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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 hottest and most intense 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 on 5 years of productivity of the dominant vegetation types in the Cerrado, namely savanna (*cerrado*) and transitional forest–savanna (*cerradão*), continuously tracked before, during, and after the El Niño. Between 2014 and 2019, we carried out intensive monitoring 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, which was reduced 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 terms of the allocation of productivity to canopy, wood, and fine-root production. Our findings demonstrate that the *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.

1 Introduction

The 2015–2016 El Niño event led to some of the most intense tropical droughts in 100 years, as well as record maximum temperatures, occurring on top of decades of long-term warming (Jiménez-Muñoz et al., 2016; Liu et al., 2017). While the 2015–2016 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, 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, in particular, requires high-fidelity process-based measurements that are sustained over time. These are exceptionally challenging to conduct and require long-term dedication to measurements before, during, and after major climate events like the 2015–2016 El Niño.

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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 ($\sim 41\,\%$ 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 toward 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 reductions 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, with the typical *cerrado* (referred to as *cerrado* hereafter) and woodland savanna (i.e., *cerradão*) being the most common in the regions (Ratter et al., 1973; Marimon et al., 2006; Oliveras and Malhi, 2016). Despite co-existing in the same space, the *cerrado* and *cerradão* vegetation formations show contrasting characteristics (Marimon Junior and Haridasan, 2005; Marimon et al., 2006). The *cerradão* is a transitional forest–savanna characterized by a closed canopy; an understory formed by small shrubs and herbs, with few grasses; and an average height of the tree stratum that varies from 8 to 15 m, with tree cover of 50 % to 90 % (Ribeiro and Walter, 2008; Oliveras and Malhi 2016), while the *cerrado* is a savanna vegetation type with a discontinuous canopy; trees and shrubs with a grass understory; and a low average height of just 3 to 6 m, with tree cover of 20 % to 50 % (Marimon Junior and Haridasan, 2005; Ribeiro and Walter, 2008).

In the *cerrado*, most species are deciduous, shedding their leaves during the dry season, whereas, in the *cerradão*, brevideciduous and/or evergreen species predominate (Ribeiro and Walter, 2008). This phenological difference has direct implications for the tolerance to water and thermal stress. The *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, 2023). In contrast, trees in the *cerradão* group 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 the *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 deficits, 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 for *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 outlined below.

1. Did the 2015–2016 El Niño affect total productivity and the productivity and partitioning of different compartments (canopy, stem, and fine root) in the *cerradão* and *cerrado*?

   We hypothesize the following:

   - *H1. Cerrado* and *cerradão* NPPs 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 that this was more severe 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 systems, 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 re-sprouting 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 the *cerradão* (a transitional forest–savanna) and another in the *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 ∼ 300 m 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 the Brazilian National Institute of Meteorology (INMET) (station no. 83319), the mean monthly temperature is 24.8 °C, and 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 and Haridasan, 2005).

Each plot covers 1 ha and was established in 2002 (Marimon Junior and Haridasan, 2005), with multiple re-censuses having been 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 and Haridasan, 2005; Marimon et al., 2014; Scalon et al., 2022). Partial carbon cycles 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 and 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 understory, and two dominant tree species: *Qualea parviflora* Mart. and *Davilla elliptica* A.St.-Hil. (Marimon Junior and 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 ($Ca^{2+} \sim 0.4$ cmolc kg^{-1}), with high levels of exchangeable aluminum ($Al^{3+} > 1.3$ $cmol_c$ 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 and 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 and Haridasan, 2005). Both plots contain 77 tree species and similar tree densities (1890 trees in the *cerrado* and 1884 trees in the *cerradão*) (Marimon Junior and 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 per month 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 and 35.4 °C, respectively) and record-low total annual precipitation (790.2 mm). Additionally, in September 2016, the an-

