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). ~~Before the El Niño total productivity was ~25% higher in the cerradão compared to the cerrado. However, c~~*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~~one~~ of the most intense tropical droughts in a hundred years~~of the last century~~ 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 t~~T~~he 2015-16 climate anomaly affected most of the tropics it~~but~~ was especially ~~potent~~ strong in ~~t~~South and Central America~~he Neotropics Amazonia (~~(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~~the productivity of savanna ecosystems is affected by El Niño events, especially~~ in the extensive Amazonia-Cerrado transition in South America. This

~~The Amazonia-Cerrado transitional region~~ contains a mixture of Amazon~~ia~~ 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~~is~~ 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~~the~~ long-term trend to longer~~lengthening of the~~ dry season (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~~carbon~~ dynamics here.

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The~~is~~ 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, completely ~~fully~~ shedding their leaves during~~in~~ the dry season, whereas in the~~while most~~ *cerradão*, ~~species are~~ 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~~Although the dominant species of both vegetation types show strong stomatal efficiency (Jancoski et al., 2022), trees in the *cerrado* have~~ smaller stomata and higher trichome density, which reduce~~than individuals occurring in the *cerradão*, anatomical features that help the leaves minimise their~~ 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).

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Among~~Furthermore, for~~ species that co-occur in both vegetation types~~cerrado and cerradão~~, individuals in *cerrado* shed~~lose~~ their leaves earlier ~~than *cerradão*~~ in the dry season than those in the cerradão, ~~. The early loss of leaves~~ a strategy that prevents damage to ~~in the *cerrado* means that the~~ photosynthetic apparatus ~~is not harmed~~ 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, ~~individuals take longer to lose their leaves, which~~ making~~es~~ them more vulnerable~~sensitive~~ to rising ~~changes in~~ temperatures~~ increases~~, both under current conditions and in future ~~and~~ projections~~ed~~ (Araújo et al., 2021a~~b~~). Trees in the ~~C~~c*erradão* ~~trees~~ are also taller than those in the *cerrado* ~~trees~~, a trait that may increase their ~~this characteristic may offer *cerradão* greater~~ sensitivity to drought.~~,~~ T~~since t~~aller 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~~*under review*~~). 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~~These~~ characteristics ~~(such ase.g., larger stomata, and greater maximum stomatal pore opening, and lower water loss control)~~ suggests ~~thatmay give the~~, of *cerradão* vegetation may make it more susceptible to ~~be more affected by extremegreater sensitivity to disturbances generated by climateic disturbancesanomalies, such as the 2015-2016 El Niño, when~~ market significant temperature increases and prolonged water deficits.

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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~~se~~ two vegetation types. Our guiding questions and hypotheses are: ~~1) Does productivity and allocation differ between *cerradão* and *cerrado*? 2~~**1) D~~How d~~id the 2015-2016 El Niño affect total productivity~~ and~~, productivity and partitioning of different compartments (canopy, stem and fine root)~~allocation~~ 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). ~~3) Did the *cerradão* and *cerrado* regain productivity after the El Niño? 42) How NPPWhat are the trade-offs in resource partitioningallocation between canopy, wood and fine roots change during El Niñodrought in the two vegetation types?~~ **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).

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2 Materials and Methods

2.1 Study sites

We conducted this study in two long-term plots: one in *cerradão* (a transitional forest-savanna~~; NXV-02, Forestplots code~~) and another in *cerrado* (*typical cerrado*; savanna~~ – NXV-01~~), both located in Bacaba Municipal Park, ~~in~~ 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 ~~~about~~ 300m apart, they experience similar climatic conditions, classified as ~~which corresponds to the~~ *Aw* (tropical with dry winters) ~~type~~ in Köppen's ~~classification~~ 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~~As measured by station #83319 of the~~ 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 ~~, and the~~ average altitude ~~of the park~~ 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 ~~The~~ plot~~s~~ covers 1 hectare and was~~ere~~ established in 2002 (Marimon Junior & Haridasan, 2005), with multiple~~and have been~~ re-censuses~~d~~ conducted since then~~multiple times~~. 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~~collaborations~~.~~, and~~ S~~s~~ince 2014, they have also been integrated into the GEM network~~part of GEM~~ (Global Ecosystems Monitoring network; Malhi et al., 2021). These plots have supported numerous~~facilitated multiple~~ studies on topics~~,~~ including~~such as~~ soil properties, species composition and diversity~~ of species~~, biomass, nutrient allocation, and tree dynamics (e.g., Marimon Junior & Haridasan, 2005; Marimon et al., 2014; Scalon et al., 2022). Partial ~~data on~~ carbon cycle~~ing~~ ~~have previously been published~~ for the cerradão plot, including~~on~~ litterfall, soil CO_2 efflux and carbon stocks in~~at~~ 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~~the carbon cycling~~ in both plots, along with~~as well as~~ an extended time series that sheds light on~~provides insight into~~ the aftermath of the 2015/2016 El Niño event.

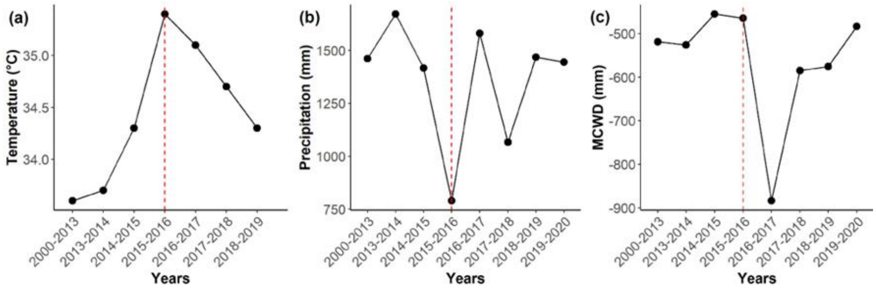
The plots have remained fire-free~~not been burned~~ since 2008. The *cerradão* plot is a transitional forest-savanna ecosystem with ~~characterized by the~~ overlapping ~~of~~ savanna and forest species, a closed canopy, and ~~with~~ dominant species such as ~~(notably~~ *Hirtella glandulosa* Spreng. and *Tachigali vulgaris* L.G. Silva & H.C. Lima~~)~~. ~~This type of *cerradão* was recognised by~~ Ratter et al. (1973) classified this vegetation type as *Hirtella glandulosa cerradão*. In contrast, the cerrado plot is characterized by an open canopy with t~~T~~rees and shrubs, a ~~with~~ grass understorey, and ~~open canopy characterize the *cerrado*. Here the~~ two dominant tree species: ~~are~~ *Qualea parviflora* Mart. and *Davilla elliptica* A.St.-Hil. (Marimon Junior & Haridasan, 2005; Marimon et al., 2014). However, t~~T~~he cerrado vegetation has been densifying, with reduced~~of the *cerrado* is becoming denser and there are not many~~ grass~~es~~ cover~~presen(Morandi et al., 2015)~~, possibly due to fire exclusion (Morandi et al., 2015).

