Contrasting strategies of nutrient demand and use between savanna and forest ecosystems in a Neotropical transition zone

Marina Corrêa Scalon[1,2], Imma Oliveras Menor[1,3], Renata Freitag[4], Karine S. Peixoto[4], Sami W. Rifai[1,5], Beatriz Schwantes Marimon[3], Ben Hur Marimon[3], Yadvinder Malhi[1]

[1]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK
[2] Programa de Pós-graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba, PR, 81531-990, Brazil
[3]AMAP (botAnique et Modélisation de l'Architecture des Plantes et des Végétations), Univ. de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier Cedex 5, France
[4]Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso – UNEMAT, Nova Xavantina, MT, 78690-000, Brazil
[5]ARC Centre of Excellence for Climate Extremes, Sydney, NSW, Australia

Correspondence to: Marina C. Scalon (marina_scalon@yahoo.com.br)

Abstract. The total demand and uptake of nutrients by vegetation is rarely quantified or compared across vegetation types. Here, we describe different nutrient use and allocation strategies in Neotropical savanna (cerrado) and transitional forest (cerradão) tree communities composed by different species, report leaf nutrient resorption and calculate ecosystem-level nutrient use efficiency. We couple net primary productivity (NPP) estimates with nutrient stoichiometry to quantify nutrient demand and nutrient flows at the whole stand scale for different components of vegetation biomass. Species from the two vegetation communities showed similar mean nutrient concentration and nutrient resorption efficiency except for wood P concentration that was 4-fold higher in cerrado than cerradão species. The cerradão showed higher canopy NPP, while fine roots and wood NPP were similar for the two vegetation types. Nutrient requirement in the two vegetation types was dominated by the demands of the canopy, with canopy resorption contributing generally more than 50% of the total canopy demand for nutrients, while less than 35% of N, P, K, Ca and Mg were allocated to wood or fine roots. Proportionally, cerrado showed higher nutrient demand from fine-roots (over 35% of total nutrient demand) and for the wood component (over 13% of total nutrient demand), while ~60-70% of cerradão nutrient demand was allocated to the canopy. The proportional difference in nutrient allocation to the different biomass components suggesting cerrado species allocate less nutrient to a given fine root biomass, but more nutrient to a given wood biomass. Our findings suggest that cerradão species are more limited in P and K than cerrado species, inducing a higher resorption to compensate for low uptake. Moreover, we found that N uptake for cerradão was higher with lower N use efficiency, i.e., the amount of production per nutrient unit, leading higher N demand compared to the cerrado. This difference in nutrient dynamics explains how similar soils and the same climate dominated by savanna vegetation can also support forest-like formations. Tree species composition is likely the major factor regulating nutrient use, limiting vegetation transitions and influencing nutrient demand at landscape scales.

1 Introduction

Net primary productivity (NPP), together with carbon and nutrient cycling are important ecosystem processes that may be primarily limited by nutrient availability (Aragão et al., 2009; Quesada et al., 2009; Fernández-Martínez et al., 2014). Even though there is a major interest in the relationship between nutrient and carbon for predictive models on how tropical ecosystems will respond to increasing atmospheric CO2 and climate change (Malhi, 2012), the influence of nutrient availability in carbon balance and sequestration is not well understood. Most studies of nutrient demand are based on simple concentrations and stocks of nutrients in, for example, leaves, wood and soil. In order to assess the *flow and demand* of nutrients in vegetation, it is necessary to couple the stoichiometry of key plant organs with the rates of production of those organs, which are assessed through measurements of NPP. By definition, nutrient use efficiency is the amount of production per nutrient unit (Chapin, 1980) and can be estimated as the ratio of. NPP per unit of nutrient demand (Bridgham et al., 1995). Nutrient demand is the sum of nutrient accumulated in above and belowground biomass and nutrient returns to the soil via litterfall including resorption efficiency, while nutrient uptake excludes nutrient resorption efficiency. Nutrient resorption is defined as the process from which plants withdraw nutrients from senescent leaves prior to leaf abscission, and its efficiency is calculated as the proportional resorption from green to senesced leaves (Killingbeck 1996).

In the context of tropical ecosystems, the availability of forest sub-component NPP data has increased substantially in recent years, most notably through the activity of the Global Ecosystems Monitoring (GEM) network (Malhi et al., 2021). The coupling of NPP and stoichiometry data opens the potential for detailed description of plant nutrient demand and nutrient cycling in a variety of ecosystems. Here we demonstrate how such coupling of NPP estimates with nutrient stoichiometry can be conducted in the context of Neotropical savanna and transitional vegetation types.

