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ABSTRACT

Fire is an evolutionary environmental filter in tropical savanna ecosystems altering functional diversity and associated C pools in the biosphere and fluxes between the atmosphere and biosphere. Therefore, alterations in fire regimes (e.g. fire exclusion) will strongly influence ecosystem processes and associated dynamics. In those ecosystems C dynamics and functions are underestimated by the fire-induced offset between C output and input. To determine how fire shapes ecosystem C pools and fluxes in an open savanna across recently burned and fire excluded areas, we measured the fol- lowing metrics: (I) plant diversity including taxonomic (i.e. richness, evenness) and plant functional diversity (i.e. func- tional diversity, functional richness, functional dispersion and community weighted means); (II) structure (i.e. above- and below-ground biomass, litter accumulation); and (III) functions related to C balance (i.e. net ecosystem carbon di- oxide (CO_2) exchange (NEE), ecosystem transpiration (ET), soil respiration (soil CO_2 efflux), ecosystem water use ef- ficiency (eWUE) and total soil organic C (SOC). We found that fire promoted aboveground live and belowground biomass, including belowground organs, coarse and fine root biomass and contributed to higher biomass allocation be- lowground. Fire also increased both functional diversity and dispersion. NEE and total SOC were higher in burned plots compared to fire-excluded plots whereas soil respiration recorded lower values in burned areas. Both ET and eWUE were not affected by fire. Fire strongly favored functional diversity, fine root and belowground organ biomass in piecewise SEM models but the role of both functional diversity and ecosystem structure to mediate the effect of fire on ecosystem functions remain unclear. Fire regime will impact C balance, and fire exclusion may lead to lower C input in open savanna ecosystems.

HIGHLIGHTS

- Alterations of fire regimes influence tropical savannas water and carbon exchange.
- Fire presence modified carbon balance increasing soil and belowground carbon input.
- Fire promotes functional diversity due to plant regeneration post-fire strategies.
- Fire exclusion leads to losses on soil carbon and functional diversity.

GRAPHICAL ABSTRACT
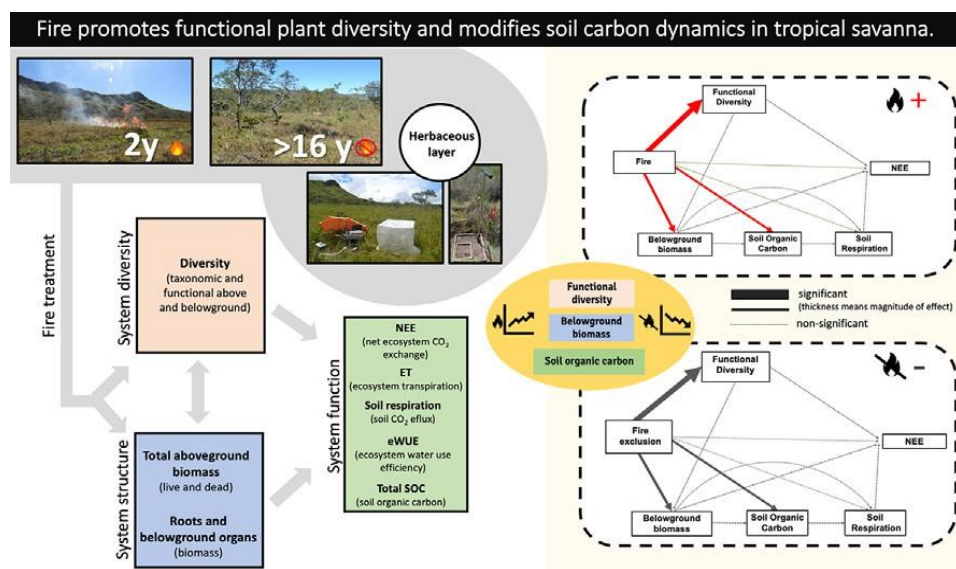
1. Introduction

Disturbances (e.g., fire) can alter carbon (C) dynamics and overall C balance by shifting the amount of C input and output from ecosystems consequently altering stocks in the biosphere and fluxes between the atmosphere and biosphere (Goetz et al., 2007). Fire is fundamental for the maintenance of C balance and ecosystem function at fire prone-ecosystems, such as open tropical savannas (McLauchlan et al., 2020). However, currently fire regimes of many fire-prone systems have been deeply changed across the globe (Archibald, 2016; Rogers et al., 2020) potentially altering C dynamics in fire-dependent ecosystems. Some studies already suggested that fire suppression in savannas will lead to changes of C dynamic equilibrium, decreasing the ecosystem C sink capacity (Beringer et al., 2015; Yin et al., 2020). Even so, the indirect and direct impacts of changes in fire regimes on C dynamics remain still poorly understood and are not explicitly analyzed addressing interfaces of fluxes between the atmosphere and biosphere alongside with C stocks to capture overall C dynamics (Pausas and Bond, 2020; Yin et al., 2020).