~~The s~~Soil properties are~~is~~ similar across the plots, consisting of ~~—~~sandy loams classified as~~of the~~ yellow latosol~~ type~~, 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}).~~ — h~~ However, the *cerradão* soil has a~~presents~~ higher ~~percentages of~~ clay content and greater ~~potential~~ water-holding capacity than the *cerrado* soil, potentially explaining the contrasting vegetation types at these adjacent sites (Marimon Junior & Haridasan, 2005). ~~These differences in soil texture may explain the different vegetation formations in these two closely adjacent sites.~~ In t~~T~~he cerrado plot, the average tree height ~~of the trees in *cerrado*~~ is 3.7 m, with~~and~~ a basal area of ~14.9 m^2 ha^{-1}, while in~~.~~ ~~For~~ the *cerradão*, ~~the average~~ trees are taller on average ~~height is (~~6.4 m) with a higher~~and~~ basal area ~~of~~ (~ 21.4 m^2 ha^{-1}~~-~~) (Marimon Junior & Haridasan, 2005). Both plots contain~~The species number was~~ 77 tree species and ~~in both and the number of trees~~ similar tree densities (*cerrado* = 1890 trees, ~~and~~ *cerradão* = 1884 trees) (Marimon Junior & Haridasan, 2005).

2.2 Site climate and the El Niño 2015/2016 event

We used ~~the~~ climate variables— ~~–~~air temperature, relative air humidity, and precipitation— ~~–~~from a~~in~~ time series recorded at~~from~~ a m~~M~~eteorological s~~S~~tation (World Weather Station 83319), located approximately~~about~~ 800 m from the plots. We calculated the maximum climatological water deficit (MCWD), a key~~climatological~~ measure of tropical forest water stress (see Aragão et al., 2007). For this ~~To~~ calculati~~one~~on ~~MCWD~~, we assumed~~considered~~ a standardized evapotranspiration (ET) rate~~value~~ ~~for wet season tropical forests~~ of 100 mm month^{-1} for wet-season tropical forests (Aragão et al., 2007).

~~The seasonality of the plots is marked by two well-defined seasons – cooler-dry (April to September) and hot-rainy (October to March).~~ We used the hydrological year to define~~d~~ the period~~twelve months~~ from May 2015 to April 2016 as representative of the climate conditions during ~~of~~ the 2015-2016 El Niño Southern Oscillation event, based on Aragão et al. (2007) and Liu et al. (2017). During the ~~the El Niño~~event, the site~~plots~~ experienced record-high mean annual and mean monthly maximum ~~annual~~ temperatures (26.0 °C and 35.4 °C, respectively) and record-low total annual precipitation (790.2 mm). Additionally, ~~, and~~ in September 2016, the ~~record low~~ annual MCWD reached a record low of ~~(~~-883.7 mm~~)~~ (Fig. 1; Table S1).



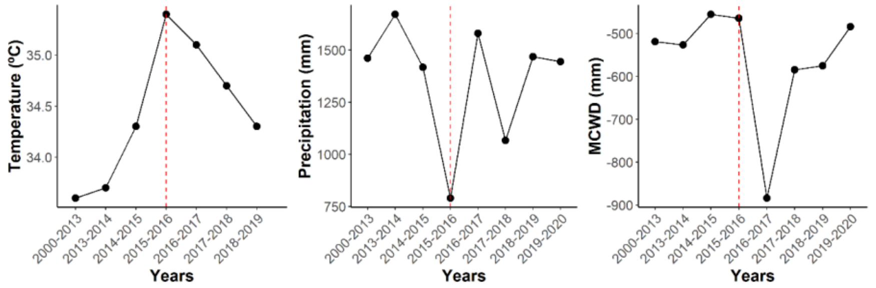


Fig. 1. Climate variables between 2000 and 2020 for *cerrado* and *cerradão*. We show~~uld~~ (a) temperature (°C), (b) precipitation (mm/year) and (c) maximum climatological water deficit (MCWD, mm in a rolling year) with the 1st month of the dry season (May) representing the

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 ~~the~~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~~(see Table 1)~~. 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 (NPPlitterfall): 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 NPPlitterfall as: NPPlitterfall = NPPcanopy – 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 (NPPherbivory): 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 (NPPstem): 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 (NPPbranch 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 (NPPcoarse 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 (NPPfine 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 the uncertainty value is calculated by error propagation with standard quadrature rules (Hughes & Hase, 2010; Malhi et al., 2015). The uncertainty of each component is explained above.

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~~**Table 1**. Field methods for intensive monitoring of NPP components from *cerradão* (NXV-02) and *cerrado* (NXV-01) plots in the transition zone between Amazonia and Cerrado. See also the RAINFOR-GEM manual (Marthews et al., 2014). nc= no collected.~~

~~**Component**~~	~~**Description**~~	~~**Sampling period**~~	~~**Sampling interval**~~
~~**Above-ground net primary productivity (*NPP*AG) and biomass**~~			