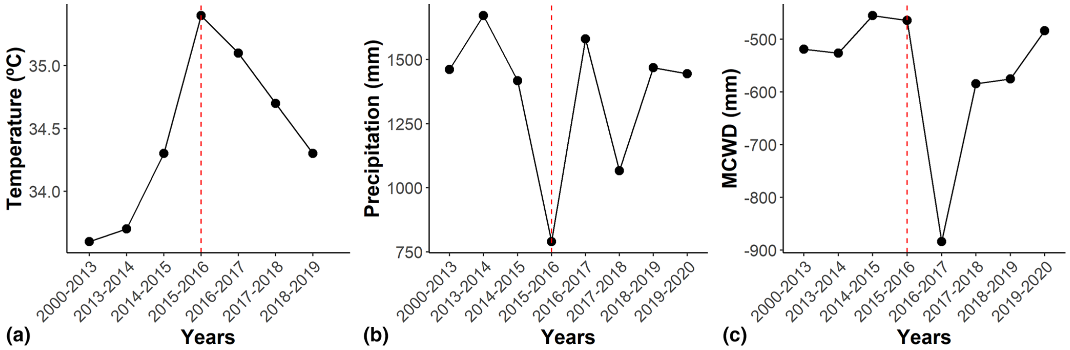

Figure 1. Climate variables between 2000 and 2020 for the *cerrado* and *cerradão*. We show **(a)** temperature (°C), **(b)** precipitation ($\mathrm{mm\,yr^{-1}}$), and **(c)** maximum climatological water deficit (MCWD, mm in a rolling year), with the first month of the dry season (May) representing 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 no. 83319 of the Brazilian National Institute of Meteorology (INMET). See Table S1 in the Supplement for data.

nual MCWD reached a record low of −883.7 mm (Fig. 1; Table S1 in the Supplement).

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 method measurements and uncertainties are described below.

- *Litterfall net primary productivity* ($NPP_{\mathrm{litterfall}}$). We collected litterfall – dead organic material production (< 2 cm diameter) – every 14 d from January 2014 to December 2019. We used $0.2827\,\mathrm{m^2}$ 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 $\mathrm{NPP_{litterfall}}$ as follows: $\mathrm{NPP_{litterfall}} = \mathrm{NPP_{canopy}} - \mathrm{loss}$ 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* ($NPP_{\mathrm{herbivory}}$). We estimated leaf herbivory loss based on Neyret et al. (2016), who 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 $H = (\mathrm{Anh} - \mathrm{Ah})\,/\,\mathrm{Anh}$, 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 the *cerradão* and *cerrado* plots. All trees ≥ 5 cm in diameter were surveyed to determine the growth rate of surviving trees and the rate of recruitment of new trees. The default measurement point was set at 30 cm (DAS30cm) above the soil surface instead of a typical forest diameter at breast height of 1.3 m. The biomass of each stem was calculated using the specific allometric equation of Rezende et al. (2006) for the Cerrado: $C = 0.24564 + 0.01456 \times (D/10)2 \times H$, where C is the 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. A systematic uncertainty of +25 % was assigned to recognize systematic error in the use of allometry.
- *Branch turnover net primary productivity* ($NPP_{\mathrm{branch\ turnover}}$). Every 3 months, between 2014 and 2019, we collected branchfall > 2 cm diameter (excluding that associated with dead trees) within four 1 m × 100 m transects in each plot (*cerrado* and *cerradão*). Small branches were cut to include only the transect-crossing component and then were 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 the RAINFOR-GEM manual (Marthews et al., 2014, p. 74) for a description of the decomposition status and surface area formulas. Errors were calculated as the standard error associated with the variation among transects.

