Science of the Total Environment 987 (2025) 179626

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The effect of fire on the carbon fluxes and productivity of Brazilian woodland savannas

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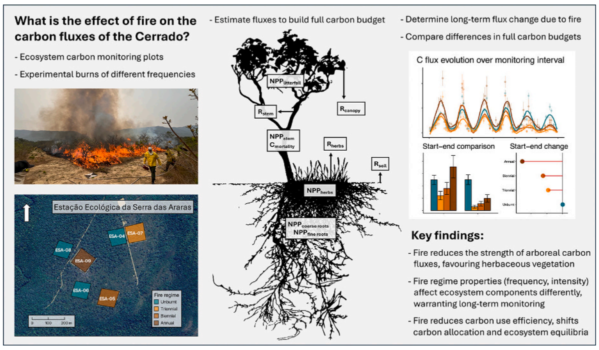
HIGHLIGHTS

- Estimated ecosystem carbon budget and fluxes in unburnt and periodically bunt plots
- Fire reduced the strength of arboreal carbon fluxes favouring herbaceous vegetation
- Specific carbon fluxes are diversely related to either fire frequency or intensity
- Fire reduces carbon use efficiency, shifts carbon allocation and ecosystem balances
- Active burning management of altered fire regimes can improve savanna conservation

GRAPHICAL ABSTRACT



What is the effect of fire on the carbon fluxes of the Cerrado?

- Ecosystem carbon monitoring plots
- Experimental burns of different frequencies

- Estimate fluxes to build full carbon budget

- Determine long-term flux change due to fire
- Compare differences in full carbon budgets

Key findings:

- Fire reduces the strength of arboreal carbon fluxes, favouring herbaceous vegetation
- Fire regime properties (frequency, intensity) affect ecosystem components differently, warranting long-term monitoring
- Fire reduces carbon use efficiency, shifts carbon allocation and ecosystem equilibria

ARTICLE INFO

Editor: Paulo Pereira

ABSTRACT

The effects of altered fire regimes within open ecosystems are poorly understood and can have serious consequences on functioning and conservation across savanna ecoregions worldwide. In South American savannas like the Cerrado, there is a gap of knowledge relating to carbon cycling in the presence of fire, meaning the impacts of altered fire regimes on the carbon fluxes and budgets are virtually unknown. We thus investigate vegetation carbon flux dynamics within the Cerrado making use of an experimental fire and carbon monitoring research project at the Estação Ecológica da Serra das Araras, Brazil. We present a thorough carbon budget of woodland-

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https://doi.org/10.1016/j.scitotenv.2025.179626
Received 23 October 2024; Received in revised form 1 May 2025; Accepted 6 May 2025

type savannas (*cerrado* sensu stricto), and investigate how annual (every year), biennial (every two years), and triennial (every three years) controlled fire frequencies have influenced net primary productivity and respiration fluxes. Six years of experimental fire had noticeable effects on the vegetation structure and carbon dynamics, reducing woody cover and productivity in favour of grass-dominated carbon balances. Woody NPP increased by 35 % in the unburnt plots from 2017 to 2019 to 2021–2023, but decreased by 75 %, 33 % and 20 % in the triennial, biennial and annual fire frequencies. By 2023, burnt plots revealed around three times higher herbaceous NPP than unburnt plots. Fluxes corresponding to different ecosystem components (canopy, stems, roots, herbs) showed varying patterns of change across the gradient of experimental fire frequencies, indicating other fire regime properties distinctively affect each vegetation segment. Fire intensity and severity appear to be linked with patterns in woody stems and the herbaceous layer. Our results indicate periodically burnt *cerrado* sensu stricto vegetation experiences different carbon dynamics than unburnt vegetation. Burning is revealed as a strategy that can successfully limit woody encroachment and help conserve open ecosystem structure in the Cerrado. Our study highlights the importance of long-term monitoring efforts in investigating the effects of management interventions and environmental shifts on ecosystem functioning.

1. Introduction

Fire regimes across tropical ecosystems are being shifted by different drivers of global change, altering ecosystem productivity, carbon sequestration and biogeochemical processes (Bowman et al., 2013; Rocha et al., 2014; Zheng et al., 2021; Friedlingstein et al., 2022). Major shifts in tropical fire regimes could alter the Earth-System functioning, as fire emission sources are disproportionately tropical – with tropical savannas contributing to approximately 62 % of total global fire emissions – and expected to increase in the face of global change (van der Werf et al., 2003; Krawchuk et al., 2009; van der Werf et al., 2017; Zheng et al., 2021). Increases in the number, intensity, severity and recurrence of fire events can be linked to extreme weather events and climate change (Westerling et al., 2006; Prichard et al., 2017; Diffenbaugh et al., 2021), as well as socioecological factors such as land abandonment or the encroachment of agricultural and urban land uses into natural areas (Prichard et al., 2017; Conciani et al., 2021; Pivello et al., 2021). Extensive burning can also affect water balances, heat fluxes and surface climate in tropical forests and savannas, promoting warmer and drier weather conditions that support more extreme fires, reinforcing global warming impacts (De Sales et al., 2023). Changing fire regimes can thus exacerbate biodiversity loss and climate change and have the potential to compromise key ecosystem services – such as nutrient cycling, water provisioning, habitat protection and carbon storage – and to permanently shift landscapes into alternative stable states (Bowman et al., 2009; Gomes et al., 2020; McLauchlan et al., 2020).

However, fire is also key natural disturbance in many open ecosystems such as woodlands, grasslands, and savannas, allowing structure, biodiversity and functioning to be maintained (Pivello, 2011; Staver et al., 2011).

Tropical savannas are important in terms of biodiversity and global functioning, covering approximately 20 % of the Earth's surface and accounting for 30 % of the total productivity of terrestrial vegetation (Dexter et al., 2015; Grace et al., 2006). Savannas play an essential role in terms of delivering of ecosystem services, providing >1 billion people with food, materials, and pollinators as well as regulating flows of air, energy and water (Marchant, 2010; Stevens et al., 2022). Savanna ecosystems are maintained by fire regimes; where natural or traditional human-induced burns are required to promote vegetation regeneration, maintain adequate nutrient cycles and control the degree of ecosystem change via woody encroachment (Miller et al., 2017; Kelly et al., 2020), which can cause significant loss of ecological functioning and diversity (Durigan and Ratter, 2016; Rosan et al., 2019; Wieczorkowski and Lehmann, 2022). Consequently, the preservation or restoration of natural fire disturbances or – where the former is not feasible – the implementation of prescribed fire regimes are emerging as potential land management strategies that could help maintain savanna biodiversity and functioning (Durigan and Ratter, 2016).

Improving fire management for ecosystem health and biodiversity conservation has been highlighted as one of the key milestones required for adequate management of the Cerrado, Brazil's savanna ecoregion (Françoso et al., 2015; Prichard et al., 2017). The Cerrado is a 2-million-km^2 biodiversity hotspot (e.g., supporting >12,000 native plant species of which about 40 % are endemic – Silva et al., 2024) that is also extremely threatened. Higher land clearance rates than the Amazon have led to about 50 % of the natural area disappearing already (Françoso et al., 2015). In terms of fire, Brazilian savannas are experiencing higher pressures and impacts from anthropogenic burning as well as ongoing ecosystem degradation from lack of prescribed fire management (Pivello et al., 2021). Burning continues to play a role as an important environmental factor influencing processes like phenology and nutrient stoichiometry (Silva and Batalha, 2008; Oliveras et al., 2012) and many Cerrado plants have successful adaptations that allow them to cope with the interacting impacts of fire and drought (Franco et al., 2008). Thus, the restoration of frequent surface fires in areas of fire suppression could represent a feasible conservation strategy for the Cerrado by reducing wildfire severity and extensive woody encroachment (Durigan et al., 2020). Yet, the effects of prescribed fires on Brazilian savannas are still poorly understood and could lead to unintended effects on ecosystem functioning and vegetation (Hoffmann, 2002; Bustamante et al., 2012; Gomes et al., 2018). Therefore, investigating the effect of altered fire regimes on the ecosystem dynamics is becoming an increasingly key research priority.

Despite the importance of determining and quantifying the impacts of fire on Cerrado ecosystem dynamics, there are disproportionately few experimental studies on controlled burning across such a large and heterogeneous area, which are mainly focused on open vegetation and grass-dominated dynamics within a handful of locations in the central and south-eastern Cerrado (see Rissi et al., 2017; Durigan et al., 2020; Zupo et al., 2021; Rodrigues et al., 2021; Teixeira et al., 2022; Fontenele and Miranda, 2024). There is a gap of knowledge surrounding key ecosystem metrics relating to carbon cycling in terms of carbon fluxes, both in the presence or absence of fire. Vourlitis et al. (2022) have been able to provide a detailed estimate of the main carbon fluxes within a mixed-grassland site in Mato Grosso, Brazil, using field methods from different sources to reconstruct a relatively complete carbon cycle. Additionally, Scalon et al. (2022) estimated net primary productivity partitioning for woodland savanna (*cerrado* sensu stricto) and afforested woodland savanna (*cerradão*) plots also in Mato Grosso, Brazil. Still, there is no available data linking detailed carbon flux dynamics to the effects of fire. This means the impacts of altered fire regimes on the carbon balance of the Cerrado are virtually unknown. Thus, the aim of this study is to investigate carbon flux dynamics within experimental fire regimes of different burning frequencies, in order to inform about the potential consequences of altered fire regimes within the Cerrado. Overall, we specifically aim to address the following objectives:

1. Quantify the main carbon fluxes within Cerrado woodland savanna, illustrating – where sampling intensity and temporal replication allows – flux seasonal changes and trends over time.
2. Determine how the cumulative effects of the annual, biennial, and triennial experimental fire frequencies have influenced the main carbon fluxes savanna by comparing estimates in burnt plots against estimates in fire exclusion plots.
3. Provide estimates of ecosystem total carbon budget metrics for Cerrado woodland savanna that has been subjected to fire suppression and compare them to metrics for plots that have experienced annual, biennial, and triennial burns.

We expect to find similar carbon flux patterns as those recorded in other Cerrado sites (Scalon et al., 2022; Vourlitis et al., 2022), with comparable distribution across ecosystem components and strong seasonal fluctuations related to water availability (Araujo-Murakami et al., 2014; Rocha et al., 2014). In terms of our hypotheses regarding the long-term effect of fire on the carbon fluxes of savannas, we expect to i) observe a reduction in the intensity of fluxes relating to the arboreal component of the ecosystem within the experimental burning plots. Reduced carbon allocation into arboreal fluxes should correspond to decreases in the survival and growth of trees with recurrent burning (Rodrigues and Fidelis, 2022), and would be consistent with carbon flux patterns observed in burnt vs unburnt plots in Amazonian transitional forests in Mato Grosso (Rocha et al., 2014). We also predict that ii) experimental burns will alter the way in which carbon is allocated into different fluxes, increasing the proportion of productivity distributed into aboveground components due to post-fire recovery and regrowth (Zupo et al., 2021); as well as the proportion of respiration from heterotrophic sources, given fire will transform part of the live biomass stock into decomposable dead matter (Brando et al., 2014). Finally, we expect iii) individual carbon fluxes to potentially show varying patterns of change across the gradient of fire frequencies, since different effects of the fire regime – such as decreased fuel load and fire intensity, or higher proportion of bare ground in more frequently burnt plots – could either exacerbate or compensate the effect of cumulative burns on the different carbon fluxes (Rodrigues et al., 2021; Chiminazzo et al., 2023).

