Meir, P., Aragão, L. E. O., da Costa, A. C., Braga, A. P., Gonçalves, P. H., ... & Williams, M. (2008). The effects of water availability on root growth and morphology in an Amazon rainforest. Plant and Soil, 311(1), 189-199.

Miller, J. B. (1967). A formula for average foliage density. Australian Journal of Botany, 15, 141-144.

Miranda, S. D. C., Bustamante, M., Palace, M., Hagen, S., Keller, M., & Ferreira, L. G. (2014). Regional variations in biomass distribution in Brazilian savanna woodland. Biotropica, 46(2), 125-138.

Morandi, P. S., Marimon-Junior, B. H., De Oliveira, E. A., Reis, S. M., Valadão, M. X., Forsthofer, M., ... & Marimon, B. S. (2015). Vegetation succession in the Cerrado–Amazonian forest transition zone of Mato Grosso state, Brazil. Edinburgh Journal of Botany, 73(1), 83-93.

Morandi, P. S., Marimon, B. S., Eisenlohr, P. V., Marimon-Junior, B. H., Oliveira-Santos, C., Feldpausch, T. R., ... & Phillips, O. L. (2016). Patterns of tree species composition at watershed-scale in the Amazon ‘arc of deforestation’: implications for conservation. Environmental Conservation, 43(4), 317-326.

Neyret, M., Bentley, L. P., Oliveras, I., Marimon, B. S., Marimon-Junior, B. H., Almeida de Oliveira, E., ... & Malhi, Y. (2016). Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients in light of community assembly. Ecology and evolution, 6(16), 5674-5689.

Nobis, M., & Hunziker, U. (2005). Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agricultural and forest meteorology, 128(3-4), 243-250.

Nogueira, D. S., Marimon, B. S., Marimon-Junior, B. H., Oliveira, E. A., Morandi, P., Reis, S. M., … & Phillips, O. L. (2019). Impacts of Fire on Forest Biomass Dynamics at the Southern Amazon Edge. Environ. Conserv. 46, 285-292.

Oliveira, B., Marimon Junior, B. H., Mews, H. A., Valadão, M. B. X., & Marimon, B. S. (2017). Unraveling the ecosystem functions in the Amazonia–Cerrado transition: evidence of hyperdynamic nutrient cycling. Plant Ecology, 218(2), 225-239.

Oliveras, I., & Malhi, Y. (2016). Many shades of green: the dynamic tropical forest–savannah transition zones. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1703), 20150308.

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., ... & Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. Proceedings of the National Academy of Sciences, 115(29), 7551-7556.

Palmer, P. I. (2018). The role of satellite observations in understanding the impact of El Nino on the carbon cycle: current capabilities and future opportunities. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1760), 20170407.

Patiño, S., Fyllas, N. M., Baker, T. R., Paiva, R., Quesada, C. A., Santos, A. J. B., ... & Lloyd, J. (2012). Coordination of physiological and structural traits in Amazon forest trees. Biogeosciences, 9(2), 775-801.

Peixoto, K. S., Marimon-Junior, B. H., Marimon, B. S., Elias, F., de Farias, J., Freitag, R., ... & Malhi, Y. (2017). Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and CO2 soil efflux in cerradao forest undergoing ecological succession. Acta oecologica, 82, 23-31.

Peixoto, K. D. S., Marimon-Junior, B. H., Cavalheiro, K. A., Silva, N. A., das Neves, E. C., Freitag, R., ... & Valadao, M. B. X. (2018). Assessing the effects of rainfall reduction on litterfall and the litter layer in phytophysiognomies of the Amazonia–Cerrado transition. Brazilian Journal of Botany, 41(3), 589-600.

Pérez-Ramos, I. M., Volaire, F., Fattet, M., Blanchard, A., & Roumet, C. (2013). Tradeoffs between functional strategies for resource-use and drought-survival in Mediterranean rangeland species. Environmental and Experimental Botany, 87, 126-136.

Phillips, O. L., Aragão, L. E., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., ... & Torres-Lezama, A. (2009). Drought sensitivity of the Amazon rainforest. Science, 323(5919), 1344-1347.