~~Aboveground coarse wood net primary productivity (*NPP*$_{stem}$) and Stem biomass~~	~~**Forest inventory** or plot census were done in the years listed. The default measurement point was set at 30cm (DAS$_{30cm}$) above soil surface, instead of a typical forest diameter at breast height at 1.3m. All trees ≥ 5 cm DAS30cm were censused, based on which, we calculated mortality and recruitment rate of new trees. **Stem biomass** for each tree was calculated. The sum of all alive trees in each census is termed stem biomass. As we have noticed trees stem shrinking, we calculate stem NPP as the change of alive trees biomass between two censuses, where dead and new recruit trees are excluded but shrinking trees are included. We have also presented 'Stem Diameter growth' which excludes shrinking trees, dead trees and new recruit trees. In 2014, five 10 m x 10 m subplots were established to census small trees (≤ 5 cm DAS30cm) to estimate the biomass fraction of smaller trees and data scaled up to 1 ha. Standing dead trees biomass is measured using similar method and not counted in Stem Biomass.~~ ~~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). The authors assumed that dry stem biomass is 50% carbon. Systematic uncertainty of +25% was assigned to values for error propagation. Errors calculated as the sampling error associated with variation between the transects.~~	~~2013 – 2021 (NXV-01)~~ ~~2013 – 2020 (NXV-02)~~	~~2013, 2015, 2018 and 2021 (NXV-01)~~ ~~2013, 2015, 2017 and 2020 (NXV-02)~~
~~Branch turnover net primary productivity (*NPP*$_{branch\ turnover}$)~~	~~Branchfall > 2 cm diameter (excluding that associated with dead trees) surveyed within four 1 m x 100 m transects; small branches were cut to include only the transect-crossing component, removed, and weighed. Larger branches had their dimensions taken (diameter at three points), and assigned a wood density value according to decomposition class (Harmon et al., 1995). Biomass of each branch was calculated. The first collection of branchfall in 2014 lead to 'woody debris biomass', which accounts for nacromass in the ground litter layer. 'Woody debris biomass' is not included in above nor belowground biomass. The biomass of branch has been implicitly included in *NPP*$_{stem.}$ Branchfall was then~~	~~2014 – 2019~~	~~Every 3 months~~

	~~collected from the same transects every 3 months which lead to $NPP_{\text{branch turnover}}$~~		
~~Litterfall net primary productivity ($NPP_{\text{litterfall}}$)~~	~~Litterfall production of dead organic material (< 2 cm diameter) calculated by collecting litterfall in 0.2827 m^2 circular collectors placed at 1 m above the ground at the center of each of the 25 subplots in each plot. Litter separated into leaves, twigs, reproductive parts (flowers, fruits, and seeds), and unidentifiable. $NPP_{\text{litterfall}}$ calculated as follows: $NPP_{\text{litterfall}} = NPP_{\text{canopy}}$ – Loss to Leaf Herbivory. Litterfall separated into different components, oven-dried at 65°C to constant mass, and weighed. Litter estimated to be 49.2% carbon, based on mean Amazonia values (S. Patiño, unpublished analysis). Errors calculated as the sampling error associated with variation between the litter traps.~~	~~Jan 2014 – Dec 2019~~	~~Every 14 days~~
~~Leaf Area Index (LAI)~~ ~~and Leaf biomass~~	~~Hemispherical photos taken with a digital camera (Nikon OP 10mm) and hemispherical lens (Nikon 10mm fisheye lens) near the center of each of the 25 subplots in each plot at a standard height of 1 m and during overcast conditions. LAI estimated from these images using Hemisfer software (licensed version 2.12; http://www.wsl.ch/dienstleistungen/produkte/software/hemisfer/index_EN). LAI estimated from hemispherical photos using the standard Li-Cor LAI-2000 method, based on the Miller (1967) equations, and correcting for non-linearity and slope effects (Schleppi et al., 2007) and canopy clumping (Chen & Cihlar, 1995). Thresholds were set to detect separately for each ring (6 rings) according to Nobis & Hunziker (2005). Errors calculated as the sampling error through variation among subplots. Leaf **biomass** calculated as leaf area index (LAI)/specific leaf area (SLA), where LAI is the plot mean over the study period, and SLA is the basal area-weighted plot mean over the study period. We used the SLA value of March 2014 (Neyret et al., 2016).~~	~~Jun 2015 – Jan 2020~~	~~Every 3 months~~

~~Loss to leaf herbivory ($NPP_{herbivory}$)~~	~~Estimated based on Neyret et al. (2016)'s observation that the loss to herbivory was 3.11% in NXV-01 and 4.43% in NXV-02. The data collection was conducted between March and May 2014. Each leaf's fractional herbivory (H) was calculated as $H = (A_{nh} – A_{h}) / A_{nh.}$ Where $A_{h,}$ is the area of each leaf, including the damage incurred by herbivory, and $A_{nh,}$ is the leaf area prior to herbivory (Neyret et al., 2016). The average value of H of all leaves collected per litterfall trap was derived, and plot-level means were calculated. Systematic uncertainty of ±50% assigned to values for error propagation.~~	~~nc~~	~~nc~~
~~Below-ground net primary productivity (NPP_{BG})~~			
~~Coarse root net primary productivity ($NPP_{coarse\ root}$)~~	~~Root biomass estimated based on Miranda et al. (2014) that is specific for the vegetation types of Cerrado. Based on this study, the Root(belowground): shoot ratio (aboveground) biomass is 1.37 to *cerrado* and 0.22 to *cerradão*. Systematic uncertainty of ±20% assigned to values for error propagation. We used these ratios, 1.37 (at NXV-01) and 0.22 (at NXV-02) to derive $NPP_{coarse\ root}$ from NPP_{stem}~~	~~nc~~	~~nc~~
~~Fine root net primary productivity ($NPP_{fine\ root}$) and fine root biomass~~	~~In each plot, sixteen ingrowth cores (mesh cages 12 cm diameter, to 30 cm depth) were installed. Roots were manually removed from the soil samples in four 10 min time steps, according to a method that corrects for underestimation of biomass of hard-to-extract roots (Metcalfe et al., 2007) and used to predict root extraction beyond 40 min (up to 120 min); typically, there was an additional 33% correction factor for fine roots not collected within 40 min. Correction for fine roots productivity below 30 cm depth (Galbraith et al., 2013) increased the value by 39%. Errors were calculated as the sampling error associated with variation between the sampling points.~~ ~~Root-free soil was then re-inserted into the ingrowth core. Collected roots were thoroughly rinsed, oven-dried at 65°C to constant mass, and weighed. This process was repeated for each measurement thereafter.~~ **~~Fine root biomass~~** ~~was calculated from harvested fine roots during the first installation of ingrowth. The subsequent fine root collection from the ingrowth cores lead to $NPP_{fine\ root}$~~	~~Sep 2014 – Feb 2020~~	~~Every 3 months~~

2.4 NPP calculation

We measured the NPP in the two plots between 2014 and 2020~~ (Table 1)~~, 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)

~~$NPP_{root} = NPP_{fine\ root}$ (4)~~

$NPP_{ACW} = NPP_{stem}$ (4~~5~~)

NPPfine $_{root} = NPP_{fine\ root}$ (5~~4~~)