Changes in tropical savanna fire regimes (i.e., increase or decrease of fire frequencies) will lead to changes in vegetation structure or soil composition for example, causing plant-soil feedback that might modify the global C dynamics (Da Silva and Batalha, 2008; Grace et al., 2006; Pellegrini et al., 2020). Those plant-soil feedback alterations may occur due to differential responses of vegetation regrowth after fire (C input) (Archibald et al., 2018), soil respiration modification (C release), variations on soil organic carbon (SOC, C input), and changes in microbial activities (C fixing, Chapin et al., 2011; Dove et al., 2021; Pressler et al., 2019). Fire exclusion may increase aboveground biomass, decreasing grasses fuel load, affecting thus fire intensity (Fidelis et al., 2013, 2018). Thus, due to changes in fuel load and vegetation structure by the replacement of grassy by woody vegetation, C input after fire as a result of regrowing vegetation may be compromised. First, because fire exclusion can negatively impact the herbaceous layer, since some species may disappear after some time without fire (Pilon et al., 2021b). Secondly, in fire-excluded areas, as a consequence to increasing woody cover, the release of C to the atmosphere will contribute more in case of fire, compromising C balance (Richards et al., 2011; Simpson et al., 2021). In addition, woody encroachment caused by fire exclusion may lead to changes in SOC pool, i.e. SOC losses and decrease in soil respiration which are fundamental properties of interconnections between the biosphere and the atmosphere (Abreu and Durigan, 2011; Chen et al., 2003; February et al., 2020; Jackson et al., 2002). On the other hand, SOC may increase after fire exclusion due to the stabilization of soil organic matter (Pellegrini et al., 2021) and thus, further studies about the effects of changes in fire regimes are needed to elucidate carbon dynamics in different fire-prone ecosystems.

Moreover, changes in fire frequency will lead to changes in biomass allocation and belowground traits, both greatly influencing soil C pools and fluxes balance (Jackson et al., 2000). Indeed, higher C investment in belowground biomass in tropical grassy biomes is partly in response to fire (De Castro and Kauffman, 1998; Fidelis et al., 2013), where plants shift their strategy by allocating resources from above to belowground (Archibald et al., 2018, 2019). The belowground biomass investment represents the major component of C input in grassy biomes (De Castro and Kauffman, 1998; Ottaviani et al., 2020). Belowground traits, especially root traits, are key functional traits that shape several ecosystem processes (Freschet et al., 2021) and are subject to be affected by fire and changes in vegetation structure (Loiola et al., 2015). For example, root traits from grasses such as higher specific root length and dense root system in the superficial soil layer promote efficiency of water and nutrients use (Case et al., 2020; Freschet et al., 2018; Linder et al., 2018) being related to ecosystem C input mainly at shallow soil layer (Jobbagy and Jackson, 2000). Root traits (e.g. rooting depth) from trees and shrubs are more correlated with tree growth and water uptake at deeper soil promoting efficiency of water use (Case et al., 2020; Zhou et al., 2020), and ecosystems C input at deep soil layer (Pellegrini et al., 2020, 2021). In addition, root traits (e.g. specific root length, root length density) also are related to ecosystem C loss due to

plant-soil respiratory processes (Bardgett et al., 2014; De Deyn et al., 2008). Further, any changes in root functional traits can have consequences on C flux balance by altering root depth, root respiration, microbial communities or nutrient uptake for example (Bardgett et al., 2014; De Deyn et al., 2008; Freschet and Roumet, 2017).

Fire modifies C flux balance by affecting both taxonomic(Abreu et al., 2017; Finn et al., 2013) and functional diversity (De Deyn et al., 2008; Hoffmann et al., 2012; Keeley et al., 2011). Fire maintains species richness and fitness in tropical savanna ecosystems (Lamont et al., 2018; Pilon et al., 2021a). Thus, fire can influence ecosystem function (Petchey and Gaston, 2006) by filtering species with functional traits that are key to ensure higher plant fitness and are related to C cycling in such ecosystems (Bardgett et al., 2014; De Deyn et al., 2008). Fire should therefore promote functional diversity through functional dispersion (Silva et al., 2013) and, by selecting plant-soil response and further positively impacting C dynamics flux balance (Freschet and Roumet, 2017; Hanif et al., 2019).

Our study aimed to integrate total environment responses -atmospheric and biosphere dynamics- by understanding whether fire impacts (I) ecosystem C and water dynamics (i.e., total SOC, net ecosystem carbon dioxide (CO_2) and water exchange, ecosystem water use efficiency and soil respiration), ecosystem diversity (i.e. plant taxonomic and functional diversity) and ecosystem structure (i.e. above and belowground biomass) on open Cerrado (Brazilian savanna) physiognomy; and (II) how changes in ecosystem diversity and/or structure in response to fire will affect ecosystem C dynamics. We hypothesized that: (a) fire occurrence modifies the overall balance between C release and input, increasing C input while reducing C output through changes in both functional diversity and biomass allocation; (b) fire increases C input in the system, by increasing biomass allocation in the belowground compartment; and (c) fire will promote higher taxonomic and functional diversity in Cerrado open physiognomy compared to areas excluded from fire.

2. Material and methods

2.1. Study site

We conducted our study at the *Reserva Natural Serra do Tombador* (RNST hereafter; 13° 35-38′ S and 47° 45′-51′ W, 8900 ha, 560–1118 m a.s.l., Fig. S1), a protected area of Cerrado (Fundação Grupo Boticário, 2011). RNST exhibits a mosaic of fire history, with a fire-interval in open savannas of ca. 2–4 years (Daldegan et al., 2014) and a prevalence of open savannas (Fundação Grupo Boticário, 2011). Our study site at the RNST is classified as open savannas (*campo sujo*), a species-rich open savanna mainly composed of C4 grasses mixed with forbs and scattered dwarf trees and shrubs, representing overall low tree cover (<5%) and basal area (Coutinho, 1978; Ribeiro and Walter, 2008). The climate is marked by two seasons: dry (May to October) and wet (November to April) (Fundação Grupo Boticário, 2011). The region of the study site has year-round average temperatures of ~23 °C, and annual precipitation of ~1778 mm, of which 82% is concentrated between the months of November and April (Fick and Hijmans, 2017).We performed all measurements during the rainy season (January–February 2019) at the peak of vegetation productivity (Cornelissen et al., 2003; Díaz et al., 2016; Pérez-Harguindeguy et al., 2013).