2. Materials and methods

2.1. Study site and experimental design

Our study was located within an area of woodland savanna at the Estação Ecológica da Serra das Araras (Serra das Araras Ecological Station, Fig. 1), in Southwestern Mato Grosso, Brazil (15°39′10.96″S, 057°12′52.54″W, ~320 m above sea level). Serra das Araras is a 27,000-ha IUCN category 1A conservation unit mostly contained within the municipality of Porto Estrella (ICMBio, 2016). The unit is managed by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and placed in a strategic location near the ecotone between the Cerrado, Pantanal and Amazonian ecoregions, playing a key role in biodiversity conservation. The area has tropical savanna climate with dry winter characteristics, having distinct dry (June–September) and rainy (November–March) seasons (Kottek et al., 2006; Pizzato et al., 2012). Mean annual temperature and rainfall for the 1979–2010 period were around 25-26 °C and 1268.4 mm respectively (Pizzato et al., 2012; Santos et al., 2018). The site was historically settled by traditional *quilombola* communities but was transformed into a protected area in 1982. No fires have been recorded within our monitoring area since 1992.

Our monitoring efforts consist of six 1-ha (100 × 100 m^2) plots (named ESA-04 to ESA-09) that have been set up and maintained since 2017. Plots are grouped in three burnt/unburnt pairs, and divided into 25 subplots (20 × 20 m^2) to provide spatial replication within the plot unit. Most carbon fluxes have been intensively monitored up to the end

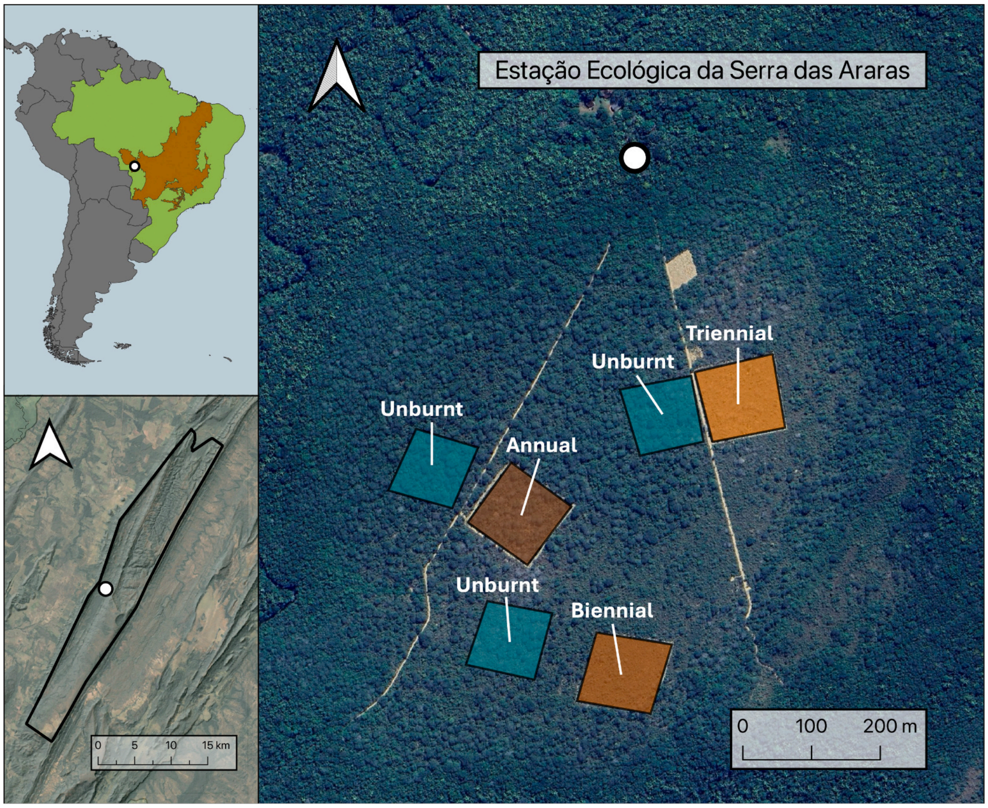

Fig. 1. location of the monitoring plots. Top left) location of the Estação Ecológica da Serra das Araras within South America (Brazil is highlighted in light green, the Cerrado ecoregion in orange). Bottom left) position of the *cerrado* sensu stricto study site within the Estação Ecológica da Serra das Araras. Right) distribution of the six monitoring plots subjected to experimental burns and fire exclusion.

of 2023 – with the exception of the 2020/2021 Covid-19 lockdowns – based on the methods provided by the RAINFOR-GEM Field Manual for Intensive Census Plots (Marthews et al., 2014). The monitoring plots have also been subjected to experimental fire, with three regularly burnt plots and three unburnt ones where all fire is excluded. Each burnt plot has been burnt at different frequencies (annual, biennial and triennial burns) to better determine the effects of different fire regimes on Cerrado vegetation. This means that by December 2023, the annual plot had burnt six times (2018, 2019, 2020, 2021, 2022, 2023), the biennial plot three times (2019, 2021, 2023) and the triennial plot had burnt twice (2018, 2021). We conceptualise each experimental regime as incorporating different fire frequencies, as well as recognising the unique return interval, behaviour, intensity and severity of each set of fires. Controlled burns were undertaken at the peak of the dry season (July – September) to take advantage of good burning conditions – low ambient moisture and high accumulation of dry fuel – and to simulate seasonality of fire within the Cerrado (Pivello, 2011).

Upon plot establishment, all six plots shared similar vegetation architecture and composition, although variable vegetation density due to the strong heterogeneity characteristic of Cerrado ecosystems (see Table S1 for details). Vegetation was classified as *cerrado* sensu stricto (typical woodland savanna) in transition towards *cerradão* (forested woodland savanna), consisting of small and medium tree species, shrubs and a relative sparce herbaceous layer. Dominant tree species include *Curatella americana* L., *Kielmeyera grandiflora* (Wawra) Saddi, *Tachigali paniculata* Aubl., *Vochysia haenkeana* Mart., *Myrcia bella* Cambess., and *Pouteria ramiflora* (Mart.) Radlk. All plots are characterized by a generally flat topography and share underlying soils formally classified as dystrophic latosols under the Brazilian soil classification system (EMBRAPA, 2018) – largely equivalent to dystric ferralsols under the World Reference Base soil classification system (IUSS Working Group WRB, 2022).

2.2. Estimation of carbon fluxes

We make use of an experimental fire and carbon monitoring research project at Serra das Araras, Mato Grosso, Brazil, to track and estimate the area's main carbon fluxes over a period of six years. These include net primary productivity – NPP, defined as the rate at which carbon is incorporated into the biomass of an ecosystem via plant growth discounting carbon loss through respiration – and respiration – R, describing the rate at which carbon is released by plants or soil as a result of metabolic processes or microbial decomposition (Girardin et al., 2010; Moore et al., 2018). NPP and R are typically measured in the field based on rates of production and gas exchange of leaves, stems, roots, etc. (Araujo-Murakami et al., 2014). The study of the productivity and respiration fluxes of these different ecosystem components gives insight into ecological performance and functioning as they relate to specific biological processes such as stem growth, leaf phenology and plant physiology (Girardin et al., 2010). In the wider ecosystem scale, productivity and respiration dynamics are used to estimate ecosystem carbon balance metrics such as plant carbon expenditure (PCE), gross primary productivity (GPP) and carbon use efficiency (CUE) which provide useful information with regards to ecosystem carbon balances and stability, as well as climate budgeting (Metcalfe et al., 2010; Malhi, 2012).

We therefore present the first detailed picture of these carbon fluxes within Brazilian woodland-type savannas (*cerrado* sensu stricto*;* Miranda et al., 2014). Since 2016, we collected long-term ecosystem monitoring data from three woodland plots subjected to different fire regimes: annual (every year), biennial (every two years), and triennial (every three years) burns, as well as three unburnt – fire exclusion plots. We used ecosystem monitoring data to estimate the main carbon fluxes within Cerrado woodland savanna: 1) litterfall NPP, 2) woody stem NPP, 3) herbaceous NPP, 4) coarse root NPP, 5) fine root NPP, 6) canopy R, 7) woody stem R, 8) herbaceous R, 9) and soil R, as well as 10) carbon accumulated in dead stems. We then compare flux estimates between burnt and unburnt plots, which allows us to study the long-term effect of the different experimental fire regimes on the carbon cycling of Cerrado woodland savanna.

The main carbon fluxes of the monitoring plots were estimated from a set of field sampling data based on the RAINFOR-GEM protocol (Marthews et al., 2014; Malhi et al., 2021). Summaries of the field methods and data processing techniques used to estimate each flux are presented in Tables 1 and 2, respectively. In broad terms, carbon fluxes can be estimated from a) census inventory data of all trees within the plots, b) spatially-replicated samples taken at monthly or trimestral intervals, or c) a combination of variables derived from both types of data. Because our objectives are to estimate the main carbon fluxes and investigate the long-term effects of fire, we attempted to compare flux estimates using a BACI-based framework (before-after control-impact approach; Christie et al., 2019) which allowed us to study the effect of fire by comparing flux change in burnt vs unburnt plots. Thus, we aimed to compare estimates for each carbon flux covering the first and last complete year of data within the experiment, allowing for sufficient data to produce adequate, representative yearly estimates. It is important to note that since the experimental fire regimes were initiated during the first year of data collection, we were unable to implement a fully typical BACI approach for some fluxes, instead comparing 'start' and 'end' flux estimates. Incorporating more reliable full-year start estimates is thus justified because short-term flux changes are negligible in comparison to estimate uncertainty and seasonal variation.

In the case of variables derived from temporally- and spatially-replicated samples, we compared fluxes using statistical models to account for groupings within the data and extract flux estimate coefficients. In the case of carbon fluxes partially or entirely derived from sums of plot-level inventory allometries, estimates were compared descriptively. Please note that for certain variables, data collection was only possible at the final stages of the monitoring period. For these fluxes, we used a control-impact (CI) or space-for-time substitution approach (Christie et al., 2019) to compare flux estimates – statistically and descriptively – and evaluate the effect of fire across regimes (Tables 2 and 3).

Due to the lack of some initial data, were only able to parametrise the full carbon cycle for the 2023/2024 focal period, around six years after the start of the experimental fires. This allowed us to calculate ecosystem carbon budget metrics, also comparing them via the CI framework. We integrated carbon fluxes to calculate ecosystem net primary productivity ($\text{NPP}_{\text{total}}$) and its aboveground/belowground partition using the following equations:

$$NPP_{aboveground} = NPP_{litterfall} + NPP_{stem} + NPP_{herbs} \tag{1}$$

$$NPP_{belowground} = NPP_{coarse\ roots} + NPP_{fine\ roots} \tag{2}$$

$$NPP_{total} = NPP_{litterfall} + NPP_{stem} + NPP_{herbs} + NPP_{coarse\ roots} + NPP_{fine\ roots} \tag{3}$$

We estimated ecosystem respiration (R_{eco}) by summing all respiration fluxes. In order to estimate total autotrophic respiration ($\text{R}_{\text{autotrophic}}$) we partitioned R_{soil} into $\text{R}_{\text{rhizosphere}}$ (autotrophic respiration from the rhizosphere) and $\text{R}_{\text{heterotrophic}}$ (heterotrophic microbial decomposition, see Table 2 for details).

$$R_{eco} = R_{canopy} + R_{stem} + R_{herbs} + R_{soil} \tag{4}$$

$$R_{autotrophic} = R_{canopy} + R_{stem} + R_{herbs} + R_{rhizosphere} \tag{5}$$

Obtaining estimates of total autotrophic respiration allowed us to complete our carbon balances by approximately isolating plant-mediated fluxes. We were thus able to derive plant carbon expenditure (PCE), the total amount of carbon expended by trees.

$$PCE = NPP_{total} + R_{autotrophic} \tag{6}$$

Table 1
sampling methodologies used for the study of carbon flux dynamics at the Estação Ecológica da Serra das Araras (adapted from the RAINFOR-GEM protocol), Includes period of measurement and sampling interval. Multiple variables were collected for some fluxes; these are indicated as separate paragraphs within a cell.