Although climatic fluctuations have major role shaping the forest and savannas occurrence and dynamics (e.g. expansions and retractions) globally, mesic and humid savannas normally persist over areas where climatic conditions could support forest formations (Cole, 1986; Solbrig, 1996). Therefore, in addition to climatic conditions, nutrient availability and species shifts are expected to be important environmental filters (Lehmann et al., 2011). It is suggested that nutrients may be the primary determinant of tree biomass worldwide, since trees experiencing higher nutrient availability can potentially have faster growth rates and therefore be more competitive against grasses and avoid the grass fire trap (Hoffmann et al., 2012). Key limiting nutrients are usually presumed to be nitrogen or phosphorus (Reich and Schoettle, 1988; Reich et al., 2009), but potassium (K), calcium (Ca), and magnesium (Mg) may also play a role (Chapin III, 1980; Grime, 2006). Savanna soils tend to be highly deficient in multiple nutrients (Bucci et al., 2006; Haridasan, 2008; Bustamante et al., 2012) and some authors attribute soil fertility as the main factor driving abrupt transitions between savannas and forests (Bond, 2010; Wang et al., 2010; Viani et al., 2011). In the Neotropical mesic savannas, when fire is excluded, gradual forest expansion occurs by encroachment of trees, forming forests-like vegetation (Durigan and Ratter, 2006; Hoffmann et al., 2012; Rosan et al., 2019), meaning that nutrient availability alone is also not the ultimate constraint on forest formation (Pellegrini, 2016). However,

nutrients might influence vegetation encroachment processes by either restricting tree growth rates, maintaining a grass layer
65 that facilitates fire; or constraining the ability of forests to form regardless of fire (Case and Staver, 2017).

Soil nutrient availability is determined not only by soil properties, but also by water availability and vegetation structure and composition. For instance, high biomass results in high nutrient turnover and availability (Nardoto et al., 2006; Pellegrini, 2016), and species-specific leaf functional traits can affect demand and turnover of nutrients (Craine et al., 2008). While savanna-like vegetation, such as the typical cerrado is defined by shrubs and trees distributed in a continuous grass and
70 herbaceous layer, savanna-forest transitional vegetation, such as the cerradão is composed by an almost continuous canopy of trees (usually 70-80% canopy cover) with a thin herbaceous understory layer (Oliveras and Malhi, 2016). Few plant species are shared between cerrado and cerradão, implying a distinct set of traits and ecological strategies (Hoffmann et al., 2003; Marimon-Junior and Haridasan, 2005; Marimon et al., 2006). There is an expected evolutionary trade-off involved in slow and fast growing species in relation to high-nutrient and low-nutrient habitats, in which plants adapted to nutrient-poor
75 habitats should be more efficient (i.e., build more organic matter for a given unit of nutrient required) than fast growing plants from nutrient-rich environments (Vitousek, 1982; Vitousek, 1984; Chapin III et al., 1986). Indeed, higher resorption rates are expected in low-nutrient environments (Aerts and Chapin, 1999; Wright and Westoby, 2003; Pellegrini, 2016).

Leaf nutrient concentration and leaf nutrient resorption are obviously major aspects that influence nutrient cycling in a plant community (Vergutz et al. 2012). However, nutrient allocation to different organs (e.g., leaves, roots, wood, and bark) can
80 also have important effects in nutrient use and supply in the ecosystem, since different species can have distinct demands for nutrients in terms of tissue stoichiometries. In addition, nutrient deposition and mineralization from different plant material will directly influence nutrient availability (Wardle et al., 2004). While wood can provide a well-defended and long-lived storage organ for nutrients, water and carbohydrates (Chapin III et al., 1990), leaves and fine roots are short-lived and much more vulnerable to herbivores, especially under high nutrient concentration (Coley et al., 1985; Moles et al., 2013).