- *Coarse-root net primary productivity* ($NPP_{\text{coarse root}}$). Root biomass was estimated based on Miranda et al. (2014), specific to the vegetation types of the Cerrado. Based on this study, the ratio of the root (belowground) to shoot (aboveground) biomass is 1.37 for the *cerrado* and 0.22 for the *cerradão*. A recent study using 144 plots found a similar relationship, with a ratio of the root (belowground) to shoot (aboveground) biomass of 1.58 in Brazilian savannas (Terra et al., 2023). A 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* ($NPP_{\text{fine root}}$). Every 3 months, from September 2014 to February 2020, we collected fine roots in each plot (*cerradão* and *cerrado*) using 16 ingrowth cores (mesh cages: 12 cm diameter, 30 cm depth). Fine roots were manually removed from soil samples in four 10 min 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 min (up to 120 min); typically, an additional 33 % correction factor was applied for fine roots not collected within 40 min. 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 the 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 Eq. (1) below), the uncertainty value is calculated by combining the uncertainty of each component by error propagation (Hughes and 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:

$$\begin{aligned}\mathrm{NPP}_{\text{total}} =& \mathrm{NPP}_{\text{coarse root}} + \mathrm{NPP}_{\text{fine root}} + \mathrm{NPP}_{\text{stem}} \\ &+ \mathrm{NPP}_{\text{branch}} + \mathrm{NPP}_{\text{litter fall}} + \mathrm{NPP}_{\text{herbivory}}, \end{aligned} \tag{1}$$

$$\mathrm{NPP}_{\text{canopy}} = \mathrm{NPP}_{\text{litter fall}} + \mathrm{NPP}_{\text{herbivory}}, \tag{2}$$

$$\mathrm{NPP}_{\text{woody}} = \mathrm{NPP}_{\text{coarse root}} + \mathrm{NPP}_{\text{stem}} + \mathrm{NPP}_{\text{branch turnover}}, \tag{3}$$

$$\mathrm{NPP}_{\text{ACW}} = \mathrm{NPP}_{\text{stem}}, \tag{4}$$

$$\mathrm{NPPfine}_{\text{root}} = \mathrm{NPP}_{\text{fine root}}. \tag{5}$$

The calculations above neglect several small NPP components, such as NPP lost through volatile organic compound emissions ($\mathrm{NPP}_{\mathrm{VOC}}$), unmeasured litter trapped in the canopy, or litter dropped from understory flora below the litter traps (1 m). However, in central Amazonia, Malhi et al. (2009) found that $\mathrm{NPP}_{\mathrm{VOC}}$ represents a relatively minor fraction of total NPP ($0.13 + 0.06\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$). For belowground NPP, we do not include root exudates and mycorrhizae, which contribute less than $2\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ 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-root NPP) for leaves, fine roots, and stems using the following equation:

$$\mathrm{Allocation}_x = (\mathrm{NPP}_x \times 100)/\mathrm{NPP}_{\text{total}}. \tag{6}$$

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-measure ANOVA. The statistical model considered the year to be 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-root 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 the *cerradão* decreased by 29 % ($6.6 \pm 0.6\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) and reached a level similar to that of the *cerrado* ($6.6 \pm 1.3\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$; 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.

Throughout the study period, NPP allocation in the *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 the *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.

3.2 Canopy NPP

Canopy productivity was affected after the El Niño event in both the *cerradão* ($F = 2.8$, $p = 0.01$, $-16.7\,\%$) and the *cerrado* ($F = 6.7$, $p < 0.001$, $-16.2\,\%$) (Fig. 4). However, the NPP of this component had fully recovered within 2 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 the 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.

3.3 Stem NPP

In the *cerradão*, the most affected component was stem net primary productivity (NPP), which declined by 58 % during and after the 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 and H.C. Lima, which contributed 22 % and 17 % to NPP after the El Niño, respectively. Before the event, *T. vulgaris* was the dominant contributor to NPP (26 %). In the *cerrado*, stem productivity was unaffected by the El Niño event (Fig. 5).

3.4 Fine-root NPP

In the *cerradão*, fine-root net primary productivity ($\mathrm{NPP_{fr}}$) increased significantly ($+42\,\%$) during the El Niño event ($F = 17.3$, $p < 0.001$) but declined in the following years (Fig. 6). In contrast, the *cerrado* exhibited the opposite pattern. $\mathrm{NPP_{fr}}$ 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.