Flux	Description	Period	Interval
$\text{NPP}_{\text{litterfall}}$	Litterfall production of dead organic material was estimated by collecting litterfall at nine litter traps (each 0.25 m^2) per plot ($N = 9$), each of them placed 1 m above ground level at the centre the nine central subplots. We did not distinguish between coarse and fine litterfall components, but classified it into types: leaves, twigs, flowers, fruits, seeds, and other objects. All components were oven dried at 80 °C to constant mass and weighed.	2018 to 2023	15 days to 1 month
NPP_{stem}	Forest inventory: All trees ≥5 cm in diameter-at-breast-height (DBH) and ≥ 3 m in height were tagged and identified to species level where possible. DBH and height of each tree were measured and re-censused every two years to describe vegetation structure and determine growth rate of existing surviving trees. Census data was also used to calculate rates of tree mortality ($C_{\text{mortality}}$).	2017 to 2023	2 years
	Seasonal growth: dendrometer bands were installed on a subset of trees at each plot ($N = 100$ at the unburnt plots, $N = 25$ at the biennial and triennial plots, $N = 50$ at the annual plot) to determine the seasonal variation in stem growth	2019 to 2023	3 months
$\text{NPP}_{\text{herbs}}$	Production of herbaceous biomass was measured at permanent quadrats set in the corners of even-numbered subplots ($N = 12$) within all plots. All herbaceous growth (2 cm above the surface) within the quadrats was harvested monthly. Herbaceous biomass was classified into live and dead matter, oven-dried at 60 °C for approximately 72 h and weighed.	Nov 2023 to Oct 2024	1 month
$\text{NPP}_{\text{coarse roots}}$	Productivity of coarse roots was not measured directly but derived from estimates of aboveground woody productivity calculated from inventory data (see Table 2 for details on analysis).	2017 to 2023	2 years
$\text{NPP}_{\text{fine roots}}$	Nine ingrowth cores (mesh cages of 14 cm in diameter, mesh size 1.5 cm) were installed in every plot ($N = 9$). They were placed in each of the central subplots to 30 cm soil depth. Cores were extracted every 3 months and roots were manually removed from the soil samples in four 10-min time steps. Root-free soil was then re-inserted into the ingrowth core, which was placed back into the soil. Collected roots were cleaned, oven-dried at 80 °C and weighed. Ingrowth cores were gradually relocated within subplots in 2022 to avoid any potential loss of productivity and fertility within the core.	2018 to 2023	3 months
R_{canopy}	Leaf area index: canopy images were recorded with a digital camera and fish-eye lens at the centre of each of the 25 sub-plots in each plot, at a height of 1 m, and during overcast weather or indirect sunlight conditions. The camera was horizontally- and north-aligned.	Dec 2022 to Nov 2023	1 month
	Leaf dark respiration: dark respiration was not measured at the Estação Ecológica da Serra das Araras. We use mean respiration values of Cerrado trees (10 species) measured at the Reserva Ecológica do IBGE near Brasilia in February 2009 (Rossatto and Franco, 2017).	n/a	n/a
R_{stem}	Stem CO_2 efflux: was measured at 15 trees in each plot ($N = 15$), using a closed dynamic chamber method. CO_2 concentration and accumulation were measured with an infra-red gas analyser (IRGA EGM-4 and EGM-5, PP Systems) and soil respiration chamber (SRC-1, PP Systems) connected to a permanent collar sealed to the bole surface.	Sep 2018 to 2023	1 month
	Stem surface area: surface area data was derived from the forest inventory data of each plot (see above).	2017 to 2023	2 years
R_{herbs}	Live herbaceous biomass: the standing stock of herbaceous biomass at each plot was sampled during the set-up of the 12 permanent herbaceous quadrats per plot (N = 12). All herbaceous material (2 cm above the surface) was harvested, classified into live and dead matter, oven-dried at 60 °C for approximately 72 h and weighed. An approximate proportion of forb and grass cover was noted.	Oct 2023	n/a
	Herbaceous dark respiration: dark respiration was not measured at the Estação Ecológica da Serra das Araras. Instead, we use dark respiration and specific leaf area (SLA) values of native Cerrado forbs (10 species) and grasses (10 species) measured at the Reserva Ecológica do IBGE near Brasilia in February 2009 (Rossatto and Franco, 2017).	n/a	n/a
R_{soil}	Total soil CO_2 efflux was measured at the centre of the nine central subplots in each plot (N = 9 per plot), using a closed dynamic chamber method. CO_2 concentration and accumulation were measured with an infra-red gas analyser (IRGA EGM-4 and EGM-5, PP Systems) and soil respiration chamber (SRC-1, PP Systems) sealed to a permanent collar in the soil.	Sep 2018 to 2023	1 month
	Soil moisture: was measured monthly at the nine central subplots in each plot alongside soil CO_2 efflux (IRGA EGM-5, PP Systems).	Nov 2023 to Oct 2024	1 month

Under steady-state conditions, the total rate of carbon utilisation by respiration and growth (PCE), should be equal to the photosynthetic carbon inputs into (and respiratory outputs from) the ecosystem (Jones et al., 2020).

$$GPP \approx PCE \approx R_{eco} \tag{7}$$

Where GPP (gross primary productivity) is the total amount of carbon entering the system via photosynthesis, usually estimated through ecosystem-level gas exchange measurements. Because gas exchange measurements are complex and costly, studies assuming steady-state conditions are able to approximate GPP as PCE, which is derived from field sampling methods. However, in non-stable or perturbed systems such as ours – where burnt plots are subjected to periodic fire and unburnt plots are experiencing woody encroachment – ecosystem-level steady-state conditions should not apply as carbon is expected to be lost or accumulated.

$$GPP \not\approx PCE \not\approx R_{eco} \tag{8}$$

In our case, because we cannot derive GPP from PCE, we estimated the ecosystem's carbon use efficiency (CUE) of both burnt and unburnt plots as the proportion of total carbon expenditure (PCE) that is invested in total NPP (rather estimating it as the proportion of GPP invested in NPP, as traditionally reported):

$$CUE = NPP_{total}/PCE \tag{9}$$

We acknowledge that our estimation of total productivity and carbon expenditure does neglect some smaller carbon flux terms. These are relatively minor flows of carbon involved in processes like leaf herbivory, decomposition of litter (in the canopy or from below litterfall traps) and volatile organic compounds (Rocha et al., 2014). We excluded these because they represent mostly negligible aspects of carbon expenditure but do recognise that they are still minor missing terms (Scalon et al., 2022).

2.3. Error analysis and propagation

Many of the carbon fluxes we estimated are calculated from multiple variables or derived from a combination of the more basic fluxes, all of

Table 2

summary of the analysis techniques used for the study of carbon dynamics at the Estação Ecológica da Serra das Araras experimental fire and ecosystem monitoring project, Brazil. Numerical transformations and statistical analyses were performed in R (version 4.3.3) via R Studio (version 2023.12.1 + 402).