Our calculations above neglect several small NPP components~~terms~~, such as NPP lost through~~as~~ 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~~was~~ a relatively minor fraction of total NPP ~~term~~ (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~~that account for <~~ 2 Mg C ha^{-1} $year^{-1}$ and~~,~~ represent~~ing~~ a modest portion~~part~~ of ~~the~~ carbon fluxes (Malhi et al., 2017). Therefore~~us~~, we focus on ~~the~~ canopy, wood, and fine root~~s~~ 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 ~~the~~ equations:

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

~~2.5 Calculation of measurements uncertainty~~

~~Estimation of measurements uncertainty for each NPP component is explained in details in Table 1. For components that are not directly measured, for example NPP_{total} as a sum of several components, we combine relevant error by error propagation with standard quadrature rules (Hughes & Hase, 2010; Malhi et al., 2015). During the above process, we also assigned significant systematic errors to capture uncertainties related to sampling methodology or scaling approaches (see Table 1); these factors were consistent with those applied in similar previous studies (Malhi et al., 2009, 2015; 2017; Girardin et al., 2010; Galbraith et al., 2013).~~

2.5~~6~~ Data analyses

Our analyses ~~were~~ focused on comparing NPP across~~among the~~ years (2014 to 2019), ~~–~~ comprising the periods before, during, and after the El Niño 2015/2016 event,~~s –~~ in both *cerrado* and *cerradão*. To~~We~~ compare~~d the stem and~~ total canopy NPP across years in each ~~biomass of the two~~ vegetation type~~s~~ (cerradão and cerrado), we performed a ~~over time using~~ repeated -measures ~~two-way analysis of variance (~~ANOVA~~-two way)~~. 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, w~~W~~e used Tukey's post hoc test to compare total canopy NPP between~~the different~~ years~~ in each plot~~. We applied~~used~~ the same analysis to compare stem and fine root NPP~~productivity and carbon allocation~~ across different years in each plot~~compartments~~. For stem NPP, we used subplots as random effects, and for fine roots NPP, we used ingrowth cores as random effects. In cases where ~~the~~ residuals violated ~~the~~ ANOVA assumptions, we applied~~used~~ Friedman's non-parametric test~~analysis~~. We performed all analyses in the R environment~~-~~, with ~~and adopted~~ a significance level of 0.05. ~~To improve the accessibility of colour figures with COLORBREWER 2.0.~~

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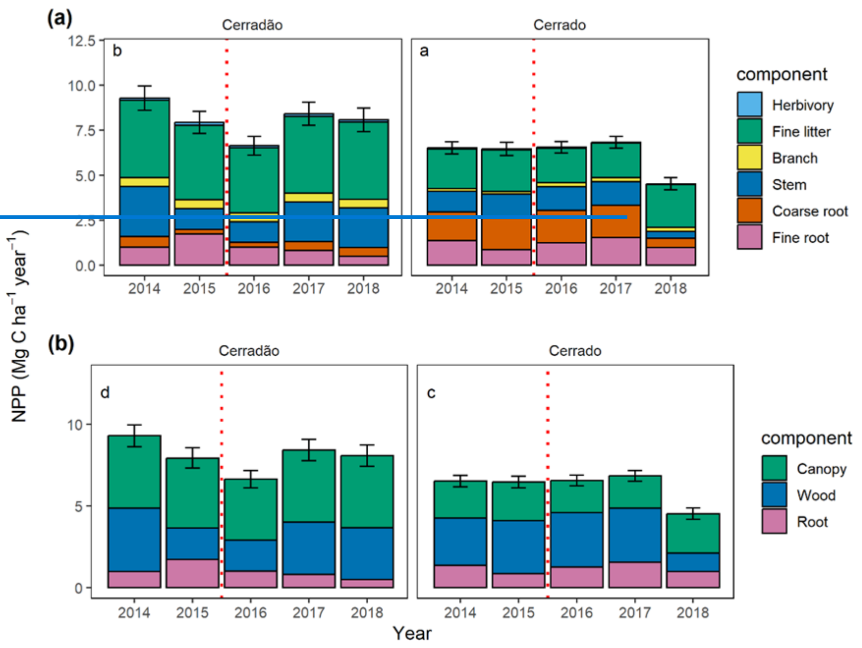
3 Results

3.1 Total NPP and its allocation~~Net primary productivity~~

~~The net primary productivity (NPP) in the *cerradão* was ~ 30% higher compared to that of the *cerrado* prior to the occurrence of El Niño (*cerradão* = ~9.3±0.57 Mg C ha^{-1} year^{-1}; *cerrado* = ~6.5±1.12 Mg C ha^{-1} year^{-1} Fig. 2; Table S2). This is due to the greater productivity in the canopy and stem in the *cerradão* (Fig. 2; Table S2).~~ During the El Niño event, ~~*cerradão*~~ total NPP in cerradão decreased by 29% (~~to~~ 6.6±0.6 Mg C ha^{-1} year^{-1}) and reaching a level ~~became~~ similar to that of ~~the~~ *cerrado* (6.6±1.3 Mg C ha^{-1} year^{-1}; Fig. 2; Table S2). ~~*Cerradão* NPP was severely affected in 2016 during the El Niño event (-29%). In~~ By 2018, it remained ~~was still~~ 13% lower than pre-El Niño conditions (Fig. 2). ~~Additionally, stem biomass declined significantly after El Niño (F= 19.3, p< 0.001) and did not return to the values registered before the event (Fig. S1).~~

In contrast, total ~~the *cerrado*,~~ NPP in ~~-~~the cerrado showed little variation~~did not vary much~~ before, ~~and~~ during, and after the El Niño. ~~However, in 2018, productivity reduced by ~30%, due especially to the reduction in stem productivity. Despite this, stem biomass was not significantly influenced by El Niño and increased significantly between 2013 and 2018 (F= 3.1; p<0.05), remaining stable until 2021 (Fig. S1).~~