85 To effectively evaluate nutrient use in forest-savanna transitions, there is the need to quantify the nutrient requirement of each vegetation type, which should consider differences in biomass investment for the distinct components (e.g., canopy, wood, roots). By calculating nutrient demand in the savanna-forest transition using literature proxy equations and data, Pellegrini (2016) found that populations of Brazilian savanna species, compared to forest species, required double the N and P to form closed canopies, but the N and P annual demand was substantially greater for forest tree species. These findings
90 suggest that even with lower nutrient requirements to form a forest, transitional forest species may experience higher limitations due to their higher nutrient demand. Species composition and vegetation structure are very distinct between the cerrado and cerradão vegetation (de Oliveira et al., 2017), and the mechanism by which these differences occur is still poorly understood, but may involve trade-offs between nutrient requirements and adaptations to fire (Silva et al., 2013), and vegetation encroachment by nucleation of keystone species, such as *Tachigali vulgaris* (Morandi et al., 2016). Here, we
95 describe different nutrient use and allocation strategies in savanna (cerrado) and transitional forest (cerradão) species, report

leaf nutrient resorption and calculate ecosystem-level nutrient use efficiency based on dynamic nutrient flows rather than one-off static estimates of nutrient stocks. We set out to test the following questions and hypotheses:

(I)   How do leaf nutrient concentration and resorption vary across savanna-forest species? At the species scale, we expect that there will be more nutrients in different plant organs in cerradão compared to cerrado species. Moreover, based on plant strategies and resource availability limitations, we expect that cerrado species will show higher nutrient resorption efficiency, both at species and community scale.

(II)   What is the nutrient demand of the cerrado and cerradão communities? We expect that cerradão will have higher NPP for all biomass components, and therefore, higher nutrient demand.

(III)   What is the partitioning of nutrient demand between canopy, wood and fine roots, and how much of this demand is met by translocation of leaf nutrients rather than by new uptake? We expect that the canopy will dominate nutrient demand in both plant communities, but that the majority of this demand will be met by nutrient translocation from senescing leaves.

2 Material and Methods

2.1 Field site

The study plots, part of the GEM intensive carbon plot network (Malhi et al., 2021), are located in a typical mosaic area of cerrado and an adjacent cerradão vegetation in the Bacaba Municipal Park (BMP; 14∘42'22" S, 52∘21'07" W), Nova Xavantina, Mato Grosso State, Brazil. The park of approximately 500 ha is located in the transition between Cerrado and Amazon biomes; the climate is Köppen's Aw (i.e., tropical savanna climate), with a highly seasonal rainfall and a prolonged and intense dry period during May to September (Marimon-Junior and Haridasan, 2005).

One 1-ha plot of each vegetation type have been monitored every year since 2010, for vegetation dynamics following standard RAINFOR protocol (Phillips et al., 2002). Plots are 100 m apart from each other. Tree identity, size, location, and growth data for each plot and census are curated and available under request at the ForestPlots.net database (Lopez-Gonzalez et al., 2011). Our plots represent long-term fire protected vegetation types, and a rare case of very well-preserved typical cerrado and cerradão vegetation in the Amazon and Cerrado transition (de Oliveira et al., 2017). Typical cerrado is a cerrado *stricto sensu* subtype with predominantly arboreal-shrubby vegetation, 20 to 50% of tree cover, and tree heights between three and six meters (Ribeiro and Walter, 1998). The cerradão is considered an ecotonal community (Ratter et al., 1973), characterized by mostly continuous canopy and the abundance of species that indicate the transition between forests and savannas on the southern Amazonian border, such as *Hirtella glandulosa* and *Emmotum nitens* (Marimon et al., 2006).

Within each 1ha plot, 25 subplots were delimited, from where soil samples at 0-10 and 10-20 cm depth were collected in all 4 corners and in the centre of each subplot, totalling 200 samples for each vegetation type. Soil chemistry data were analysed according to EMBRAPA procedure (EMBRAPA, 1997) and were provided by ForestPlots database Lopez-Gonzalez et al.

2011 (Table S1). Despite slightly sandier soils in the cerrado, the soil in both areas are very similar, and characterized as dystrophic yellow oxisols, with low nutrient concentration, reduced sum of the bases, and low cation exchange capacity (Marimon-Junior and Haridasan, 2005). They are highly acidic, Alic, well drained and without concretions up to two meters deep (Table S1).