We selected one area (~3600 m²) subjected to long-term fire experiment established in the area since 2013 (for more details, see Rissi et al., 2017), and one area with long-term fire exclusion (~ 0.36 ha). Before the establishment of the fire experiments, the area was subjected to high fire frequency (i.e. 2–3 year fire interval, Daldegan et al., 2014). Both areas presented two contrasting fire frequencies: the first area was experimentally burned every two years (fire hereafter) in the middle of the dry season (July since 2013) and mimic *campo sujo* historical fire interval (Pivello, 2011). Fire intensity in the area is 1850–2700 kW.m⁻¹, being characterized by a surface fire with high combustion efficiency (>90%, Rissi et al., 2017; Rodrigues et al., 2021). The second area was excluded from fire for 16 years (one fire event in the last 20 years, referred as fire exclusion

hereafter) (Fig. S1). Within each area, we randomly selected 12 1m^2 plots (12 plots × 2 treatments = 24 plots), with a minimum distance of 2 m between plots. All measurements for both fire frequencies were carried within those 1m^2 plots, 18 months after fire experiments in the burned plots.

2.2. Method

2.2.1. Net ecosystem C fluxes and soil C pools

We determined fire effects on interconnected fluxes between the atmosphere and the biosphere by measuring net ecosystem exchange by assessing CO_2 and water (H_2O) vapor exchange between the biosphere and the atmosphere by tracking the net ecosystem C exchange (NEE; μmols CO_2 m^{-2} s^{-1}) and water exchange (ET; ecosystem evapotranspiration; μmols H_2O m^{-2} s^{-1}). We estimated NEE at each plot in both fire frequencies before biomass sampling, during the rainy season (March 2019) by recording the flux of CO_2 and H_2O vapor on three separate sunny days (March 23rd, 25th, and 26th 2019) between 11 a.m. and 2 p.m. to ensure maximum ecosystem-level photosynthetic activity. NEE and ET from each plot was measured using the LiCOR 7500 infrared gas analyzer (Li-Cor Inc.,) mounted on a tripod and two 15 cm diameter electric fans to mix the air within a chamber (0.49m^2 total area and 0.37m^3 volume) covered with woven rip-stop polyethylene that reduced PAR by 25% while maintaining temperatures constant (e.g., temperature increasing during measurement period did not exceed <1 °C). The chamber was placed in each plot for 120 s where CO_2 was recorded overtime for 90 s - the first 30 s we allowed for the air to mix and stabilize (Arnone and Obrist, 2003; Huxman et al., 2004; Potts et al., 2006a). Linear declines in CO_2 and in- creases in H_2O vapor concentrations during the measurement periods dem- onstrate the alterations in water vapor were not significant to alter stomatal conductance, canopy photosynthesis or soil respiration (Huxman et al., 2004). NEE of CO_2 and H_2O vapor were analyzed using Jasoni et al. (2005) approach to estimate fluxes at the system level. As the NEE inte- grated both CO_2 uptake by the vegetation via plant photosynthesis and CO_2 release by soil respiration (roots and microorganism respiration, re- spectively), to clearly measure soil CO_2 release, alone we measured soil res- piration which is soil average efflux (μ mol CO_2m^{-2} s^{-1}) with a LI-6400 gas analyzer (Li-Cor Inc., Lincoln, NE, USA). Finally, ecosystem water use effi- ciency (eWUE, μ mol CO_2/μ mol H_2O m^{-2} s^{-1}) was determined by calcu- lating the ratio of NEE per amount of ET.

2.2.2. Plant and soil C stocks

Within each 1m^2 plot, we harvested all the aboveground biomass in one subplot of 0.5 m × 0.5 m and we sampled the belowground biomass in one subplot of 0.25 m × 0.25 m with 0.2 m depth. to quantify biomass of coarse roots (roots >2 mm) and belowground organs (i.e., rhizomes, bulbs, xylopodia). Within each subplot used for the belowground biomass, fine roots (roots <2 mm) were quantified based on a soil core sample using an auger of 5 cm diameter and 20 cm depth since 50% of root biomass is found in the top 20 cm of the soil (De Castro and Kauffman, 1998; Delitti et al., 2001; Loiola et al., 2015).

We sorted all aboveground biomass into litter, live and dead biomass, and then dried the samples at 80 °C for 48 h. The sum of live and dead bio- mass represented the total aboveground biomass. We washed the below- ground biomass to remove soil particles and separate coarse root biomass from belowground organs. Fine root (<2 mm) samples were sieved at 2 mm, 1.40 mm and 850 μm before being washed. For assessing fine root biomass, we considered all fine roots (roots <2 mm) as a result of the sum of acquisitive and transport roots (McCormack et al., 2015). The total be- lowground biomass was the sum of belowground organs, coarse and fine roots.

We used total aboveground biomass, live and dead biomass, litter, total belowground biomass, belowground organs biomass, coarse and fine root biomass measurements to characterize the system structure metrics. To evaluate biomass allocation, we considered the ratio of total aboveground: total belowground biomass and live aboveground: fine root biomass to evaluate biomass allocation for each plot.

We determined total SOC through total soil organic matter (SOM) of sieved soil samples taken in each plot (remaining soil from fine root sam- ples sieve at 850 μm). SOM was determined by the Soil Lab from the Universidade de São Paulo – ESALQ, Brazil, through organic matter titra- tion of dichromate solution added to soil samples (Camargo et al., 2009). We used the WB method (Walkley and Black, 1934) to determine total SOC using the following formula: SOM (g.kg^{-1}) = SOC (g.kg^{-1}) × 1.724.

2.2.3. Plant diversity

In the 24 1m^2 plots, we determined overall plant community species richness and percentage cover of each plant species (see Table S4) using a modified Braun-Blanquet scale (Wikum and Shanholtzer, 1978, using inter- vals of 10%). Species richness, Simpson's index and evenness index were used as the system taxonomic diversity metrics. The taxonomic diversity metrics were obtained by using the R package *vegan* (Oksanen et al., 2019).