Component	Description
$NPP_{litterfall}$	Dry litterfall biomass values were converted into carbon content by multiplying by the 0.49 biomass to carbon ratio (IPCC, 2006). Carbon accumulation was then standardised by interval length and scaled up to obtain estimates per hectare per year. Since litterfall data was spatially and temporally replicated ($N = 9$ subplots per plot per month/fortnight), we obtained annual $NPP_{litterfall}$ estimates at each fire regime for the earliest (2018) and latest (2023) years with complete data using a linear mixed model (Section 2.4; Table 3, model 1). The standard error of the regime-level marginal means of the mixed model was taken to represent sampling uncertainty. No further value of systematic uncertainty was assigned (Girardin et al., 2014).
NPP_{stem}	Forest inventory: aboveground woody carbon stocks were estimated using the Rezende et al. (2006) allometric equation for *cerrado* sensu stricto: $C = 0.24564 + 0.01456 \cdot H \cdot D^2$, where C is aboveground carbon (kg), H is tree height (m) and D is DBH (cm). NPP_{stem} for each tree was calculated as the difference in aboveground woody carbon stock between a census and the previous one, standardised by the interval length between measurements. Total plot NPP_{stem} for a given interval was calculated as the sum of individual-level, positive NPP_{stem} values for stems present at both censuses. Mortality carbon was described as the sum of carbon stock of trees that died by the following census date, as a per-year rate. We compared the earliest (2017–2019) and latest (2021–2023) estimates of NPP_{stem} and $C_{mortality}$ for all experimental fire regimes (using a mean for the unburnt plots). Since these are calculated as a plot-level sum, we did not perform any statistical test as there is no within-plot replication. Following Girardin et al. (2014), we assigned a systematic uncertainty value to our final NPP_{stem} estimates; in our case, 26 % error based on the allometric model error reported by Rezende et al. (2006). Since NPP_{stem} is derived from complete plot inventories, it was not assigned sampling uncertainties. Seasonal growth: growth increment values obtained from dendrometer bands were used as a proxy variable to gain insight on seasonal variation in NPP_{stem}. Circumference increments were converted to diameter (DBH) increments and standardised by interval length. Because dendrometer measurements were spatially and temporally replicated ($N = 25$ to 100 stems per plot per trimester, see Table 1), we analysed them statistically. Since dendrometer data is zero-inflated, we undertook two separate statistical analyses, one using binary data to study the proportion of growing trees, another with positive non-zero data to investigate growth rate of actually growing trees. We thus obtained model estimates for 1) the proportion of growing trees and 2) growth rates of growing trees at each fire regime during the earliest (2019) and latest (2023) years with complete data using mixed-effects models (Section 2.4; Table 3, models 2 and 3). The standard error of the regime-level marginal means of the mixed models were taken to represent sampling uncertainty. No further value of systematic uncertainty was assigned (Girardin et al., 2014).
NPP_{herbs}	Total dry herbaceous biomass values were converted into carbon content by multiplying by the 0.49 biomass to carbon ratio (IPCC, 2006). Herbaceous carbon production was standardised by interval length and scaled up to obtain monthly estimates in relevant units (per hectare per year). Since herbaceous biomass data was spatially and temporally replicated ($N = 12$ quadrats per plot per month) but was only measured at the end of the experiment (from November 2023) we used a linear mixed model to obtain and compare annual estimates of NPP_{herbs} at each fire regime (Section 2.4; Table 3, model 7). The standard errors of the regime-level marginal means of the model were taken to represent sampling uncertainty. No further value of systematic uncertainty was assigned.
$NPP_{coarse\ roots}$	Estimated by assuming that coarse root biomass and productivity was 1.37 ± 0.93 times larger than above-ground woody stems. This root-to-shoot ratio was based on a review of coarse root and above-ground biomass studies from the Cerrado (Miranda et al., 2014). We assigned this root-to-shoot ratio a systematic uncertainty value of ±0.93 (calculated by propagating the standard errors of mean root and shoot biomass estimates presented by Miranda et al. (2014). Total plot $NPP_{coarse\ roots}$ was calculated by multiplying total NPP_{stem} by the root-to-shoot ratio and propagating their uncertainties (this is equivalent to estimating the tree-level coarse root biomass by multiplying stem biomass by 1.37, then calculating the interval difference standardised by time and summing individual $NPP_{coarse\ roots}$ across the entire plot). We then compared the earliest (2017–2019) and latest (2021–2023) $NPP_{coarse\ roots}$ estimates for all regimes, avoiding statistical tests due to the lack within-plot replication. Because they are derived from complete plot inventories, our estimates of $NPP_{coarse\ roots}$ were not assigned sampling uncertainties.
$NPP_{fine\ roots}$	Values of root biomass over the four 10-min time steps were used to model the pattern of cumulative extraction for each ingrowth core sample, using logarithmic regression. Total root biomass in each core was then estimated by solving to 120 min (approximate amount of time required to remove all of the fine roots from a core, see Metcalfe et al., 2007a, 2007b). Estimated biomass was converted into carbon content by multiplying by the 0.45 biomass to carbon ratio for tropical fine roots (Huaraca Huasco et al., 2021), standardised by interval length and scaled up to obtain productivity estimates per hectare. We applied a depth correction proportion of 1.125 to account for additional root growth beyond 30 cm depth based on Yoda (1983) and Kho et al. (2013). Since fine root data was spatially and temporally replicated ($N = 9$ subplots per plot per trimester), we obtained annual $NPP_{fine\ roots}$ estimates at the earliest (2018) and latest (2023) years with complete data using a linear model (Section 2.4; Table 3, model 4). The standard errors of the regime-level marginal means of the mixed model were taken to represent sampling uncertainty. No further value of systematic uncertainty was assigned (Girardin et al., 2014).
R_{canopy}	Leaf area index: LAI of each plot was estimated from fisheye lens images using 'ilastik' (Berg et al., 2019), matlab and 'CANEYE' (Weiss and Baret, 2017) software for pixel classification, image cropping and LAI calculations respectively (see Supplementary Materials for details). Annual LAI estimates (alongside standard error) for each regime were obtained through linear mixed models (Section 2.4). Since plot-level LAI data was temporally replicated but was only measured at the end of the experiment (from December 2022) we used a linear mixed model to obtain and compare annual LAI estimates at each fire regime (Section 2.4; Table 3, model 9). The standard errors of the regime-level marginal means of the mixed model were taken to represent sampling uncertainty. Leaf dark respiration: mean leaf dark respiration (1.34 ± 0.30 $\mu mol\ m^{-2}\ s^{-1}$) was transformed and multiplied by LAI estimates to obtain canopy respiration for each regime (Girardin et al., 2014). The standard error of the mean of respiration values provided by Rossatto and Franco (2017) was used as an estimate of systematic uncertainty, and propagated with LAI sampling uncertainty. We then applied the inhibition factor from Malhi et al. (2009) to account for daytime light inhibition of leaf dark respiration: 67 % of daytime dark respiration, 34 % of total dark respiration. Dry season respiration values were linearly scaled by soil moisture to allow for drought inhibition and continuous variation in respiration (in dry season months, respiration was scaled down by multiplying it by the proportion of that month's moisture with regards to the wet season soil moisture).
R_{stem}	Stem CO_2 efflux: For each EGM sample, the rate of stem CO_2 efflux ($\mu mol\ m^{-2}\ s^{-1}$) was calculated from the linear rate of increase in CO_2 concentration within the chamber (Metcalfe et al., 2007a, 2007b). Since stem CO_2 efflux data was spatially and temporally replicated ($N = 15$ stems per plot per month), we obtained annual estimates at each fire regime for the earliest (Sep 2018 to Aug 2019 for plots ESA-04, ESA-07, ESA-08 and ESA-09, and Sep 2019 to Mar 2020 for ESA-05 and ESA-06) and latest (2023) years with complete data using a linear mixed model (Section 2.4; Table 3, model 5). The standard errors of the regime-level marginal means of the mixed model were taken to represent sampling uncertainty. Stem surface area: Surface area (SA) of every stem was estimated with the Chambers et al. (2004) equation: $\log(SA) = -0.105 - 0.686 \cdot \log(D) + 2.208 \cdot \log(D)^2 – 0.627 \cdot \log(D)^3$, where D is DBH in cm. Individual surface area was then summed to calculate regime tree surface area per hectare. Surface area estimates were assigned a systematic error of 10 % based on similar studies (Girardin et al., 2014). R_{stem} was estimated by scaling up start and end stem CO_2 efflux estimates with total tree surface area in 2019 and 2023 respectively. We compared the earliest and latest R_{stem} estimates for all regimes, propagating stem CO_2 efflux sampling uncertainty and surface area systematic uncertainty. Since R_{stem} was calculated from a plot-level sum, we did not perform any statistical analysis.
R_{herbs}	Live herbaceous biomass: dried live herbaceous biomass values were converted into carbon content by multiplying by the 0.49 biomass to carbon ratio (IPCC, 2006). Since herbaceous biomass data was temporally replicated ($N = 12$ quadrats) but was only measured once at the end of the experiment (October 2023) we used a linear mixed model to obtain and compare estimates at each fire regime (Section 2.4; Table 3, model 8). The standard errors of the regime-level marginal means of the mixed model were taken to represent sampling uncertainty. Herbaceous dark respiration: leaf dark respiration of each species was multiplied by SLA to obtain dark respiration values in terms of dry biomass. We obtained a weighted mean of dark respiration – where grasses were assigned a total weight of 0.8 and forbs 0.2 based on the approximate proportion of biomass (0.031 $\mu mol\ g^{-1}\ s^{-1}$) and multiplied it by the herbaceous live biomass estimates for each regime to obtain R_{herbs} (based on the canopy respiration methodology included in Girardin et al., 2014). The standard error of this weighted mean of grass and forb respiration values provided by Rossatto and Franco (2017) was used as an estimate of large systematic

(*continued on next page*)

Table 2 (*continued*)

Component	Description
	uncertainty (± 0.003 μmol g^{-1} s^{-1}), and propagated with live herbaceous biomass sampling uncertainty. We also applied the inhibition factor from Malhi et al. (2009) to account for daytime light inhibition of leaf dark respiration: 67 % of daytime leaf dark respiration. Dry season respiration was linearly scaled by soil moisture to account for drought inhibition and allow for continuous variation of leaf respiration (in dry season months, respiration was scaled down by multiplying it by the proportion of that month's moisture with regards to the wet season soil moisture).
R_{soil}	For each EGM sample, soil CO_2 efflux rates were calculated from the linear rate of increase in CO_2 concentration within the chamber (Metcalfe et al., 2007a, 2007b). CO_2 efflux rates were then scaled up to R_{soil} at the hectare level. We then obtained R_{soil} estimates (alongside standard error) at the earliest (Sep 2018 to Aug 2019) and latest (2023) annual periods with complete data using mixed models (Section 2.4). Since R_{soil} data was spatially and temporally replicated (N = 9 subplots per plot per month), we obtained annual estimates at each fire regime for the earliest (Sep 2018 to Aug 2019) and latest (2023) years with complete data using a linear mixed model (Section 2.4; Table 3, model 6). The standard errors of the regime-level marginal means of the mixed model were taken to represent sampling uncertainty. No further value of systematic uncertainty was assigned to R_{soil}. We estimated the partition of total R_{soil} into $R_{rhizosphere}$ (autotrophic respiration from plant roots) and $R_{heterotrophic}$ (heterotrophic respiration from microbes) using a ratio of R_{soil} to $R_{heterotrophic}$ based on the values reported by Butler et al. (2012) at another *cerrado* sensu stricto site in Mato Grosso. To calculate the systematic uncertainty associated with this ratio, we extracted the standard errors of the mean for R_{soil} (17.41 ± 1.47) and $R_{heterotrophic}$ (6.49 ± 0.87) reported by Butler et al. (2012), and propagated them accordingly (R_{soil}:$R_{heterotrophic}$ = 0.37 ± 0.06). We then applied this ratio and its complement ratio to our estimate of R_{soil}, propagating their respective systematic and sampling uncertainties to obtain our own estimates of $R_{rhizosphere}$ and $R_{heterotrophic}$.

which incorporate error/uncertainties. Systematic and sampling uncertainties of our carbon flux estimates were thus taken into consideration following the methodological uncertainty analysis provided by Malhi et al. (2009). Systematic uncertainties of key variables – associated with unknown biases in measurements or scaling methods – were assigned a conservative error estimate based on similar studies or on reported error values of allometric equations and ratios (Table 2). Sampling uncertainties arising from heterogeneity and random variation in spatially replicated samples were derived using linear mixed models and marginal means. Using marginal means (and their standard errors) derived from mixed models provided better estimates than those provided through simple arithmetic means (and their standard errors) because these variables were sampled repeatedly and in groupings (see Section 2.4. and Table 2).

Errors were then propagated by taking the square root of the sum of squared absolute errors for addition and subtraction, and relative errors for division and multiplication (Taylor, 1997), assuming independence and normal distribution of uncertainties (where A and B are example variables, and δ represents their associated uncertainty):

$$\delta(A+B) \text{ or } \delta(A-B) = \sqrt{(\delta A)^2 + (\delta B)^2} \tag{10}$$

$$\delta(AB) \text{ or } \delta(A/B) = \sqrt{(\delta A/A)^2 + (\delta B/B)^2} \tag{11}$$

2.4. Statistical modelling and analysis

Statistical models were used to investigate the long-term effect of fire on carbon fluxes ($NPP_{litterfall}$, NPP_{herbs}, $NPP_{fine\ roots}$ and R_{soil}) and flux-related variables (stem DBH growth, stem CO_2 efflux, live herb biomass, and leaf area index – LAI, see Tables 1 and 2) that were spatially and temporally replicated within the monitoring plots. We preferentially used the stronger BACI approach to compare data encompassing the start and end years of the burning experiment, allowing us to extract the fire regime effects as the changes in flux intensity for $NPP_{litterfall}$, stem DBH growth, $NPP_{fine\ roots}$, stem CO_2 efflux, and R_{soil}. We could statistically model the interaction between start-end change and fire regime using linear mixed model (LMMs), which allowed us to account for groups in the data. We also used a binomial generalised linear mixed model (GLMM) to examine changes in the percentage of growing stems to better fit proportional data. For fluxes and variables whose data only covered the end phases of the experiment (NPP_{herbs}, live herb biomass, and LAI), we used the CI or space-for-time substitution framework enabling us to examine spatial differences between fire regimes without being able to actually isolate the specific fire-regime effect. In this case, we investigated differences between experimental fire regimes by using one-way LMMs (Table 3).

Mixed effects models were implemented using the lme4 (version 1.1–35.1) and lmerTest (version 3.1–3) packages in R (Bates et al., 2015; Kuznetsova et al., 2017). The random effects included within the LMMs, and the transformations used to achieve acceptable homoskedasticity and residual normality were specific to each variable being tested (see Table 3). For models using untransformed response variables, we extracted marginal means and their standard error using the emmeans package (version 1.10.0, Lenth, 2024). If response variables were transformed, we extracted back-transformed marginal means and approximate standard errors via the delta method using the car package (version 3.1–2, Fox and Weisberg, 2019). We also used the emmeans package to determine if the carbon flux or variable change at each experimental fire regime is significant by obtaining marginal contrasts for the start/end periods at the regime level.

We decided to undertake an additional analysis to complement our BACI and CI frameworks by accounting for the potentially confounding effect of ecosystem heterogeneity between the monitoring plots, as initial differences in vegetation structure could have influenced the intensity of carbon fluxes and the way in which different variables are affected by fire. We therefore calculated the total basal area – standard indicator of vegetation structure – for each plot using census data from 2017 and included it as an additional additive fixed effect in duplicate versions of models 1 to 9. We then compared models with and without this 'initial basal area' effect using the Akaike information criterion (AIC; Akaike, 1974). Indistinguishable models (where difference in AIC is smaller than 2) were discarded, whilst distinct ones (ΔAIC >2) were run and interpreted.