2.2 Nutrient sampling

In each plot, we randomly selected five individuals of the seven most abundant species representing ca. 70% of the community basal area (Table 1). Calculation of relative dominance was based on previous census collected in the plots (2009, 2012, 2014), by dividing the species dominance (i.e., total basal area of the species) and the sum of the dominance of all species multiplying by 100. The IVI was calculated as the sum of the relative frequency, the relative density and the relative dominance of each species within the community. We chose only adult trees with at least 5cm in diameter at breast high (dbh) in the cerrado and 10 cm dbh in the cerradão, following standardized criteria for individual inclusion in forest and savanna vegetation. For each species, 5 individuals were chosen, from which we collected samples from different tissues: heartwood and sapwood, inner and outer bark, branch, mature and old leaves, and fine roots. Inner and outer bark can be easily visually distinguished, but we also used magnified lenses to confirm our classification whenever there was any uncertainty. Ten fully expanded mature sun leaves were collected during the wet season (January 2018) and 10 recently senescent leaves were collected from the same individuals during dry season (July 2018) because of the deciduousness of most species. We considered senescent leaves to be those that fall with a gentle flick to the branch (Wright and Westoby, 2003). Collected branches were approximately 1cm diameter without bark, which was removed before analysis. Wood core samples and bark were collected at breast height (DBH ≈ 1.30 m). Wood samples were extracted using a 4.3 mm Haglof increment borer to a depth of half the DBH of the tree.

Table 1. Species, importance value index (IVI) and basal area contribution (BA, %) for Cerradão (transition forest) and typical Cerrado (savanna) permanent plots in Nova Xavantina, Brazil.

Cerradão	IVI	BA (%)	Typical Cerrado	IVI	BA (%)
Hirtella glandulosa Spreng	46.37	28.82	*Qualea parviflora* Mart.	27.49	18.28
Tachigali vulgaris L.G .Silva & H.C.Lima	25.38	19.51	*Davilla elliptica* A. St.-Hil.	18.09	14.04
Emmotum nitens (Benth.) Miers	11.18	9.94	*Roupala montana* Aubl.	14.48	9.86
Xylopia aromatica (Lam.) Mart.	18.46	6.13	*Byrsonima pachyphylla* A. Juss.	9.02	9.67

Chaetocarpus echinocarpus (Baill.) Ducke	10.39	3.52	*Eriotheca gracipiles*	8.12	9.48
Tapirira guianensis Aubl	12.04	2.84	*Qualea grandiflora* Mart.	10.59	8.12
Myrcia splendens (Sw .) DC	10.66	2.66	*Aspidosperma tomentosum* Mart	10.91	7.71

150   Fine root samples were collected at 20 cm depth soil near the coarse root of each individual. While this might include roots from outside the target individual, we were interested in root nutrient composition at the community scale; therefore, this approach was sufficient to address our key question. Samples were sieved and washed with tap water. After being oven dried at 70 ℃ until constant weight, dried samples were sent to Laboratório de Análises de Viçosa-MG, for nutrient concentration analyses. N and P (g kg – 1) were determined by Kjedahl digestion and UV-Vis spectroscopy, respectively, and the other

155   nutrients (Ca, Mg and K, g kg – 1) were determined by atomic absorption spectrometry.

Nutrient resorption efficiency (RE) was calculated following Eq. (1):

$$RE = \left(1 - \frac{Nut_{old}}{Nut_{mat}} MLCF\right) \times 100 \tag{1}$$

where Nut_{mat} is the nutrient concentration of mature leaves and Nut_{old} is the nutrient concentration of senesced leaves and *MLCF* is the green to senesced leaf Ca ratio (Vitousek and Sanford, 1986). This calculation is based on the assumption that

160   Ca is not translocated, and enables correction for differences in leaf mass per area between mature and senescent leaves.

2.3 Estimation of NPP

Net primary productivity is the rate of organic material production, and can be quantified at the scale of an individual plant or an ecosystem (Malhi et al., 2011). Here we quantified the major components of NPP, including the canopy (leaves, twigs and reproductive parts), wood (stem, coarse roots and branches), and fine roots during 2014 to 2016. Data were collected

165   following GEM protocols (Malhi et al. 2021) and methods are described in detail in Mathews et al. 2014 and Malhi et al. (2021). Briefly, for the canopy NPP component estimation, litter traps sampled biweekly together with monthly canopy leaf area index were used. For wood component estimation, annual census and dendrometers measuring growth rates were converted into woody biomass production. Fine root production was measured with ingrowth cores installed and sampled every three months. Estimates of NPP are usually biased because it is very challenging to measure small NPP terms, such as

170   volatile emissions, herbivory losses, and mycorrhizae exudates. Nevertheless, these terms are likely minor components of carbon budget (Malhi et al., 2021), and here we focus on major components of NPP (canopy, wood and fine roots), recognising that, inevitably, these missing terms exist.