We measured three above and three belowground plant functional traits on the dominant species from each fire and fire exclusion plots (30 m × 30 m) to determine functional diversity, richness, evenness, commu- nity weight means (CWM) and dispersion. We measured (i) aboveground functional traits: growth-form, specific leaf area (SLA), individual height; and (ii) belowground traits: root specific length (SRL), root dry matter content (RDMC) and root tissue density (RTD). Plant functional traits selected are as- sociated with C dynamics (e.g. C stock) because they reflect individual eco- physiological adaptations and trade-off mainly related to resources allocations and acquisition (Bardgett et al., 2014; De Deyn et al., 2008; Pérez-Harguindeguy et al., 2013).

We considered as dominant plant species, those plants which repre- sented 80% of vegetation cover at community level from each fire fre- quency. For fire plots, 25 species represented 80% of total cover, and 12 species accounted for 80% of total cover in the fire exclusion area (see Table S5). Aboveground functional traits have been assessed in 10 different individuals for each species and belowground in 5 different individuals for each species (Cornelissen et al., 2003). Since in savannas several plants may have clonal growth (Lamont et al., 2011; Pausas et al., 2018), each individ- ual was sampled at least three meters from the nearest neighbor of the same species to avoid measuring the same genet.

To measure the roots functional traits, roots were first washed under water and then fine roots (<2 mm) were classified in acquisitive (first three root order) and transport roots (McCormack et al., 2015). To measure the root morphological traits (i.e., SRL, RDMC and RTD), a sub-sample of acquis- itive roots was used. Each sub-sample was weighed (fresh roots), digitized using a scanner EPSON Perfection V800 (Copyright© 2015 Epson America, Inc.) at resolution of 1200dpi. Root volume, diameter, and length was assessed with the software WinRHIZO™ 2013e (Copyright© 1996–2019 Ré- gent Instruments Inc., Canada) (Bouma et al., 2000; Rose and Lobet, 2019) using digitized images. After image analysis, each sub-sample was dried 72 h at 50 °C in an oven and weighed to determine dry biomass. Specific root length (SRL, m g^{-1}) was measured as the ratio between root length and root dry mass, root dry matter content (RDMC, mg g^{-1}) was measured as the ratio between fresh wet (in mg) and dry weight (in g), and root tissue density (RTD, g cm^{-3}) was assessed as the ratio between root dry mass and root volume.

System functional diversity metrics were represented by functional richness (FRich) (Villéger et al., 2008), functional evenness (FEve), func- tional dispersion (FDis) (Laliberté and Legendre, 2010), functional diver- sity (FDp) (Petchey and Gaston, 2002, 2006) and the CWM index which is the abundance-weighted mean trait value for a community (Kleyer et al., 2012). FRich, FEve, FDis and CWM index were obtained by using the R package *FD* (Laliberté et al., 2014) and FDp using package *picante* (Kembel et al., 2010).

2.3. Data analysis

To quantify the direct effect of fire frequencies on system diversity, structure, and ecosystem C balance, we performed the Effect-size test using Cohen's D index (Cohen, 1988). We calculated the standardized effect

size (d) by assessing the standardized mean difference between the fire plots (m_t) and fire exclusion plots (control, m_c) of the value of a given system metric, using the pooled standard deviation of the same component in the treatment (sd_t) and control (sd_c) plots, with a correlation of the two samples (fire exclusion and fire) to make it less biased (McGrath and Meyer, 2006), as the following formula:

$$d = \frac{(m_t - m_c)}{\sqrt{\frac{sd^2_t - sd^2_c}{2}}} \quad (1)$$

A positive value of Cohen's D index for a given system metric means that fire increases the ecosystem metric in relation to fire exclusion. A value of Cohen's D index near zero means that fire has no effect on the given system metric. All NEE values were multiple by -1 to simplify results interpretation. To examine how changes in diversity and structure promoted by fire will lead to direct and indirect changes on ecosystem C balance we used a piecewise structural equation model (piecewiseSEM; Lefcheck, 2016). Piecewise SEM's has a non-significant p-value ($p > 0.05$) as an indicative of a well-fit model, similarly to the lower AIC value (Lefcheck, 2016). We built four different piecewise SEM models based on our hypothesis from the results of our effect-size analyses, using variables that have shown significant effect according to fire and supporting our theoretical hypothesis (Fig. 1, hypothesis one is in brown, hypothesis two is in black). Also, to ensure good explanatory power at each of our piecewiseSEM models, we respected the general rule of the ratio of the total number of observations to the number of variables as d = 5 (Grace et al., 2015). Based on this, each of the four piecewise SEM model, representing our hypothesis,

considered only one system structure metric at a time respectively the live aboveground biomass (first piecewise SEM and first hypothesis), fine root (second), coarse root (third), and belowground organ (forth) representing our second hypothesis.