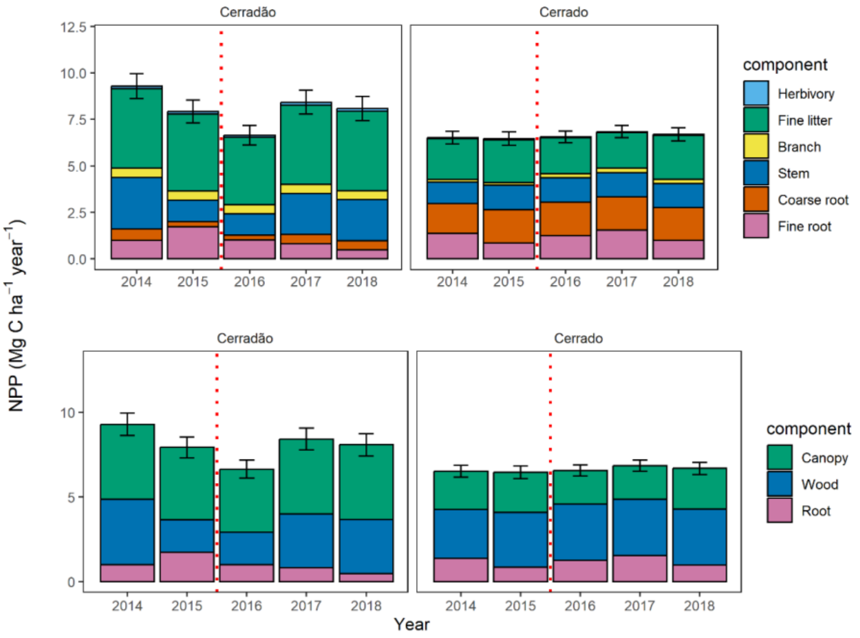


Fig. 2. Mean total annual net primary productivity (NPP) between 2014 and 2018 split into its components (a) and annual NPP allocation into the canopy, wood, and root components (b) at *cerradão* and *cerrado*. The branch data from *cerradão* was collected in 2014 and repeated in

other years. The error bars represent the standard error for total NPP. The dashed red line indicates the El Niño periods.

~~In general, NPP allocation differed significantly between *cerradão* and *cerrado* plots (Fig. 7), but this varies within the components (F= 41.7, p< 0.001). The allocation to canopy was greater in *cerradão* (53±3%) than in *cerrado* (37±10%). In contrast, allocation to woody and roots was greater in the *cerrado* (woody= 44±11%; roots= 19±4%) than in the *cerradão* (woody= 34±8%; roots= 13±6%). Over~~ Throughout the study~~ied~~ period~~time~~, ~~the~~ NPP allocation in cerrado exhibited little ~~showed~~ inter~~-~~annual variation ~~in *cerrado* but~~and showed no clear drought signal. ~~t~~The primary~~main~~ axis of interannual variation was ~~a trade-off~~ between canopy investment and root allocation, w~~ith~~hile woody allocation remained~~ing~~ constant (Figs. 2~~7~~ and 3). ~~However, in 2018, ~ three years after El Niño, the allocation of canopy and wood changed drastically, showing an opposite pattern to previous years.~~ However, i~~I~~n ~~the~~ *cerradão*, ~~there is~~ a clear drought signal was observed, with increased investment in fine roots during the drought~~,~~ and reduced investment in woody growth. ~~; c~~Canopy allocation remained relatively~~fairly~~ constant.

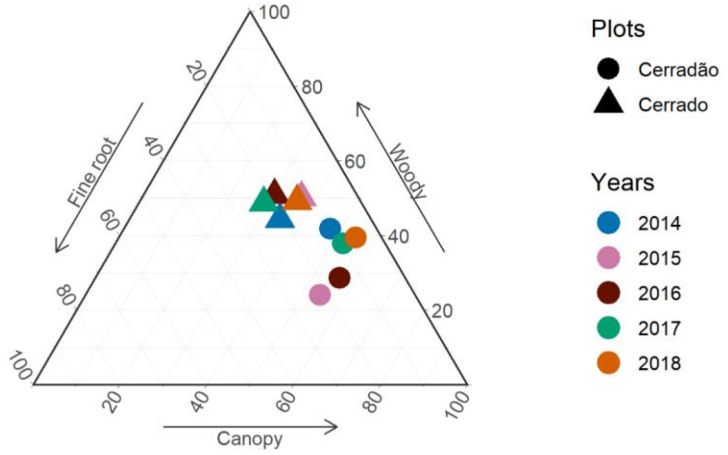


Fig. 3~~7~~. Relative allocation (% of total) of net primary productivity (NPP) to canopy, woody, and fine root NPP in *cerrado* and *cerradão*. ~~2014= blue, 2015= pink, 2016= red, 2017=orange and 2018= grey.~~ Woody components include stem, coarse root and branch turnover; Fine root includes fine root 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~~5~~). However, ~~the~~ NPP of this component

Formatado: Recuo: Primeira linha: 0.04 cm, Espaço Antes: 12 pt had fully recovered~~was re-established~~ within two years after the event. ~~For the *cerradão*, it is worth highlighting the drop in fruit production after the event, which had not yet re-established itself two years after El Niño (Fig. 6). Furthermore, after El Niño, both plots show declining and then recovering LAI (Fig. S2). We also noted that following El Niño, the variability of LAI increased among subplots, potentially due to clearings emerging from heightened tree mortality. The average annual mortality rate increased during and after El Niño, especially in the *cerradão* (Fig. 6).~~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.

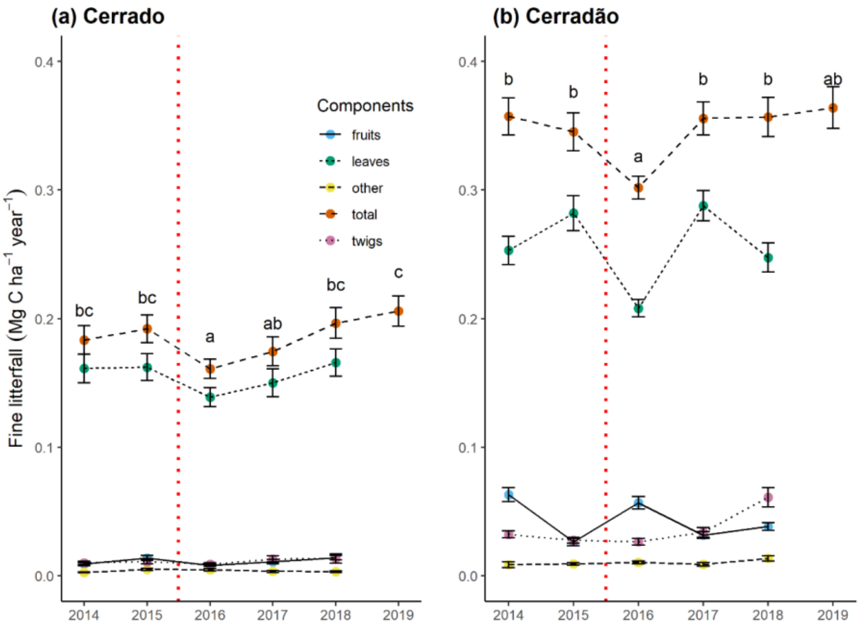
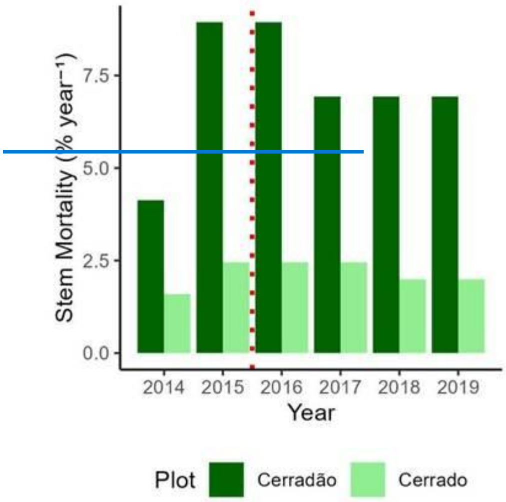