3. Results

Overall, we measured a total of 4630 different stems, belonging to 71 species and 33 botanical families (Table S1). At the first census (2017) the monitoring plots supported 39 number of species, stem density of 627 stems ha^{-1} and aboveground stem carbon stocks of 3.86 MgC ha^{-1} on average. There was substantial heterogeneity between plots despite proximity – with plot ESA-04 (unburnt) having highest carbon density (5.78 MgC ha^{-1}) in contrast to the least dense (triennially burnt) ESA-07 plot (2.16 MgC ha^{-1}, see Table S1). Fire had noticeable effects on the vegetation structure by 2023, reducing stem density by 113 stems ha^{-1} in the triennial plot, 119 stems ha^{-1} the biennial plot, and 119 stems ha^{-1} annual plot (corresponding to decreases of 0.16 and 0.49 MgC ha^{-1} in the triennially and biennially burnt plots, but an increase of 1.15 MgC ha^{-1} in the annual burns regime, Table S1). We also obtained long-term datasets of different intensively sampled variables (e.g., 5895 datapoints for $NPP_{litterfall}$ or 3312 for stem CO_2 efflux) which allowed us to examine trends and fire-related changes in carbon fluxes.

Table 3
description of the mixed effects models used to examine differences in fluxes and related variables across experimental fire regimes and start-end monitoring periods at the Estação Ecológica da Serra das Araras. All ecologically justified random effects are listed, however, those that did not explain enough variation or increased model complexity beyond convergence were discarded, and have been shown as deleted: ~~(1|factor)~~. Random effects represented groupings within the data and included: plot pair (since plots were set up in pairs), plot (since unburnt plots were grouped within the unburnt fire regime), subplot (for measurements sampled in different subplots over time), stem (for measurements sampled in different tree stems over time) and species (to account for functional/phylogenetic similarities between stems).

	family	response variable	fixed effects	random effects
1	gaussian	$\log_{10}(\text{NPP}_{\text{litterfall}} + 0.1)$	regime * period	~~(1| plot pair)~~ + (1|plot) + (1|subplot)
2	binomial	binary DBH growth	regime * period	~~(1|plot pair)~~ + ~~(1|plot)~~ + ~~(1|subplot)~~ + ~~(1|species)~~ + (1|stem)
3	gaussian	$\log_{10}$(positive DBH growth)	regime * period	~~(1|plot pair)~~ + (1|plot) + ~~(1|subplot)~~ + (1|species) + (1|stem)
4	gaussian	$\log_{10}(\text{NPP}_{\text{fine roots}} + 0.2)$	regime * period	~~(1| plot pair)~~ + ~~(1|plot)~~ + ~~(1|subplot)~~
5	gaussian	stem CO_2 efflux	regime * period	~~(1|plot pair)~~ + (1|plot) + ~~(1|subplot)~~ + (1|species) + (1|stem)
6	gaussian	R_{soil}	regime * period	~~(1| plot pair)~~ + (1|plot) + (1|subplot)
7	gaussian	$\log_{10}(\text{NPP}_{\text{herbs}} + 0.05)$	regime	~~(1| plot pair)~~ + (1|plot) + (1|subplot)
8	gaussian	$\log_{10}$(live herb biomass +1)	regime	~~(1| plot pair)~~ + (1|plot)
9	gaussian	LAI	regime	~~(1| plot pair)~~ + (1|plot)

3.1. *Changes over time and fire regime effects*

Upon observation of trends in Fig. 2, repeatedly sampled variables showed seasonal fluctuations, with peaks corresponding to the dry (NPP$_{\text{litterfall}}$) or wet (stem DBH growth, NPP$_{\text{fine roots}}$, stem CO_2 efflux and R$_{\text{soil}}$) seasons. Comparison of estimates at the start and end of the experiment allowed us to determine if changes in key variables is different in burnt vs unburnt plots, and thus attributable to the fire effect. NPP$_{\text{litterfall}}$ within unburnt plots remained constant from 2018 to 2023, but decreased within the burn plots (Fig. 2; Table S2; Table S3). Stem DBH growth in the unburnt plots – only including positive growth – decreased by 0.09 cm/year between 2019 and 2023 (Fig. 2; Table S4; Table S5) but stayed constant in the burnt plots. The proportion of growing stems was statistically similar in all regimes, in 2019 and 2023 (Table S6; Table S7). NPP$_{\text{fine roots}}$ decreased from 2018 to 2023 in all fire regimes (Fig. 2; Table S8, Table S9), with a stronger change in the triennial and annual burns plots (−1.41 and − 1.46 MgC ha^{-1} year $^{-1}$) compared to the unburnt plots (−1.04 MgC ha^{-1} year $^{-1}$). Stem CO_2 efflux decreased only within the biennially burnt regime (Fig. 2; Table S10; Table S11). R$_{\text{soil}}$ was reduced in all but the biennial burns plot (Fig. 2; Table S12; Table S13).

Fluxes derived from census inventory data also showed different rates of change as a result of fire frequency. Total woody productivity (the sum of NPP$_{\text{stem}}$ and NPP$_{\text{coarse roots}}$) increased by 35 % in the unburnt plots from 2017-2019 to 2021–2023, but decreased by 75 %, 33 % and 20 % in the triennial, biennial and annual fire regimes (Fig. 3). C$_{\text{mortality}}$ remained constant in the unburnt plots but increased by 0.69, 0.76 and 1.19 MgC ha^{-1} year^{-1} in plots with triennial, biennial and annual burns. Stem respiration increased by 0.48 MgC ha^{-1} year^{-1} in unburnt plots but decreased by 0.59, 0.73 and 0.29 MgC ha^{-1} year^{-1} in the triennial, biennial and annual plots as a result of the reduction in plot-level woody stem surface area (−34 % on average from 2019 to 2023).

Variables measured at the later phases of the fire experiment showed seasonal variation peaking in the wet season (NPP$_{\text{herbs}}$, LAI) and revealed consistent patterns across fire frequencies (Fig. 4). Linear mixed models testing for regime differences in log-transformed NPP$_{\text{herbs}}$ and live herbaceous biomass stock did not reveal any significant fire regime effect (Table S14; Table S15). However, despite being statistically indistinguishable, burnt plots showed higher NPP$_{\text{herbs}}$ and live herbaceous stock values, with those corresponding to the triennially burnt plot being 3.6 and 9.4 times larger than the unburnt plots (Fig. 4). LAI estimates displayed the reverse trend, as LAI in the unburnt plots was approximately 10, 4 and 2 times larger than in the triennial, biennial and annual fire regimes; though only the biennial and triennial regime coefficients were significant (Table S16; Fig. 4). As a result, R$_{\text{canopy}}$ in the unburnt plots was 3.91 MgC ha^{-1} year^{-1} higher than in the triennially burnt regime, whereas R$_{\text{herbs}}$ in the triennially burnt plots was 4.70 MgC ha^{-1} year^{-1} higher than in the unburnt plots. Mean tree, forb and grass dark respiration values obtained from Rossatto and Franco (2017) were 1.34 ± 0.30, 2.25 ± 0.49 and 3.08 ± 0.37 μmol m^{-2} s^{-1} (± standard error).

Estimates of the plots' carbon fluxes at the end of the experimental period are visually represented in Fig. 5. Estimates of carbon fluxes and key variables both at the start and end of the experiment (where relevant) are found in Tables S20 to S23, and displayed in Fig. S2 to S4.

3.2. *Importance of initial vegetation density*

We then compared the fit of our mixed effect models with and without initial basal area as a fixed effect. Models incorporating initial basal area were all indistinguishable (ΔAIC <2; Table S17), except for models estimating NPP$_{\text{herbs}}$ and live herbaceous biomass. Mixed models studying the regime-level differences in log-transformed NPP$_{\text{herbs}}$ and live herbaceous biomass revealed the distribution of stocks and productivity could be explained by a gradient in initial basal area, with triennially and annually burnt plots presenting significantly higher estimates than those just predicted by initial basal area (Table S18; Table S19).

3.3. *Total net primary productivity, respiration, plant carbon expenditure and carbon use efficiency*

The individual components of NPP were added to give an estimate of NPP$_{\text{aboveground}}$, NPP$_{\text{belowground}}$ and NPP$_{\text{total}}$ (Fig. 5). NPP$_{\text{total}}$ for the unburnt plots was 3.72 ± 0.71 Mg C ha^{-1} year^{-1}, 0.92 ± 0.15 Mg C ha^{-1} year^{-1} for the triennial plot, 1.31 ± 0.22 Mg C ha^{-1} year^{-1} for the biennial plot and 2.40 ± 0.63 Mg C ha^{-1} year^{-1} for the annually burnt plots. The proportion of NPP$_{\text{aboveground}}$ within NPP$_{\text{total}}$ was 0.53 ± 0.12 in the unburnt plots, 0.43 ± 0.11 in the triennial burns plot, 0.42 ± 0.11 in the biennial burns plot, and 0.48 ± 0.16 in the annual burns plot. We partitioned total R$_{\text{soil}}$ using the proportion of R$_{\text{rhizosphere}}$ and R$_{\text{heterotrophic}}$ where R$_{\text{heterotrophic}}$ represents 0.37 ± 0.06 of R$_{\text{soil}}$. Subsequently, the components of R were also summed to give estimates of R$_{\text{eco}}$ and R$_{\text{autotrophic}}$. R$_{\text{eco}}$ in the unburnt plots was 14.57 ± 1.21 Mg C ha^{-1} year^{-1}, and 13.74 ± 3.43, 11.55 ± 1.32 and 12.72 ± 1.12 Mg C ha^{-1} year^{-1} for the triennially, biennially and annually burnt plots. The proportion of R$_{\text{autotrophic}}$ within R$_{\text{eco}}$ was 0.81 ± 0.11 in the unburnt plots, 0.80 ± 0.32 in the triennial burns plot, 0.73 ± 0.14 in the biennial burns plot, and 0.77 ± 0.11 in the annual burns plot. The sum of NPP$_{\text{total}}$ and R$_{\text{autotrophic}}$ yielded an estimated PCE of 15.58 ± 1.44 Mg C ha^{-1} year^{-1} for the unburnt plots, and 11.96 ± 3.42, 9.79 ± 1.33 and 12.18 ± 1.28 for the triennially, biennially and annually burnt plots respectively The ratio of NPP$_{\text{total}}$ to PCE gave an estimated CUE of 0.24 ± 0.05 in the unburnt plots, 0.08 ± 0.03 in the triennial burns plot, 0.13 ± 0.03 in the biennial burns plot, and 0.20 ± 0.06 in the annual burns plot (Fig. 5).

4. Discussion

This study provides the most detailed carbon flux dataset within South American savannas and represents one of the few tropical studies to thoroughly examine the effect on fire on net primary productivity and respiration dynamics using field-based ecosystem monitoring – similar studies exploring fire responses in NPP, R, and GPP have been undertaken in fire-sensitive tropical forests in Amazonia (Rocha et al., 2014; Berenguer et al., 2021). Until now, findings from the Cerrado have either focused on quantifying natural ecosystem nutrient and carbon balances (Scalon et al., 2022; Vourlitis et al., 2022) or investigating the effect of fire on individual fluxes and vegetation components (e.g., Meirelles and Henriques, 1992; Le Stradic et al., 2021). We thus focus our discussion on the main insights that our experimental burning and monitoring project bring to the understanding of how carbon fluxes are affected by altered fire regimes in Brazilian woodland savannas.