Each SEM model was built from five linear mixed effect models (*lme*) (see Supplementary material, Table S3). The first *lme* aims to explain total SOC as the response variable according to system structure (i.e., fine roots biomass, belowground organ biomass, coarse roots biomass, live aboveground biomass) and fire frequencies as predictor variables. The second *lme* aims to explain system structure (i.e., live aboveground biomass, fine roots biomass, belowground organ biomass, coarse roots biomass) as the response variable according to fire frequencies and functional diversity (FDp index). The third *lme* used NEE as the response variable, and the functional diversity, soil respiration, total SOC, fire frequencies and system structure (i.e., aboveground biomass, fine root biomass, belowground organ biomass, coarse root biomass) as explanatory variables. The fourth *lme* aims to explain soil respiration according to system structure, fire frequencies and NEE as predictor variables. Finally, the fifth *lme* examined functional diversity as a response to fire frequencies. We log-transformed all response and predictor variables to achieve normality assumptions. We kept fire frequency as a categorical variable, and to check the contribution of each category in the model (fire and fire exclusion), we performed an estimated marginal mean analysis for each significant model (Lefcheck, 2019). We used Fisher's C to assess the completeness of our model. We included plot as a random variable in all model regressions and we did not remove non-significant links in our final SEM.
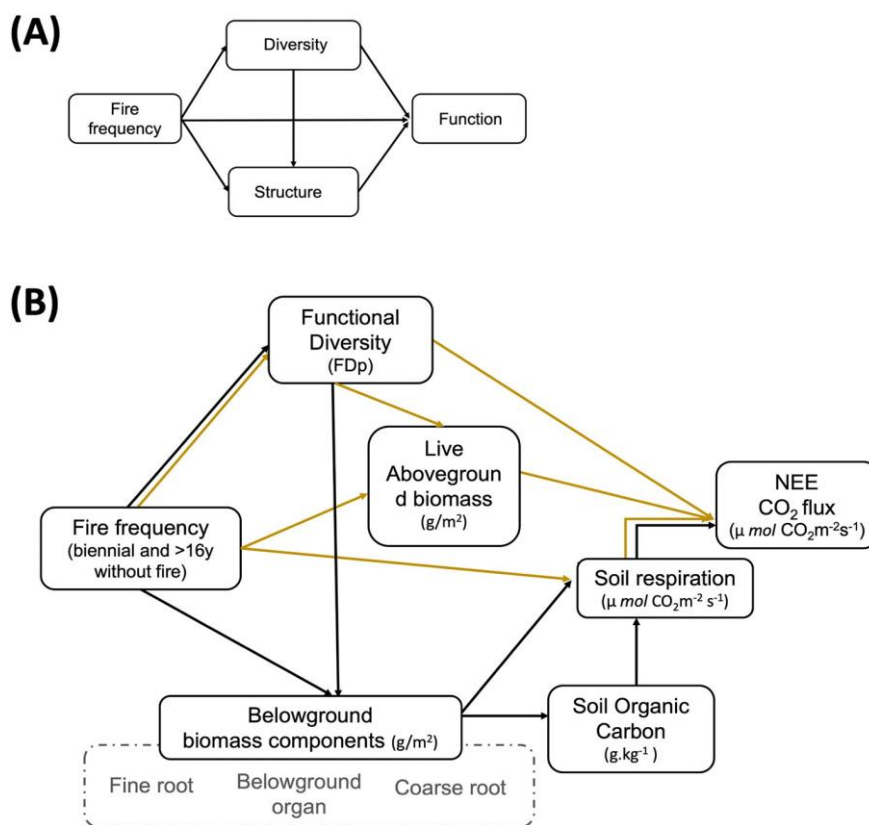

Fig. 1. Conceptual model based on our hypothesis examined within our piecewise SEM models. (A) Hypothetical model regarding the general pathways of the effect of fire presence on system diversity, structure and thus system function to carbon balance. (B) Detail of our hypothetical model, considering the metrics we used in our piecewiseSEM models. Hypotheses one and two are represented by the brown and black arrows, respectively. To ensure good explanatory power at our piecewiseSEM models, belowground biomass components from our second hypothesis, were separately analyzed in our piecewiseSEM models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

All analyses were conducted using the R version 3.6.3 environment (R Development Core Team, 2020) and package *piecewiseSEM* (Lefcheck, 2016), *nlme* (Pinheiro et al., 2020) and package *effsize* (Torchiano, 2017).

3. Results

3.1. Direct effect of fire on ecosystem diversity, structure & function

Fire impacted all three system components: system diversity, structure, and system function (Fig. 2). Fire has a positive effect on diversity by promoting functional diversity and functional dispersion. However, fire did not impact taxonomic diversity metrics (Fig. 2, Tables S1–S2).

Fire promoted live biomass and all belowground biomass components including belowground organs, coarse and fine roots biomass (Fig. 2). The ratio between above- and belowground biomass responded negatively to fire, indicating a higher biomass allocation to belowground with fire (Fig. 2). Fire had no effect on dead biomass and litter, as well as on the ratio between live aboveground biomass and fine roots.

Finally, fire impacted system function, positively affecting NEE and total SOC while negatively impacting soil respiration. Fire had no effect on ET and eWUE.

3.2. Fire impacts on ecosystem C dynamics through shifts in structure & diversity

Models consistently indicated a fire-induced increase on SOC (Fig. 3, Table S3) and a decline in soil respiration (Fig. 3C). All piecewise SEM models showed strong positive and direct relation between fire and plant functional diversity (Fig. 3, Table S3). The models also showed that fire induced greater belowground biomass input, especially fine root and belowground organ biomass (Fig. 3B and D) whereas coarse roots biomass was minimally affected by fire (Fig. 3C). NEE in most models (except Fig. 3D) was positively, besides marginally, affected by fire (Fig. 3).

Overall, the model that included fine root biomass was the best model to explain how fire impacted ecosystem C stocks and fluxes (Fisher's C = 2.194, AIC = 58.194, p-value = 0.7, Fig. 3B). In that model, fire marginally reduced soil respiration while promoting NEE, leading towards higher ecosystem C flux input. Further, fire affected positively and directly both functional diversity and fine root biomass (Fig. 3B). Although our models showed a marginal positive relationship between fire and NEE, they did not allow us to establish a direct relationship between fire and NEE, or a clear indirect relation mediated by functional diversity, belowground biomass, soil respiration or SOC.