4 Discussion

The *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 the 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. The total productivity of the *cerradão* was more affected ($-29\,\%$) than that of 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 ($-58\,\%$; $-1.62\,\mathrm{Mg\,C\,ha^{-1}}$) than that estimated for tropical forests as a whole ($-8.3\,\%$ in 1997–1998 and $-9\,\%$ in 2015–2016, Rifai et al., 2018; $-0.40\,\mathrm{Mg\,C\,ha^{-1}}$, Bennett 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 changes under drought were very scarce. Doughty et al. (2014) found that NPP portioning to roots decreases while partitioning to leaves increases during drought. On the other hand, we see such a pattern only very slightly in the *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 the El Niño. However, both the *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 *cer-*

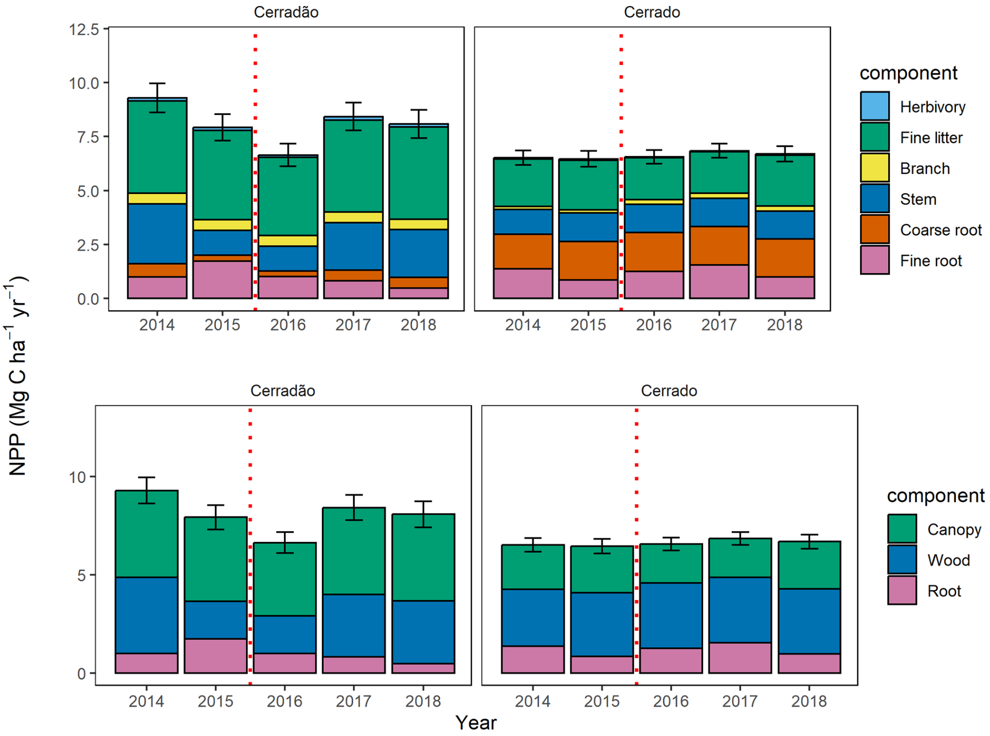

Figure 2. Mean total annual net primary productivity (NPP) between 2014 and 2018, split into its components (above) and annual NPP allocation into the canopy, wood, and root components (below) for the *cerradão* and *cerrado*. The branch data from the *cerradão* were collected in 2014 and repeated in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