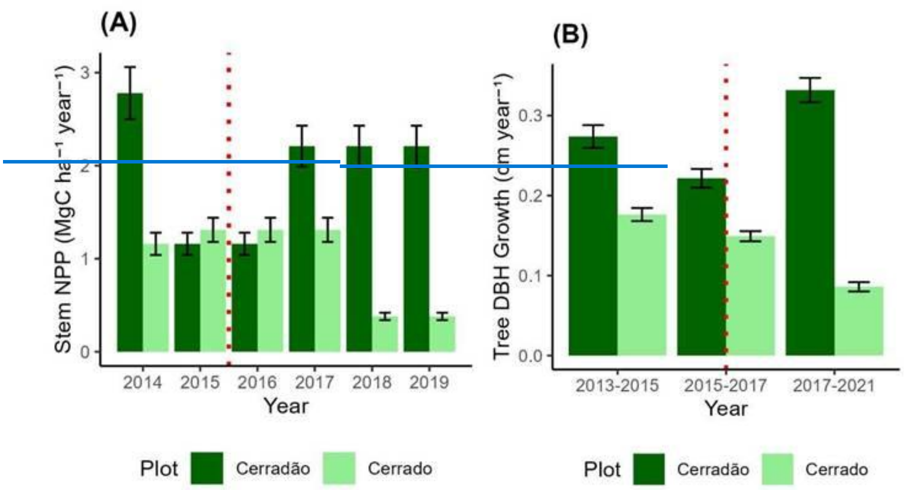
Fig. 4~~5~~. Mean monthly productivity in canopy litterfall and its components for *cerrado* (a) and *cerradão* (b) between 2014 and 2019: (fruits) flower, fruit, and seed fall; (leaves) leaf fall; (other) not identified and (total) total canopy fine litterfall (as measured in litter traps); (twigs) 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).



~~**Fig. 6**. Stem mortality, shown as the percentage of dead trees to the number of trees in the first census divided by time. The dashed red line indicates the El Niño periods.~~

3.3 Stem NPP

In ~~the~~ *cerradão*, the most affected component was stem net primary productivity (NPPs), which ~~was~~ declined~~reduced~~ by 58% during and after El Niño (F= 15.6, p< 0.001; Fig. 5~~3A~~). ~~In~~By 2019, it remained~~was still~~ ~~-~~21% lower than pre-El Niño conditions. ~~When we consider only those trees that were alive before El Niño and remained alive after the event, the *cerradão* reduced NPPs significantly during the event, but after the event, NPPs was greater than before the El Niño (Fig. 53B; F= 25.6, p< 0.001).~~ This decline was primarily driven by~~is mainly due to~~ two key~~critical~~ species in~~for~~ 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~~El Niño~~, *T. vulgaris* was the dominant ~~species that most~~ contributor~~ed~~ to NPPs (26%). In ~~the~~ *cerrado*, ~~trees showed less diameter growth during and after the event (Fig. 53B; F= 109.7, p< 0.001). However,~~ stem productivity was unaffected by the El Niño~~not affected during the~~ event (Fig. 5~~3A~~).



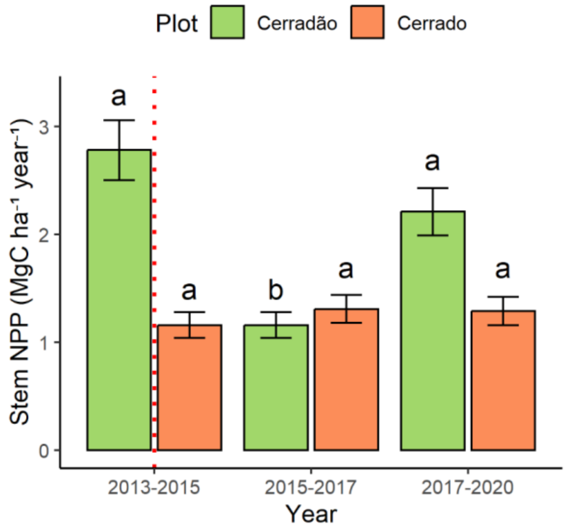
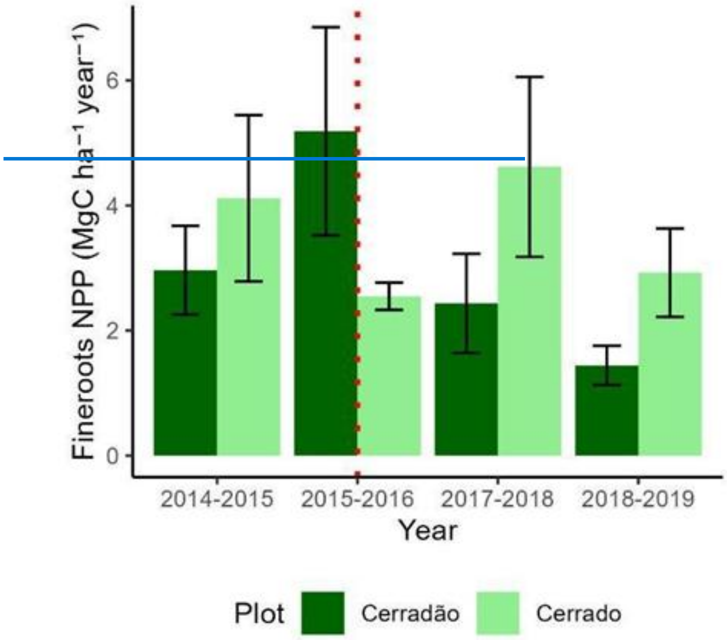