4. Discussion

In Cerrado open savanna, fire is promoting C input in the system through increases in live above- and belowground biomass as well as a higher biomass allocation belowground, ultimately promoting the input of C into soils. Our results also showed a higher NEE and total SOC with fire whereas soil respiration declined i.e., soil C efflux (C output), corroborating the higher C input in burned compared to unburned areas. While fire enhanced functional diversity, our results did not support positive fire effects on taxonomic diversity as found in other studies (Abreu et al., 2017; Gomes et al., 2020; Pilon et al., 2021a). Although our results support direct
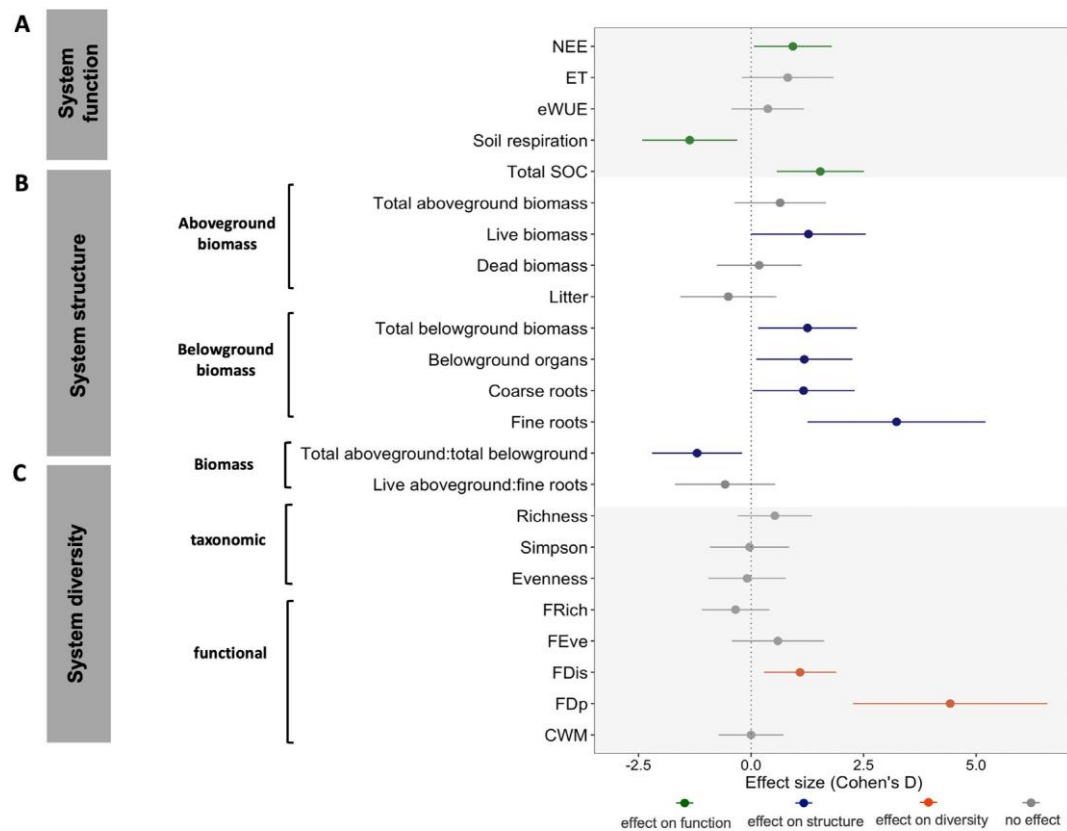

Fig. 2. Effect of fire on (A) system function to carbon balance considering total soil carbon content (SOC), rates of net ecosystem exchange (NEE), ecosystem evapotranspiration (ET), ecosystem water use efficiency (eWUE) and soil respiration, (B) system structure considering total aboveground biomass as well as live and dead biomass, and total belowground biomass in addition to fine root, coarse root and belowground organs biomass, total aboveground biomass:belowground biomass ratio and live aboveground biomass:fine root biomass, and litter biomass; and (C) system diversity considering plant community taxonomic diversity (i.e. richness, Simpson, and evenness index) and functional diversity: functional richness (FRich), functional evenness (FEve), functional dispersion (FDis); functional diversity plot-based dendrogram (FDp), community weighted means (CWM). (C) Positive values mean that fire promotes the system variable while negative values indicate that fire negatively affects the system variable. Values near zero indicate that fire did not have a significant effect. The values were based on Cohen's D index (ci = 95%), obtained from plots located in burned and fire excluded areas.

effects of fire in ecosystem functions associated with C dynamics (i.e., NEE, total SOC or soil respiration), how ecosystem structure and diversity mediated these relationships remain less straightforward.

Our results highlighted that fire modifies C balance with higher NEE in burned plots, illustrating a higher C input and lower C release. C flux is very cyclic in the Cerrado (Santos et al., 2003; Vourlitis and da Rocha, 2010) and compared to unburned savanna areas, frequently burned savannas rapidly become a stronger sink for CO$_2$ (Santos et al., 2003). However, after 12 months, the negative impact of fire (i.e. C release, biomass lost) on the open savannas is eliminated, indicating the potential of the system to compensate for C losses due to combustion (Potts et al., 2006a, 2006b; Potts et al., 2012). The increase of photosynthetic activities promoted by the

newly produced leaves from the vegetation regrowth compensates the C loss, providing the whole system C uptake (e.g., greater NEE in burned than unburned plots) (Baldocchi, 2008; Huxman et al., 2004; Potts et al., 2012).

Fast regeneration in open savanna is primarily ensured by the quick regeneration of grass species that produce newly photosynthetic leaves (Pilon et al., 2021a), since grasses are the most resilient growth form to fire in savannas (Bond, 2004). Graminoids morphological architecture that protects buds and meristems ensures fast recovery (Linder et al., 2018; Pilon et al., 2021a; Wigley et al., 2020), being also the most flammable element of the fuel load (Simpson et al., 2016). Also, high annual productivity of grasses can be related to the energetic cost investment of resprouting, that is focused on the production of photosynthetically active tissue (Linder et al., 2018; Simpson et al., 2021). Frequent fires will promote mainly grasses live aboveground biomass as shown in our results. In savannas, fire occurrence is closely related with grass abundance (De Castro and Kauffman, 1998), favoring grass species over woody species (Bond et al., 2005; Bond and Keeley, 2005).