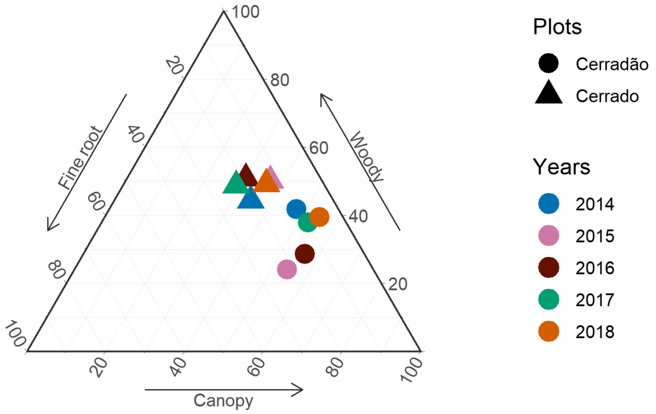

Figure 3. Relative allocation (% of total) of net primary productivity (NPP) to canopy, woody, and fine-root NPP in the *cerrado* and *cerradão*. Woody components include stems, coarse roots, and branch turnover. Fine root includes fine-root NPP only (no root exudates). Canopy includes litterfall and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

rado 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 the 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 the 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

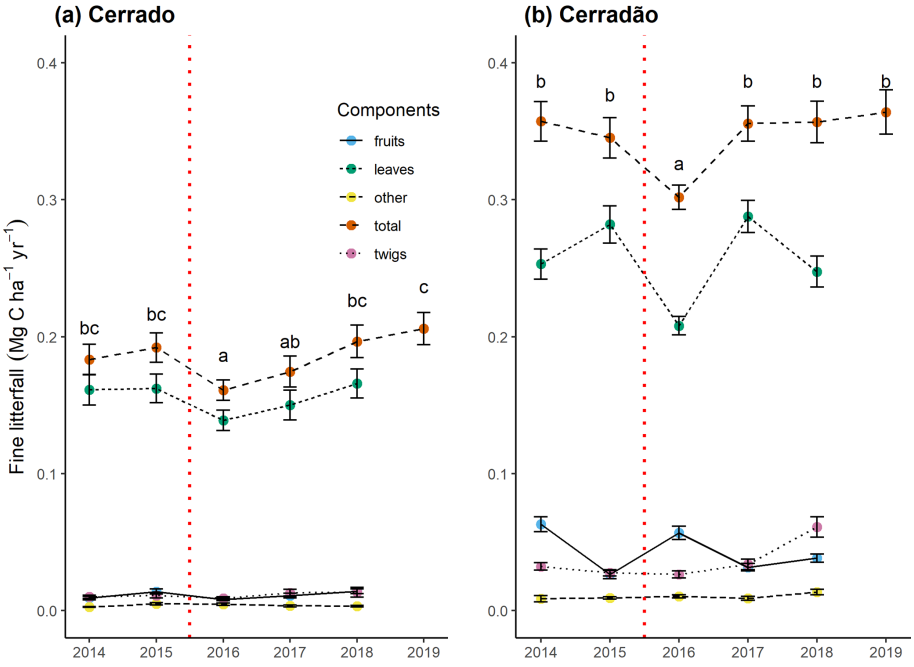

Figure 4. Mean monthly productivity in canopy litterfall and its components for the *cerrado* (**a**) and *cerradão* (**b**) between 2014 and 2019: fruits – flower, fruit, and seed fall; leaves – leaf fall; other – not identified; total – total canopy fine litterfall (as measured in litter traps); and 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's post hoc test).