Fig. 5~~3~~. ~~Stem dynamics in *cerrado* (light green) and *cerradão* (dark green). (a) ~~Stem net primary productivity (NPPstem, MgC ha^{-1} year^{-1}) for stems larger than 5cm diameter in cerradão and cerrado. ~~We note that there are negative stem NPP values due to those trees that lose bark or water from the stem in the dry periods, especially in *cerrado* after 2017. (b) The growth of tree diameter (measured at 30cm above soil surface) (cm year^{-1}), calculated as the increase in DAS between two censuses divided by time. Only growth is included, in other words, trees with shrinking stems are excluded ~~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 ~~the~~ *cerradão*, fine root net primary productivity (NPPfr) ~~production~~ increased significantly (+42%) during the El Niño event (F= 17.3, p< 0.001), but ~~in later years productivity~~ declined in the following years (Fig. 64). In contrast, ~~The~~ *cerrado* *exhibited*~~presented~~ the opposite pattern ~~observed in the *cerradão*~~. NPPfr decreased~~reduced~~ by 38% during the event (F= 5.6, p= 0.001; Figs. 2 and 64). However, ~~the NPPfr of~~ this component re-established itself shortly~~soon~~ after the El Niño, but experienced another~~a~~ decline of approximately ~~∼~~ 38% in 2018.



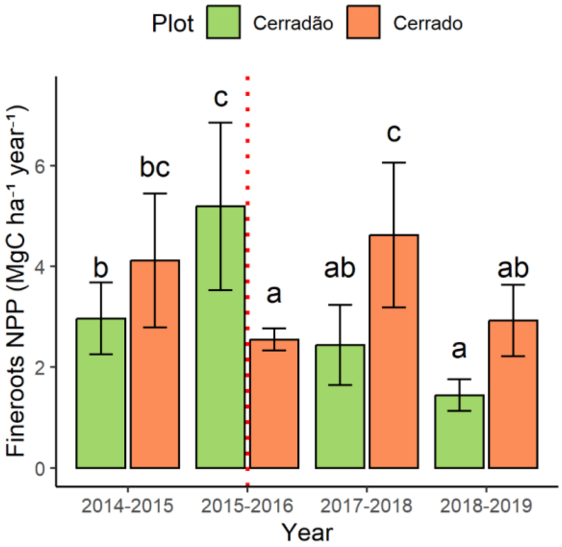
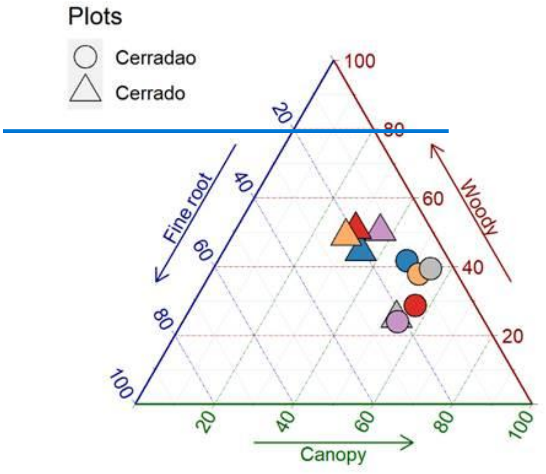


Fig. 64. Fine root net primary productivity (NPPfr) for *cerrado* (light green) and *cerradão* (orange~~dark green~~) between September 2014 and August 2019. The error bars represent the standard error. The dashed red line indicates the El Niño periods. Different letters denote significant differences between years in each plot (Tukey post hoc test).

~~*3.2. Allocation between plots, components, and years*~~

~~In general, NPP allocation differed significantly between *cerradão* and *cerrado* plots (Fig. 7), but this varies within the components (F= 41.7, p< 0.001). The allocation to canopy was greater in *cerradão* (53±3%) than in *cerrado* (37±10%). In contrast, allocation to woody and roots was greater in the *cerrado* (woody= 44±11%; roots= 19±4%) than in the *cerradão* (woody= 34±8%; roots= 13±6%). Over the studied time, the NPP allocation showed inter annual variation in *cerrado* but no clear drought signal the main axis of interannual variation was a trade-off between canopy investment and root allocation, with woody allocation remaining constant (Fig. 7). However, in 2018, ~ three years after El Niño, the allocation of canopy and wood changed drastically, showing an opposite pattern to previous years. In the *cerradão*, there is a clear drought signal with increased investment in fine roots during the drought, and reduced investment in woody growth; canopy allocation remained fairly constant.~~



~~**Fig. 7**. Relative allocation (% of total) of net primary productivity (NPP) to canopy, woody, and fine root NPP in *cerrado* and *cerradão*. 2014= blue, 2015= pink, 2016= red, 2017=orange and 2018= grey. Woody components include stem, coarse root and branch turnover; Fine root includes fine root NPP only (no roots exudates); Canopy includes litterfall and herbivory~~

4 Discussion

Cerradão and *cerrado* showed contrasting responses to the 2015/2016 El Niño-associated drought event. The *cerrado* *appears*~~proved~~ to be more resistant~~-~~, as total NPP and stem NPP were not impacted by the El Niño event, and the components ~~resilient, i.e., most of the parameters assessed (e.g., stem carbon stock, canopy productivity) changed little during the event, and those~~ that experienced a reduction (e.g., production of fine roots and canopy productivity) soon re-established themselves~~ (e.g., production of fine roots and canopy productivity)~~. In contrast, the *cerradão* exhibited~~showed~~ lower resistance, as all NPP components were affected during the El Niño event, including total NPP and ~~and resilience:~~ 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.~~carbon stock and mortality, productivity and allocation were affected during and after the El Niño event and even three years after, most of the parameters assessed were not similar to those observed before the event.~~ Our findings demonstrate the high sensitivity of the *cerradão* to extreme drought events.

4.1 Total NPP and its allocation

~~The productivity found in our *cerradão* (9.3±0.57) was similar to that observed in transitional forests in Africa (9.2 to 13.1; Moore et al., 2018), and insome low-fertility humid forest sites in lowland Amazonia in Colombia and Brazil (~8.1 to 10.3; Aragão et al., 2009; Girardin et al., 2010).~~

~~However,~~~~It is markedly greater than observed in seven premontane and montane sites in Peru (~3.9 to 6.4; Girardin et al., 2010) and~~ it was ~~lower than observed in lowland tropical forest plots in south-western Amazonia (15.1 ± 0.8 and 14.2 ± 1.0; Malhi et al., 2015) and nutrient-rich soils forests (17.0±1.4; Aragão et al., 2009).~~ 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. T~~Nevertheless, the t~~otal productivity of *cerradão* was more affected (-29%) than the Amazonian~~Amazoni~~n~~a~~ 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.