C input in burned plots is also shown through the increase in belowground biomass. Our results showed that fire enhanced total belowground biomass, especially fine root and belowground organ biomass and promoted biomass allocation in the belowground compartment, corroborating with our hypothesis. In open tropical savannas, plants allocate a large proportion of biomass in belowground compartments (Fidelis et al., 2013; Jobbagy and Jackson, 2000; Poorter et al., 2011). Fire is indeed expected to lead towards plant investment to belowground organs, for bud protection, resource storage and resource acquisition, allowing plants to survive and quickly resprout after fire (Clarke et al., 2013; Enright et al., 2014; Lawes and Clarke, 2011). Further, fire stimulates fine root biomass production at the shallow soil layer (0-20 cm depth) to improve the nutrient acquisition (Jackson et al., 2002; Le Stradic et al., 2021; Oliveras et al., 2013; Pellegrini et al., 2020). However, at deeper soil (>30 cm–100 cm), Cerrado open savannas areas with different fire histories and frequencies did not show differences on fine root biomass (Le Stradic et al., 2021).

Higher total SOC in burned areas illustrates the overall increase in C input in tropical open savannas. Grassy ecosystems can boost SOC at the shallow soil layer because of the higher grass root biomass in the upper 20 cm of the soil (Berhongaray et al., 2019; February et al., 2013, 2020; Le Stradic et al., 2021). Indeed, the increase of total SOC may be related to higher grass fine root decomposition which represents the great deal of organic matter input in the soil (De Deyn et al., 2011). However, in burned sites we also observed a reduction of soil respiration which suggests a reduced microbial activity. Fire can enhance plant microbiome diversity and composition (Dove et al., 2021) that might affect C input into soil
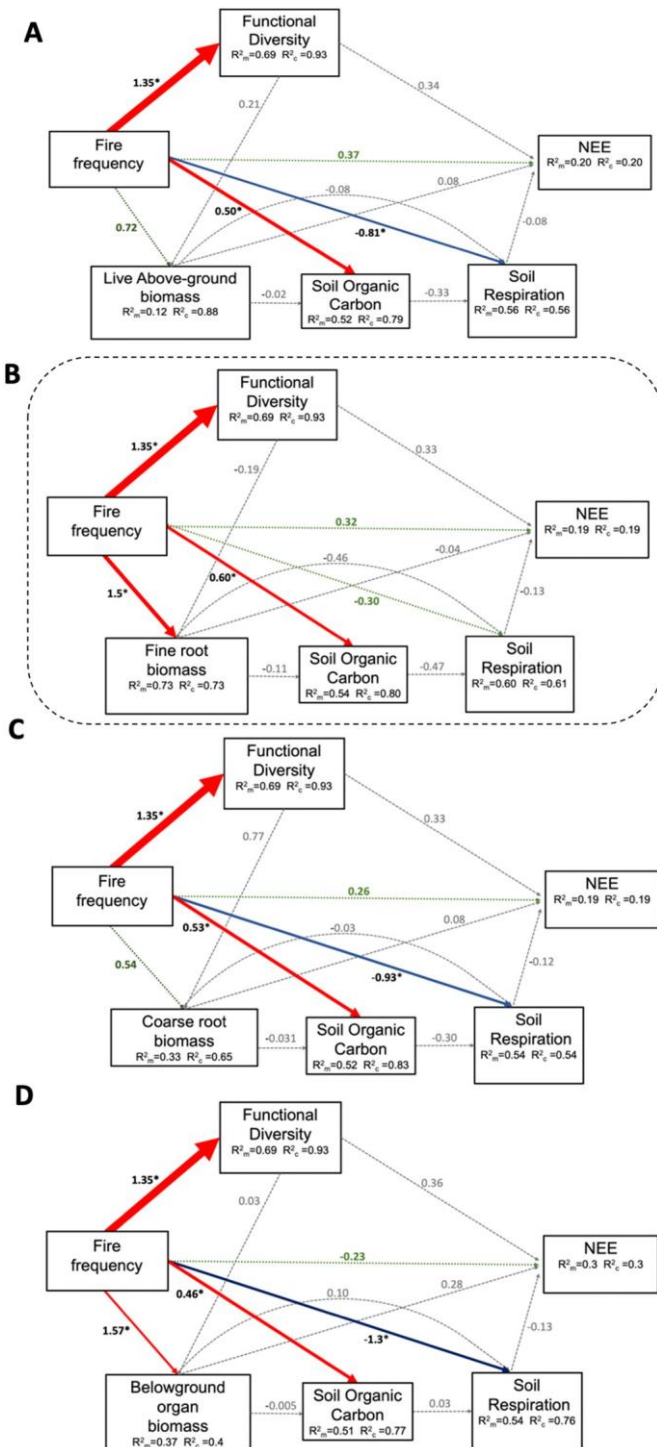
Fig. 3. Piecewise structural equation model (SEM) depicting the direct and indirect effects of fire frequency on system diversity, structure and system function associated with carbon balance. (A) Piecewise SEM based on our first hypothesis that considers live-aboveground biomass as a system structure metric. The model presented the lower goodness of fit for our data: Fisher's C = 3.266, AIC = 59.266, p-value = 0.514. The following piecewiseSEM models were based on our second hypothesis that considered separately the different belowground biomass components: (B) fine roots biomass, (C) coarse roots biomass and (D) below organs biomass. (B) The model considering the fine root biomass presented the best good fit for our data: Fisher's C = 2.194. AIC = 58.194, p-value = 0.7.
(C) The model with coarse roots biomass, also presented a good fit for our data: Fisher's C = 6.757, AIC = 62.757, p-value = 0.149. (D) The last model considered below organs biomass and has a good fit for our data: Fisher's C = 5.364, AIC = 59.266, p-value = 0.252. Partial R2 values are under each predicted variable, and standardized path estimates are provided next to each path with line thickness scaled based on the magnitude of the estimated variable. Red and dark blue arrows indicate positive and negative relationships, respectively. Grey dashed arrows represent non-significant paths (p > 0.05), and the green represents the marginally significant paths. Asterisks (*) indicate significance (p < 0.05). Black dashed block indicates the model with the best fit for our data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