4.1. Fire reduces the strength of arboreal carbon fluxes

The results presented in this study provide useful insight into the dynamics of arboreal carbon fluxes ($NPP_{litterfall}$, NPP_{stem}, $NPP_{coarse\ roots}$, R_{canopy} and R_{stem}) in the Cerrado, both in the presence and absence of fire. NPP_{stem} is notably lower than the estimate of 2.79 ± 0.45 provided by Scalon et al. (2022), giving the first insight into the potential range of values of NPP_{stem} within Cerrado woodland savannas. In comparison to other vegetation types, our unburnt plot estimates show lower stem productivity than more afforested formations like *cerradão* (2.77 ± 0.58; Scalon et al., 2022) and gallery forests (1.67; Vourlitis et al., 2022), but higher estimates than those with more open structures like *campo sujo* (0.345; Vourlitis et al., 2022). Our results also reveal that in unburnt plots, NPP_{stem} is not constrained by competition arising from denser vegetation structure (Falster et al., 2011; Ma et al., 2020), but that NPP_{stem} appears to increase with basal area and stem density (Fig. S2). Values of litterfall productivity fit those previously estimated by Peres et al. (1983), Wilcke and Lilienfein (2002), Nardoto et al. (2006) and Kozovits et al. (2007) all reporting total annual $NPP_{litterfall}$ for *cerrado* sensu stricto within the 1.5 MgC ha^{-1} $year^{-1}$ range. We present one of the first estimates of $NPP_{coarse\ roots}$, R_{canopy} and R_{stem} within South American savannas. We recognise that the $NPP_{coarse\ roots}$ results here presented are broad estimates derived from a proportion of NPP_{stem} that might hide important dynamics across time and fire regimes. Coarse root harvests could reveal distinct patterns in root productivity arising as a result of the variation in R:S across environmental gradients within the Cerrado (Terra et al., 2023) or due to changes in belowground carbon allocation after frequent fires (Zhou et al., 2022).

Our findings are consistent with our initial hypothesis, confirming the fact that recurrent burning within cerrado sensu stricto vegetation causes a reduction in vegetation density, number of trees and live biomass, and limits the strength of tree-mediated fluxes. These patterns are linked to the increases in stem mortality rates within the experimentally burnt plots and reveal that the growth and performance of surviving trees are also affected by fire (Reis et al., 2015; Rodrigues and Fidelis, 2022). Experimental burning also appears to have led to higher herbaceous biomass and productivity. This is consistent with patterns presented by Meirelles and Henriques (1992), Gomes et al. (2020) and Teixeira et al. (2022), and provides supporting evidence towards the use of controlled burning as a management strategy against woody encroachment (Pivello et al., 2021).

We are confident that our comparison of estimates at the start and end of the experiment – following a BACI-type approach – allowed us to better isolate the ecological effect of our experimental fire regimes by acknowledging the background variation in flux patterns due to stochasticity – that is the degree of change in the unburnt plots. Future analyses could focus better predicting the dynamics of fire regime impacts using improved frameworks such as the BACI paired-series or progressive-change BACI approaches (Thiault et al., 2017), although the integration of strong seasonal fluctuations and uneven sampling intervals remains challenging. It is also important to note that since variables have been measured at distinct periods, we capture the ecological effect of somewhat different aspects of each regime. We also acknowledge that extracting accurate fire regime effects was further difficulted by differences in arboreal vegetation density across plots. Spatial replicates within our monitoring plots allowed us to account for substantial within-plot heterogeneity, although, as a form of pseudoreplication, we cannot reliably conclude fire regime impacts will exhibit similar dynamics across areas of vegetation with different composition and structure. Still, in most cases, incorporating an initial structural indicator variable such as basal area did not improve model fit, confirming patterns of flux change appear unaffected by vegetation structure. Distribution of herbaceous biomass and productivity could be partially explained by a gradient in initial basal area, as the weaker space-for-time substitution analysis used for these variables does not incorporate before-impact spatial differences. Still, the presence of significant fire regime coefficients in the basal area models confirms strong experimental fire effects on herbaceous fluxes.

4.2. Fire regime properties affect ecosystem components differently, warranting long-term monitoring

Our second main finding is that fluxes corresponding to the different ecosystem components (canopy, stems, roots, herbs and soil) showed varying distributions and patterns of change across the gradient of experimental fire frequencies, meeting our expectations and indicating different fire regime properties distinctively affect each vegetation component. By definition, each fire regime incorporates a range of patterns including the timing, duration, seasonality, behaviour, distribution, intensity and severity of the fire events (Kelly et al., 2023). Our experimental fire regimes also encompassed the particular characteristics of each fire event, as experimental burns are unique, non-replicable disturbances with singular temporal and energetic dynamics that limit the applicability of the traditional treatment-control experimental design. In our experiment, controlled fire events exhibited substantial differences between fire regimes, where smaller intervals between fires in the annually burnt plot led to patchy, low-intensity surface fires due to lower accumulation of fuel and higher proportion of bare soil (Rodrigues and Fidelis, 2022). Alternatively, fires in the biennially and triennially burnt plots were quicker, more severe and homogeneous, and affected the canopy to a greater extent (Rissi et al., 2017). The trade-off between fire frequency and intensity allowed us to determine which fluxes are primarily influenced by these broad fire regime axes. Fire intensity and severity seem to be more strongly linked with patterns in fluxes of woody stems and herbs, the two vegetation components that are most affected by burning under the low-intensity fire regimes of the Cerrado (Chiminazzo et al., 2023). In contrast, long-term changes in $NPP_{litterfall}$ and mortality carbon appear to be more strongly related to fire frequency rather than fire intensity. Reduced litterfall productivity and higher mortality in the annually burnt plot could be explained by the negligible impact of short-term leaf charring and consumption on overall leaf production, by more cumulative burns with short recovery interval having stronger tree-wide impacts on fitness, or by an interactive effect between fire impacts and stem density. The mismatch between trends in mortality and NPP_{stem} – where a stronger decline in the triennial plot reveal more intense fires disproportionately reduce aboveground growth in surviving trees – warrants a more detailed analysis on tree vulnerability across species and functional strategies.

It is important to note that the herbaceous layer exhibits short-term responses and recovery after fire (Fontenele and Miranda, 2024). This explains why the biennial plot exhibits lower herbaceous biomass and productivity, as it was burnt shortly before herbaceous monitoring was implemented. On the contrary, fire had a more delayed effect on tree fluxes. Despite burning in 2018, the annual and triennial plots showed negligible mortality rates along the 2017–2019 interval, and supported

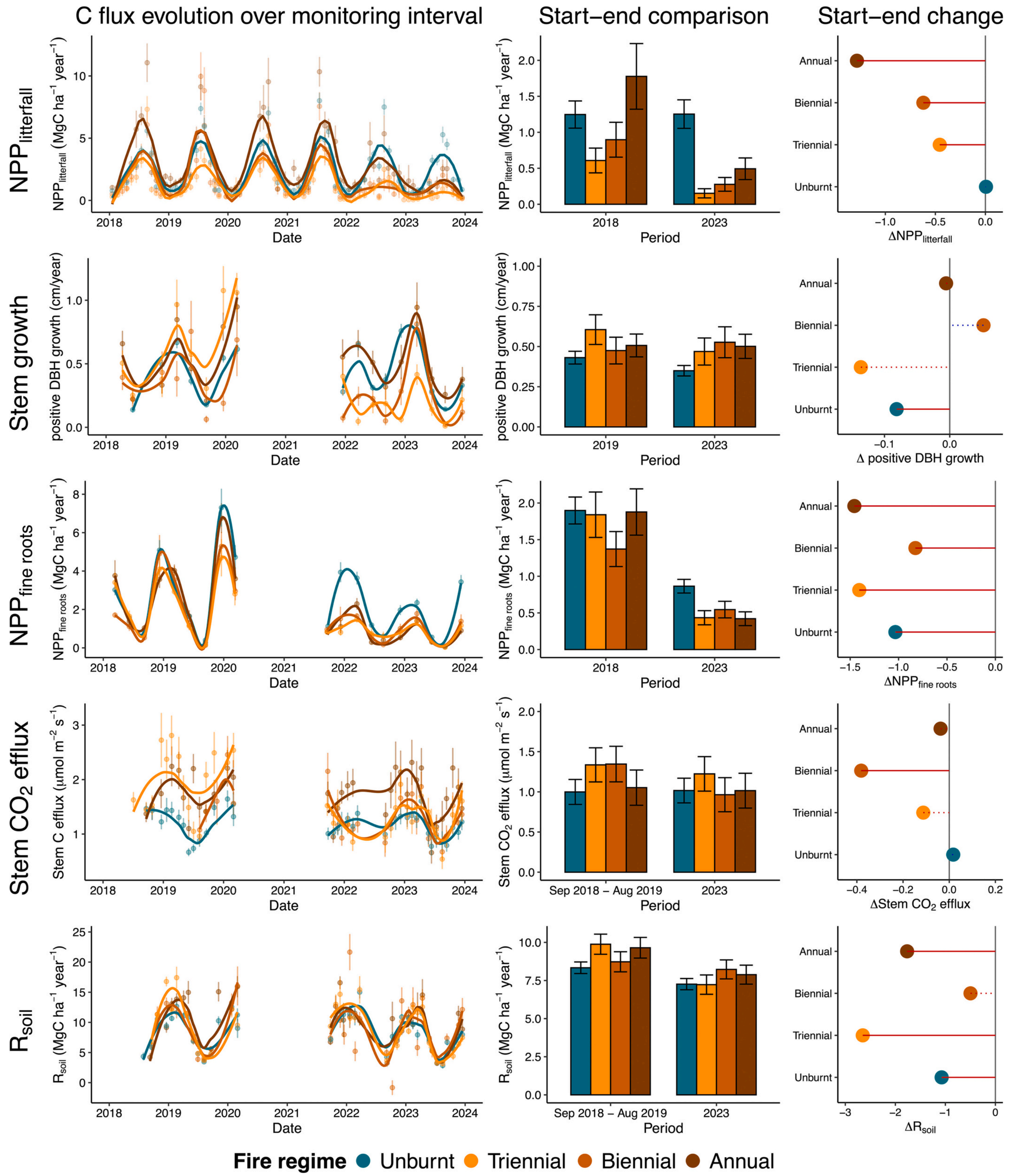

Fig. 2. influence of experimental fire regimes on variables that were intensively sampled throughout the duration of the experiment at the Estação Ecológica da Serra das Araras. Plots on the left present the trends over time using monthly averages and loess smoothers (error bars represent arithmetic standard error values per fire regime per sampling date, see Table 1 for sample size details). Plots in the centre show the estimates, in absolute terms, for each regime at the start and end periods (error bars represent marginal mean standard error derived from the linear mixed models; please see Tables S2 to S13 for model output details). Plots in the right illustrate the start-end change in variables (represented by delta Δ, same units as absolute values), with solid lines indicating statistically significant contrasts between periods.