Powers, J. S., Vargas G, G., Brodribb, T. J., Schwartz, N. B., Pérez-Aviles, D., Smith-Martin, C. M., ... & Medvigy, D. (2020). A catastrophic tropical drought kills hydraulically vulnerable tree species. Global Change Biology, 26(5), 3122-3133.

Ratter, J. A., Richards, P. W., Argent, G., & Gifford, D. R. (1973). Observations on the vegetation of northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 266(880), 449-492.

Reis, S. M., Lenza, E., Marimon, B. S., Gomes, L., Forsthofer, M., Morandi, P. S., ... & Elias, F. (2015). Post-fire dynamics of the woody vegetation of a savanna forest (Cerradão) in the Cerrado-Amazon transition zone. Acta Botanica Brasilica, 29, 408-416.

Reis, S. M., de Oliveira, E. A., Elias, F., Gomes, L., Morandi, P. S., Marimon, B. S., ... & Lenza, E. (2017). Resistance to fire and the resilience of the woody vegetation of the “Cerradão” in the “Cerrado”–Amazon transition zone. Brazilian Journal of Botany, 40(1), 193-201.

Reis, S. M., Marimon, B. S., Marimon Junior, B. H., Morandi, P. S., Oliveira, E. A. D., Elias, F., ... & Phillips, O. L. (2018). Climate and fragmentation affect forest structure at the southern border of Amazonia. Plant Ecology & Diversity, 11(1), 13-25.

Reis, S. M., Marimon, B. S., Esquivel-Muelbert, A., Marimon Jr, B. H., Morandi, P. S., Elias, F., ... & Phillips, O. L. (2022). Climate and crown damage drive tree mortality in southern Amazonian edge forests. Journal of Ecology, 110(4), 876-888.

Reis, S. (2023). Savanna is more resistant and resilient to tropical drought than transitional forest. Dryad Dataset: https://doi.org/10.5061/dryad.rjdfn2zhw

Rezende, A. V., Vale, A. D., Sanquetta, C. R., Figueiredo Filho, A., & Felfili, J. M. (2006). Comparação de modelos matemáticos para estimativa do volume, biomassa e estoque de carbono da vegetação lenhosa de um cerrado sensu stricto em Brasília, DF. Scientia Forestalis, 71(2), 65-73.

Ribeiro, J. F., Walter, B. M. T. (2008). As principais fitofisionomias do bioma Cerrado. Cerrado Ecologia e Fauna. Brasília: Embrapa Informação Tecnológico 1, 153 – 221.

Rifai, S. W., Girardin, C. A., Berenguer, E., del Aguila-Pasquel, J., Dahlsjö, C. A., Doughty, C. E., ... & Malhi, Y. (2018). ENSO Drives interannual variation of forest woody growth across the tropics. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1760), 20170410.

Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M., ... & Ewers, R. M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. Global Change Biology, 24(7), 2913-2928.

Scalon, M. C., Oliveras Menor, I., Freitag, R., Peixoto, K. S., Rifai, S. W., Marimon, B. S., ... & Malhi, Y. (2022). Contrasting strategies of nutrient demand and use between savanna and forest ecosystems in a neotropical transition zone. Biogeosciences, 19(15), 3649-3661.

Schleppi, P., Conedera, M., Sedivy, I., & Thimonier, A. (2007). Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. Agricultural and Forest Meteorology, 144(3-4), 236-242.

Silvério, D. V., Brando, P. M., Bustamante, M. M., Putz, F. E., Marra, D. M., Levick, S. R., & Trumbore, S. E. (2019). Fire, fragmentation, and windstorms: A recipe for tropical forest degradation. Journal of Ecology, 107(2), 656-667.

Sippel, S., Reichstein, M., Ma, X., Mahecha, M. D., Lange, H., Flach, M., & Frank, D. (2018). Drought, heat, and the carbon cycle: a review. Current Climate Change Reports, 4, 266-286.

Zhang-Zheng, H., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Addo-Danso, S. D., Amissah, L., ... & Malhi, Y. (2024). Contrasting carbon cycle along tropical forest aridity gradients in West Africa and Amazonia. Nature Communications, 15(1), 3158.