through modification in microbial activities and increase in microbial by-product (Rossi et al., 2020). In addition, increases in belowground organ and fine roots at the shallow soil layer due to fire, can overtime contribute towards greater soil C through slow decomposition and mycorrhizal association (Freschet et al., 2013; Godbold et al., 2006). Although the belowground communities seem to play an important role in the soil respiration and for soil C input, further studies are needed to understand how they may affect C flux and storage in a fire-prone environment (Pressler et al., 2019).

In Cerrado open savannas, litter deposition and decomposition is relatively slow (Carvalho et al., 2012; Kauffman et al., 1994; Valenti et al., 2008), especially due to recalcitrant compounds of C4 grasses that decompose more slowly relative to C3 plants (Martin et al., 1990). Indeed, most of the dead grass material remains attached in the tussocks (Wragg et al., 2018) which slows down substrate quantity deposition and may decrease soil respiration (Chapin et al., 2011). In addition, in case of recurrent and frequent fires like in Cerrado, litter accumulation is limited and removed frequently by fire, which may reduce microbial activity related to litter decomposition. Cerrado soils are relatively nutrient poor with acidic pH (Pivello et al., 2010), which may also limit soil microbial activities, lowering therefore soil respiration, and thus C loss from microbial activities (Fierer and Jackson, 2006; Funakawa et al., 2014; Rousk et al., 2010). Finally, microbial activity associated with soil respiration may also be limited in post-fire environments since fire may have burned superficial microbial communities.

Overtime, fire promoted functional diversity in plant communities with greater trait variability across species (Dantas et al., 2013). Post-fire conditions promote new opportunities for plant colonization (Fidelis et al., 2012; Pausas et al., 2003), due to higher environmental heterogeneity and higher resource availability (He et al., 2019; Krawchuk and Moritz, 2011; Pivello et al., 2010), and increasing niche availability generating species coexistence and greater diversity. High diversity of post-fire strategies is associated with higher trait diversity, dispersion and consequently trait divergence (Lhotsky et al., 2016; Mason et al., 2013) as highlighted by our results. In addition, functional diversity can be stimulated by fire because over time species could complement each other in the resource use by capturing resources with different strategies (Garnier et al., 2016). Functional diversity associated with functional divergence may influences plant-soil feedback responses, such as plant and soil respiration, and efficiency on water and nutrients use, and thus impacting the ecosystem function of C balance (De Deyn et al., 2008; Jackson et al., 2000; Petchey and Gaston, 2006), besides our results did not allow to conclude about that. However, we may hypothesize belowground communities seem to play an important role in the processes of plant-soil feedback responses and C balance. Further studies are needed to understand how belowground community dynamics affect C flux and storage in a fire-prone environment (Pressler et al., 2019).

Finally, in a context of climate changes and modification of fire regimes, it seems essential to better understand mechanisms between fire and the ecosystem C cycle which are complex in different fire-prone ecosystems. Quantifying tropical open savannas potential C pools and fluxes is not trivial and identifying system pathways trajectories and mediation will provide a way to assess and describe fluctuations in ecosystem function in response to modification in fire regime under climate change. Furthermore, our findings also should help ecosystem base restoration and fire management plans in savanna open ecosystems to maintain system structure, diversity, and function. We acknowledge that our results dealt with the C pool at the shallow soil layer of an open savanna, and we did not account for C in the deeper soil layers, which may have a higher contribution of trees and shrubs. Whereas our results showed that fire promoted SOC at the soil surface, fire may decrease SOC in deeper soil layer, as shown by other study in a temperate savanna (Pellegrini et al., 2020). In addition, in savannas where the woody cover has a higher importance, the presence of trees and shrubs is expected to differently affect C balance. In woody tropical savannas, fire may decrease C stock in soil and plant biomass due to a reduction on nutrient mineralization rates, and nitrogen viability, that decreases tree net primary production and consequently soil and plant C input (Cook et al., 2005; Richards et al., 2011; Williams et al., 2004).

5. Conclusions

Our study showed that high fire frequency in Cerrado open savannas lead overall to C input into the system by increasing soil C, plant belowground biomass and by declining C fluxes from the biosphere back to the atmosphere. However, we need to acknowledge that the relationship and the underlined mechanisms between functional diversity, changes in biomass allocation and changes in ecosystem functions remained unclear. In addition, our findings also highlight the importance of fire to promote functional diversity on Cerrado open ecosystems. Once fire is excluded, functional diversity was reduced, so potentially the diversity of response to disturbances and environmental changes. Functional diversity losses could be an issue in terms of regeneration possibility after a fire, should limit system resilience in areas excluded from fire for long-time, limiting vegetation regeneration and jeopardizing the ability of the natural system to compensate for the C lost during combustion altering biosphere and atmosphere dynamics.

Data availability statement

All the data that support the findings of this study are available on the Zenodo Repository (https://doi.org/10.5281/zenodo.5796239).

CRediT authorship contribution statement

Juliana Teixeira: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. Lara Souza: Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing, Supervision. Soizig Le Stradic: Conceptualization, Methodology, Writing – review & editing, Supervision. Alessandra Fidelis: Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition, Supervision.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.152317.

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