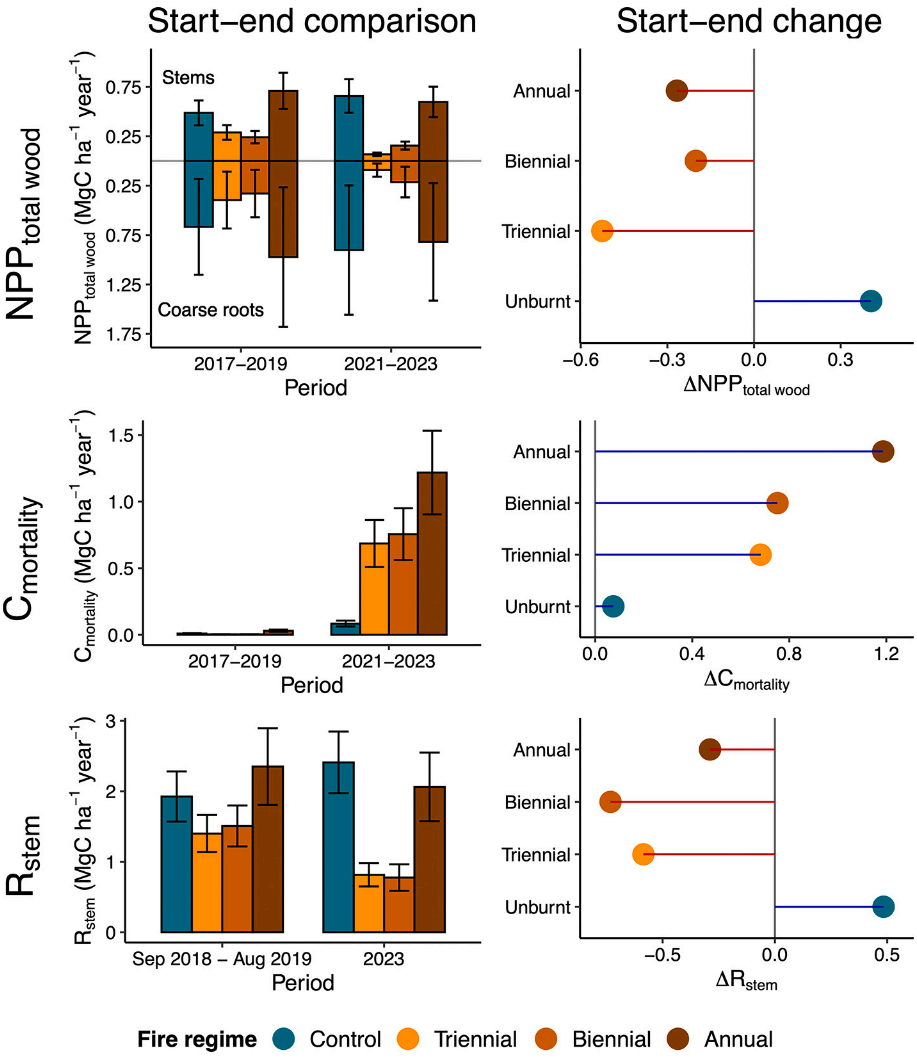

Fig. 3. influence of fire regimes on carbon fluxes (MgC ha^{-1} year^{-1}) that were derived from tree inventory data. Plots in the left show the regime-level comparison of each variable at the start and end of the experiment in terms of absolute values. Plots in the right reveal the degree of change in fluxes over time (represented by the delta symbol Δ, same units as absolute values). Error bars indicate systematic uncertainty in the case of NPP$_{stem}$ and C$_{mortality}$, and propagated error including systematic uncertainty and sampling error for NPP$_{coarse\ roots}$ and R$_{stem}$ (see Table 2 for details).

relatively constant stem respiration rates 6 years into burning, indicating lags in fire mortality and physiological resilience of surviving trees (Berenguer et al., 2021). Overall, in the long term, we observe the most dramatic differences in herbaceous vs arboreal dominance within the triennially burnt plot, as indicated by the fire regime ‘control-impact’ comparisons of herbaceous biomass and LAI. However, the lack of data at the start of the experiment prevents us from determining the degree of change of these variables as a result of fire, meaning we are unable to synthetically addresses the overall trade-off between fire intensity and frequency effects in terms rate of change. Still, LAI distribution in is consistent with end-period NPP$_{litterfall}$ values across regimes, and inversely related with both herbaceous biomass and productivity values. Patterns of herbaceous vegetation and LAI also suggest the implementation of controlled fire could have further influenced carbon fluxes and ecosystem processes in indirect ways, as a more open canopy could have increased temperature and water deficit (De Sales et al., 2023), whilst grass dominance could have increased competition against seedling establishment and resprouting (Sankaran et al., 2004). We therefore conclude that less frequent but more severe fires, coupled with a smaller proportion of surviving stems in the plots, could be providing a positive feedback dynamic that leads to more drastic changes in vegetation structure towards grass-dominated savanna systems in the Cerrado. However, less clear patterns of change in several other carbon fluxes could also indicate that ecosystem shifts might not be consistent and unidirectional across different ecological processes.

Analysing positive stem growth values revealed diameter growth significantly decreased within the unburnt plots, which seems to contradict our plot-level NPP$_{stem}$ results. We recognise that dendrometer bands focus only on diameter growth, and were only installed within larger individuals, therefore capturing only part of the woody productivity dynamics. Dendrometer measurements would have also incorporated water swelling and shrinking dynamics, as well as bark loss to fire, limiting the adequateness of data as a proxy for seasonal stem productivity. Similarly, smaller sampler sizes in the burnt plots, alongside high tree mortality, could have restricted the representativeness of our data.

Lower stem CO$_2$ efflux could have arisen as a result of compromised plant metabolism after the intense 2023 fire in the biennially burnt plot (Cernusak et al., 2006), although large variation in efflux values as a result of confounding variables relating to time of day, temperature, species composition, hydrology and metabolism (Rowland et al., 2018) support the need for more detailed investigation into stem respiration patterns. More detailed, long-term research into soil respiration and fine root productivity will also help us determine why the intensity of these two fluxes decreases regardless of fire regime. High dynamism in soil

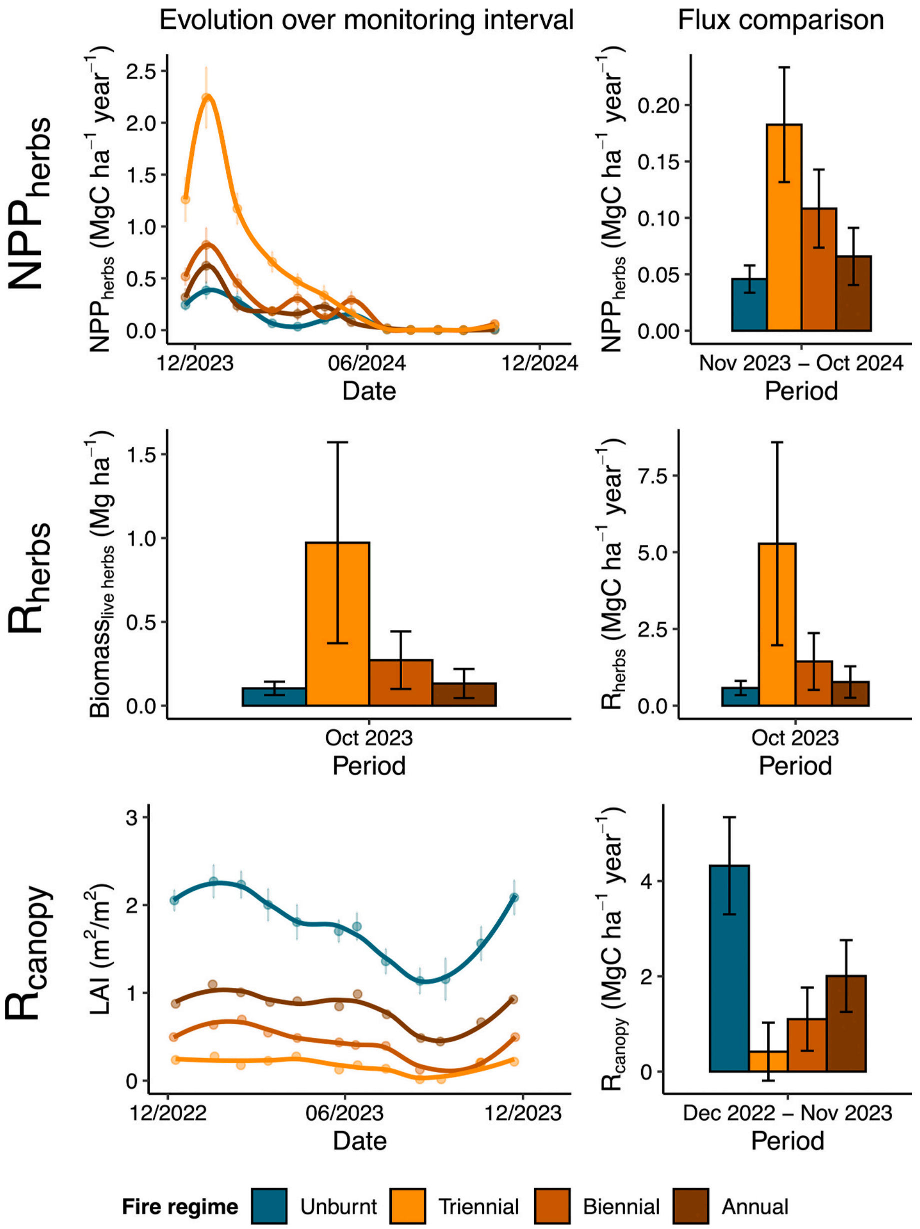

Fig. 4. regime-level comparison of carbon fluxes and related variables that were sampled at the end of the experimental fire project at the Estação Ecológica da Serra das Araras. Plots on the left represent the evolution of sampled variables over time using monthly averages and loess smoothers (error bars represent arithmetic standard error values per fire regime per sampling date, see Table 1 for sample size details). Please note R_{herbs} and R_{canopy} were not measured directly; biomass of live herbs and LAI were respectively measured as proxy variables, then scaled up to using dark respiration values. Also note biomass of live herbs was measured once; error bars instead represent marginal mean standard error derived from the linear mixed model. Plots in the right include the regime-level comparison of the scaled-up fluxes (error bars represent sampling error as marginal mean standard error derived from the linear mixed model in the case of NPP_{herbs}, and propagated error including sampling and systematic uncertainty for R_{canopy} and R_{herbs}; see Tables 2 and S12 to S16 for details).

ecosystem processes (Nottingham et al., 2015) and the onset of warmer and drier El Niño conditions at the end of 2023 could have explained this trend. We therefore highlight the importance of continuing long-term studies in order to disentangle the ecological effects of fire, as well as the interactions between burning and other pressures.

4.3. Fire influences on carbon flux allocation, carbon use efficiency and ecosystem disequilibria

Long-term monitoring of the main ecosystem components allowed us to study if experimental burns have influenced the way in which carbon is allocated into different fluxes, partially supporting our expectations and hypotheses. Comparison of NPP components across the fire regimes revealed burning appears to have reduced the proportion of productivity distributed into aboveground fluxes. This pattern was not consistent with our expectation of higher aboveground productivity due to post-fire resprouting and regrowth (Le Stradic et al., 2018), as increasing herbaceous productivity has not yet compensated for reduced arboreal growth. Carbon allocation into total heterotrophic respiration appears to have increased within the burnt plots – despite estimate uncertainty – supporting our hypothesis of stronger influence of microbial metabolism as live biomass stock is replaced by decomposable dead matter (Brando et al., 2014). The use of a respiration partition ratio derived from data from a nearby site allowed us to construct a full carbon balance but might not adequality represent the real ecological dynamics in our plots. The implementation of root exclusion methods in situ would enable us to