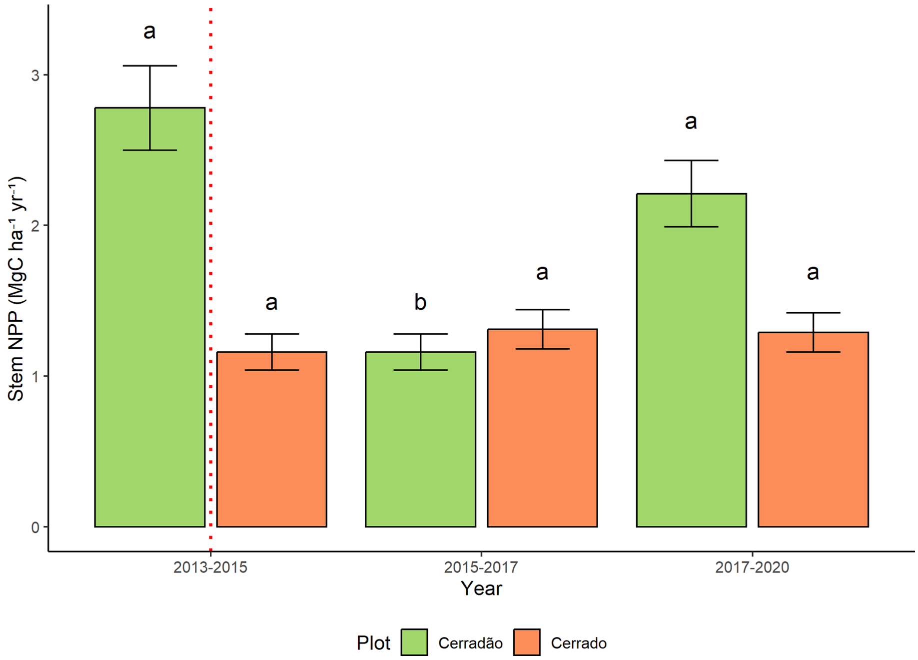

Figure 5. Stem net primary productivity (NPP$_{\text{stem}}$, Mg C ha^{-1} yr^{-1}) for stems larger than 5 cm diameter in the *cerradão* and *cerrado*. The dashed red line indicates the El Niño periods. Different letters denote significant differences between years in each plot (Tukey's post hoc test).

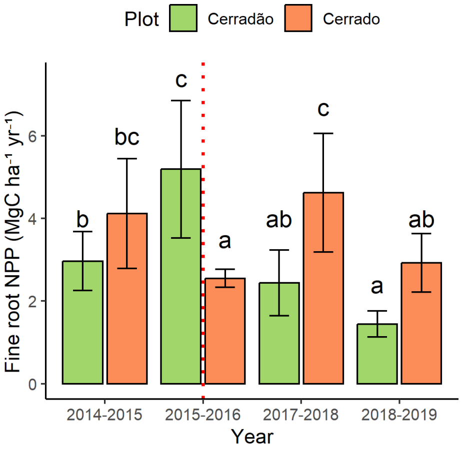

Figure 6. Fine-root net primary productivity (NPP_{fr}) for the *cerrado* (light green) and *cerradão* (orange) between September 2014 and August 2019. The error bars represent the standard error. The dashed red line indicates the El Niño periods. Different letters denote significant differences between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

the reduction in litterfall may initially appear to be 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 the 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 (NPP) in the *cerradão* during and after the El Niño event highlight the vulnerability of this ecosystem to extreme climatic conditions. The 58 % reduction in NPP, 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 NPP 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 NPP 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 the El Niño, allowing for sustained stem productivity (Jancoski et al., 2022; Araújo et al., 2023). The contrasting responses of stem NPP 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 NPP in the *cerradão* has implications for carbon storage and overall ecosystem health. As stem productivity is closely linked to biomass accumulation, the reduced NPP 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, $\mathrm{NPP}_{\mathrm{fr}}$ 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 $\mathrm{NPP}_{\mathrm{fr}}$ 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 $\mathrm{NPP}_{\mathrm{fr}}$ 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 and 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 $\mathrm{NPP}_{\mathrm{fr}}$ 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, consistently with a regional-scale atmospheric result for southeastern 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.

Data availability. The data used to produce the figures are available as a data package on ForestPlots.net: https://doi.org/10.5521/2025_4 (Reis et al., 2025) and in the Supplement. The data used to do the analyses are available on request from ForestPlot.net: https://www.forestplots.net/en/join-forestplots/working-with-data (ForestPlots.net, 2025).

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

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