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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. ~~The canopy-wood-fine root changes in allocation identified here are different from those reported by Doughty et al. (2014) for a somewhat similar Amazonian forest-dry forest transition in Bolivia, with similar rainfall but more fertile soils. There, the site with better water availability (related to soil properties) hosted an Amazonian forest which showed wood-canopy trade-offs during drought. The drier site hosted *chiquitano* dry forest with wood-fine root trade-offs during drought. Our *cerradão* site shows similar wood-fine root trade-offs to the *chiquitano* forest, whereas our *cerrado* site shows a different canopy-fine root trade off.~~ One possibility is that these shifting ~~trade-off~~ strategies reflect points on an aridity continuum from sub-humid Amazonian forest ~~(wood-canopy changes in allocation)~~ through transitional or seasonally dry forests ~~(wood-fine root changes in allocation)~~ through to savanna~~(wood-canopy changes in allocation)~~. 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~~Both *cerrado* and~~ *cerradão* adopted the strategy of shedding~~losing~~ more leaves at the onset of~~during~~ 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, i~~I~~t is well known that ~~during periods of water stress in the soil, ~~plants often shed~~lose~~ their leaves as a strategy to minimize~~avoid~~ water loss and avoid potential ~~consequent~~ 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, t~~T~~his leaf loss strategy can also have benefits for nutrient cycling~~ benefits~~;~~:~~ when ~~the nutrients released to the litter layer and soil after ~~leaves~~f~~ drop, the nutrients they contain are ~~and can later be~~ released into litter layer and soil, where they can be reabsorbed by the plants as~~when~~ they re-establish leaf growth after the~~a~~ 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.~~The high leaf loss during El Niño may have contributed to lower photosynthetic activity of plants (e.g., Luo et al., 2018; Kaewthongrach et al., 2020), consequently affecting carbon accumulation.~~

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4.3 Stem NPP

~~The higher mortality of *cerradão* may be related to the hydraulic characteristics of the main species, such as *Tachigali vulgaris*, a pioneer species with stomatal control tending to an anisohydric condition and, therefore, more susceptible to hydraulic failure (Jankoski et al., 2022). In addition, many species are brevi-deciduous, so the plants continue to photosynthesize even during water scarcity (e.g., Jancoski et al., 2022). Other factors, such as a lack of strategies to avoid water loss, may also contribute, like low trichome density in their leaves and smaller stomata (Araújo et al., 2021b). Another possible cause of the high mortality in the *cerradão* is the unusually intense winds that hit trees with xylem tissue already weakened by the effects of drought and heat~~

~~due to the El Niño event (Reis et al., 2022). *Cerradão* trees are taller than *cerrado* trees, which makes them more susceptible to wind disturbances. Once broken, even just part of the crown, the tree is at greater risk of death (Reis et al., 2022).~~

~~Despite the high mortality, the trees that remained alive showed higher stem productivity than before the El Niño. This may be related to the greater opening of clearings, favouring carbon uptake and plant growth due to the greater availability of light, water and nutrients to the remaining trees. During the El Niño drought, a decline in the growth of *Tachigali vulgaris* trees was observed, leading to a shift in the primary contributor to stem productivity from *T. vulgaris* to *Hirtella glandulosa*. The role reversal of these two species can be explained by the high mortality and low growth rate of *T. vulgaris* during and after El Niño. *T. vulgaris* is considered a key species for *cerradão* due to its high biomass gain after disturbances such as fire (Reis et al., 2015; 2017), but it is sensitive to drought. The high sensitivity of *T. vulgaris* to drought events may be attributed to the increased xylem tension required to extract water from the soil, making it more prone to embolism (Jancoski et al., 2022). Consequently, this results in reduced growth and higher mortality compared to *H. glandulosa*. On the other hand, *H. glandulosa* proved to be more resistant: it has high foliar trichome density, which works as a strategy to prevent water loss (e.g. Gianoli & González-Teuber, 2005; Araújo et al., 2021b). In the *cerrado*, we observed the opposite pattern; the productivity of trees that remained alive continued to decline after the event. In this vegetation type, plant mortality was low, and the surviving plants had to compete to stay alive, which may explain the lower productivity after El Niño. Furthermore, many trees in the *cerrado* shed their outer bark, which may have affected the diameter measurement and, consequently, the productivity of the stem. The loss of bark from *cerrado* plants, especially after fire and drought events, makes the measurement of trunk productivity inaccurate.~~

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,

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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.

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4.4 Fine root NPP

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The observed changes in fine root net primary productivity (NPPfr) 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 NPPfr 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~~The high production of fine roots in *cerradão* during drought is probably~~ a strategy to enhance~~increase soil~~ water absorption capabilities~~uptake~~ during a~~the~~ period of soil elevated atmospheric demand and potential soil moisture deficits~~water scarcity~~ (Metcalfe et al., 2008). However, this strategy does not~~on partially~~ ameliorate~~s~~ drought risk, as tree mortality was high (Prestes et al., 2024) despite~~even with~~ a high investment in fine roots. Yet, following the El Niño event, NPPfr 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 ~~showed the~~ opposite pattern, with a marked reduction in NPPfr during the El Niño~~strategy, investing less in fine roots during the event~~. 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 NPPfr 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 NPPfr 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.~~However, shortly afterwards, the productivity of this component was similar to that observed before El Niño. Lowland *terra firme* have less root growth during the dry season but had greater specific root length and surface area where soil moisture was depleted (Metcalfe et al., 2008), and the *cerradão* presented a strategy similar to these Amazonia forests, but not the *cerrado*.~~

5 Conclusions

Cerradão is an important~~vital~~ 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 tree species, *T. vulgaris*, which plays a key role in carbon uptake, showed strong~~exhibited significant~~ sensitivity to El Niño ~~the climatic~~ 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 ~~as observed~~ a regional scale atmospheric result for south-east Amazonia (Gatti et al., 2021)~~here~~. Moreover, as a transitional zone between the Cerrado and the Amazon, the *cerradão* plays an important~~vital~~ 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.

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