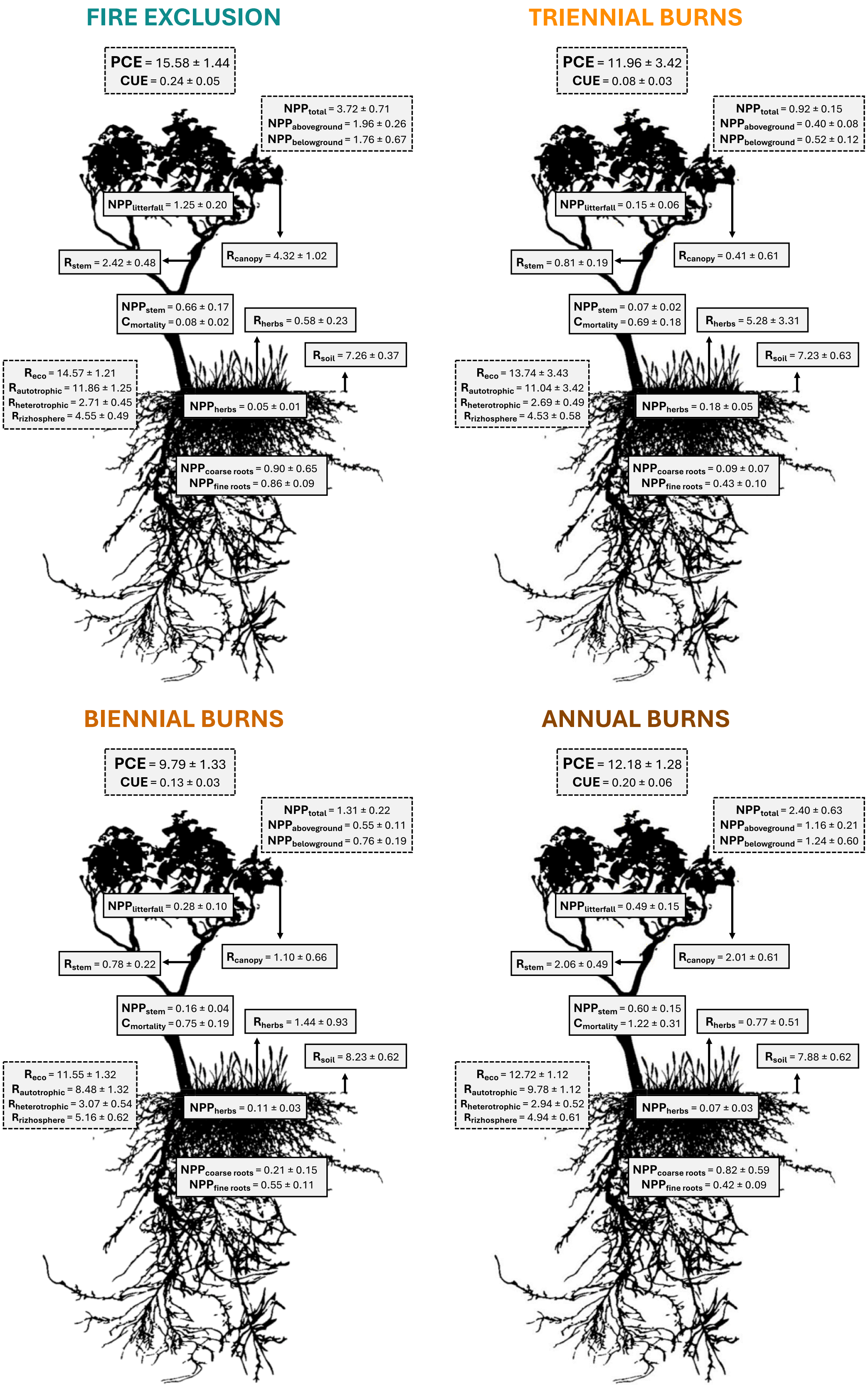

Fig. 5. main carbon fluxes (MgC ha^{-1} year^{-1}) and associated uncertainties within the experimental burning plots at the Estação Ecológica da Serra das Araras. Fluxes were estimated approximately six years into the experimental fire regimes.

provide better estimates of $R_{heterotrophic}$ and $R_{autotrophic}$. More accurate soil respiration partitioning between rhizosphere and microbial sources would account for temporal variations and changes in the soil environment across fire regimes (Butler et al., 2012). Similarly, measuring site-specific dark respiration values across local species of trees and herbs would provide more reliable estimates of R_{herbs} and R_{canopy}, helping tackle the critical lack of information on plant respiration rates across South American savannas. We acknowledge that using dark respiration measurements from another site measured in the wet season and in the absence of fire only lets us produce a very rough estimate of annual respiration fluxes, and this is reflected in the disproportionately large uncertainty of R_{herbs} and R_{canopy} estimates. Still, the use of LAI and herbaceous biomass to scale up leaf respiration – adapting a well-established methodology (Malhi et al., 2009) – allows us to bring forth a first approximation of respiratory dynamics and quantify the ecosystem-level carbon balance of mixed tree-grassland ecosystems despite carrying significant uncertainty at this stage.

The ecosystem-level carbon fluxes presented in this study seem to fit within the aridity and vegetation cover gradients observed in South American ecosystem monitoring plots (Zhang-Zheng et al., 2024), where values for NPP_{total}, GPP or PCE, and CUE are lower than those reported for seasonally dry forests in the margins of Amazonia in Bolivia (Araujo-Murakami et al., 2014) and Mato Grosso (Rocha et al., 2014). Total NPP was also substantially smaller than the sum of $NPP_{litterfall}$, NPP_{stem} and $NPP_{fine\ roots}$ presented by Scalon et al. (2022), for both *cerrado* sensu stricto and *cerradão*. Plot-specific results within the fire exclusion regime also suggest more efficient use of carbon is dependent on higher woody vegetation density at the local scale as a result of woody encroachment. Our values for the carbon use efficiency of the burnt plots fall closer to some of the estimates provided by Vourlitis et al. (2022) for grassland savannas near Cuiabá, Mato Grosso (0.16 and 0.29 using inventory-based estimates, and 0.08 and 0.15 from eddy covariance methods). Although substantial interannual variation, mismatch between eddy covariance and inventory methods, and differences in sampling methodology imply any comparison should be taken with caution, lower CUE estimates could indicate experimental fire is shifting ecosystem-wide balances towards those of grass-dominated savannas.

Experimental burning also appears to be switching ecosystem equilibrium dynamics from carbon accumulation to carbon losses, as illustrated by the comparison of $R_{heterotrophic}$ and NPP_{total}, which represent the overall inputs and outputs of carbon into the soil, approximately matching one another in steady-state conditions (Raich and Nadelhoffer, 1989). Within the unburnt plots, NPP_{total} exceeds $R_{heterotrophic}$ by >1 MgC ha^{-1} $year^{-1}$, yet $R_{heterotrophic}$ is larger than total productivity in all burnt plots. We recognise, however, that this exercise simplifies complex ecosystem dynamics by assuming no lags in the dynamics of carbon inputs and outputs, and ignores heterotrophic respiration arising from other ecosystem components. Several unknowns remain regarding the role of dead wood and charcoal in the carbon balance of burnt plots, given the high proportion of standing dead stems and the amount of partially combusted wood that is inputted into the soil (Gomes et al., 2020; Teixeira et al., 2022). Further study of the dynamics of the deadwood and soil carbon pools, as well as quantification of the direct carbon emissions through fire combustion, would allow for a better evaluation of the carbon impacts of altered fire regimes in the face of intensifying global change. (Terra et al., 2023).

5. Conclusions

The findings presented by this study have provided useful insight into the net primary productivity and carbon flux dynamics within the Cerrado biodiversity hotspot. It represents an initial step towards the understanding of how altered fire regimes are influencing its ecosystem functioning and carbon budgeting. Experimental burning regimes affected the vegetation structure and carbon dynamics by reducing woody cover and arboreal productivity, leading to a shift towards more open, grass-dominated vegetation. Our findings indicate periodically burnt *cerrado* sensu stricto would experience overall carbon losses, although the different patterns of change across ecosystem components reveal shifts are not consistent across ecological processes as a result of interactions between fire regime variables and other environmental factors. Our work complements previous studies revealing the variability of productivity and respiration of South American savanna vegetation, emphasising the diversity of ecological processes and responses to pressure between ecosystems. Long-term research on the effect of fire on carbon should therefore be extended into different locations and vegetation types incorporating a diverse range of geographies, vegetation characteristics, and experimental burning strategies, and be integrated across regional and biome scales with the help of technological advances in automation and remote sensing. Our results can aid and inform fire management programmes that prioritise biodiversity and landscape conservation. In that respect, controlled burning strategies within savannas and other open ecosystems should adjust fire frequencies depending on the reduction on woody cover and arboreal productivity that is desired. Nonetheless, fire management programs must also account for the effect on fire on species performance, biodiversity and ecosystem services, as well as social considerations and political constraints. Only then will we obtain a coherent and improved understanding of fire management for the conservation of fire-mediated ecosystems worldwide.

CRediT authorship contribution statement

Francisco Navarro-Rosales: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Maria Antonia Carniello:** Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Wesley Jonatar Alves da Cruz:** Writing – review & editing, Methodology, Investigation, Data curation. **Flavio de Campos Oliveira:** Investigation, Data curation. **Huanyuan Zhang-Zheng:** Writing – review & editing, Software, Methodology. **Valéria Lucélia de Oliveira Corrêa:** Investigation, Data curation. **Marcelo Leandro Feitosa de Andrade:** Resources, Investigation. **Yadvinder Malhi:** Writing – review & editing, Methodology. **Andrew Hector:** Writing – review & editing, Writing – original draft, Methodology. **Imma Oliveras Menor:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Funding sources

This work was supported by the University of Oxford (John Fell Fund 163/03), the UKRI Natural Environment Research Council (Standard Grant NE/W00058X/1), the Fundación Rafael del Pino, Madrid, Spain (Postgraduate Excellence Scholarship to Francisco Navarro-Rosales), and the EU Marie Skłodowska-Curie Action awarded to FIRE-ADAPT (project no. 101086416).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Davi Rodrigo Rossatto and Augusto César Franco for sharing their data; and Simone Matias Reis, Carlota Segura-García, Manoela Machado and Cecilia Dahlsjo, for support in fieldwork and writing. We are grateful to ICMBio professionals assisting in site conservation and controlled burns, and to the many interns and volunteers associated with UNEMAT and the HPAN (Herbario do PANtanal) who contributed to botanical and data collection activities. We are thankful to our institutions and colleagues for their continued support, highlighting the transport and logistical assistance provided by UNEMAT and ICMBio.

Appendix A. Supplementary data

The supplementary file attached to this article contains additional details on i) the methodology used to derive leaf area index values, ii) the structural and compositional characterisation of the monitoring plots, and iii) the statistical model outputs, as well as iv) start and end summaries of carbon fluxes and related variables.Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179626.

Data availability

Carbon flux and related variable data is available within the supplementary material. Raw data will be available upon request to the authors. Tree inventory data is available through Forestplots.net.

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Update

Science of the Total Environment

Volume 1018, Issue , 25 February 2026, Page

DOI: https://doi.org/10.1016/j.scitotenv.2026.181538

Science of the Total Environment 1018 (2026) 181538

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Corrigendum

Corrigendum to "The effect of fire on the carbon fluxes and productivity of Brazilian woodland savannas" [Science of The Total Environment volume 987 (2025) 179626]

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The authors inform that the species identification of *Tachigali paniculata* Aubl. has been revised, and updated to *Tachigali vulgaris* L.G. Silva & H.C. Lima. Original voucher specimens and botanical samples of *Tachigali* from the Estação Ecológica da Serra das Araras have been shared with taxonomic specialists. Based on morphological characteristics, experts have agreed the identity of the species is *T. vulgaris*. The paragraph describing vegetation structure upon the establishment of ecosystem monitoring plots should therefore read 'Dominant tree species include *Curatella americana* L., *Kielmeyera grandiflora* (Wawra) Saddi, *Tachigali vulgaris* L.G. Silva & H.C. Lima, *Vochysia haenkeana* Mart., *Myrcia bella* Cambess., and *Pouteria ramiflora* (Mart.) Radlk.'. The species' identity has also been corrected in Table S1 describing ecosystem characteristics of each monitoring plot at Serra das Araras, and the updated Supplementary Materials have been attached to this corrigendum.

The authors would like to apologise for any inconvenience caused.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.181538.

DOI of original article: https://doi.org/10.1016/j.scitotenv.2025.179626.

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https://doi.org/10.1016/j.scitotenv.2026.181538