For stoichiometric calculations, carbon was assumed to be 50% of the biomass for wood and canopy components, 48% for fine roots and 39% for litter (Biot et al., 1998; Paiva et al., 2011). Nutrient uptake (kg ha^{-1} year^{-1}) and nutrient demand (kg ha^{-1} year^{-1}), were calculated following Eq. (2) and Eq. (3), respectively:

$$Nut_{uptake} = \left(\left(\frac{NPP_{canopy}}{C:Nut_{mat}} \right) (1 - RE) \right) + \left(\frac{NPP_{wood}}{C:Nut_{wood}} \right) + \left(\frac{NPP_{fine\,roots}}{C:Nut_{fine\,roots}} \right) \tag{2}$$

$$Nut_{demand} = \left(\left(\frac{NPP_{canopy}}{C:Nut_{mat}} \right) \right) + \left(\frac{NPP_{wood}}{C:Nut_{wood}} \right) + \left(\frac{NPP_{fine\,roots}}{C:Nut_{fine\,roots}} \right) \tag{3}$$

where NPP is plot-mean NPP (Mg C ha^{-1} year^{-1}), and C:Nut is plot-mean nutrient stoichiometry.

Thus, we calculated nutrient use efficiency (kg C per kg nutrient) as the ratio of total NPP (NPP$_{canopy}$ + NPP$_{wood}$ + NPP$_{fine\,roots}$) and Nut$_{uptake}$ (NutUE$_{uptake}$) and Nut$_{demand}$ (NutUE$_{demand}$). Hence, NutUE$_{demand}$ takes into account that a large part of nutrient demand can be met by translocation from senescing leaves and therefore does not require uptake from the soil.

2.4 Statistical analyses

To upscale species value for the whole communities, we calculated the community-weighted mean (CWM) for each organ using species relative dominance to weight the nutrient concentration (Muscarella & Uriarte, 2016). To compare nutrient concentration average means and resorption efficiencies between the two vegetation types and between different organs, we performed a two-way multivariate analysis of variance (MANOVA) followed by two-way univariate analysis of variances (ANOVA's) and Tukey HSD post-hoc test. The independent variables were site and plant organ while the dependent variables for the MANOVA were the different nutrient concentrations (N, P, K, Ca, Mg) or resorption. Data normality and homogeneity of variances assumptions were previously checked with Shapiro-Wilk multivariate normality test using package 'mvnormtest' (Jarek and Jarek, 2009) and Levene test using package 'car' (Fox et al., 2012), respectively. All statistical analyses were performed in R software version 4.0.1 (R Core Team, 2019).

To account for the systematic uncertainties intrinsic to the methods used to NPP calculations for the different components, we assigned sampling uncertainties to each measurement and propagated them through our calculations. Following the standard rules of quadrature (Hughes and Hase, 2010), we calculated the standard error of the mean (SE), and propagated it by adding the components in quadrature, assuming the uncertainties in the independent variables were uncorrelated. To calculate differences between sites for NPP, nutrient demand to different components and nutrient use and uptake efficiencies, we performed z-tests using the average value for each site and the propagated error.

3 Results

3.1 Savanna-forest differences

200 For species mean comparisons, transition forest species showed higher leaf (green and old leaves), branch and root N concentration, while savanna species showed higher wood nutrients in general (higher N, P, K) for both sapwood and heartwood (MANOVA: F = 1.52, P = 0.029, Fig. 1). Cerrado species also showed higher leaf Mg concentrations and higher P and K inner bark concentrations. For community-weighted means, however, we did not find an identifiable interaction effect between the different plant organs and vegetation types (MANOVA: F = 1.28, P = 0.134), meaning that generally

205 there was no difference in nutrient concentration between cerrado and cerradão across the different tree components when species abundance and basal area were taken into account. Moreover, despite slightly higher nutrient resorption in the savanna, there were no differences between the two vegetation types (MANOVA: F = 0.23, P = 0.916; Fig. 2A). In general, we found higher P resorption (cerrado: 58.50 ± 18.97% and cerradão: 50.44 ± 15.72%) than N (cerrado: 49.46 ± 19.44% and cerradão: 39.58 ± 15.39%) for both sites and all species (Fig. 2).

210
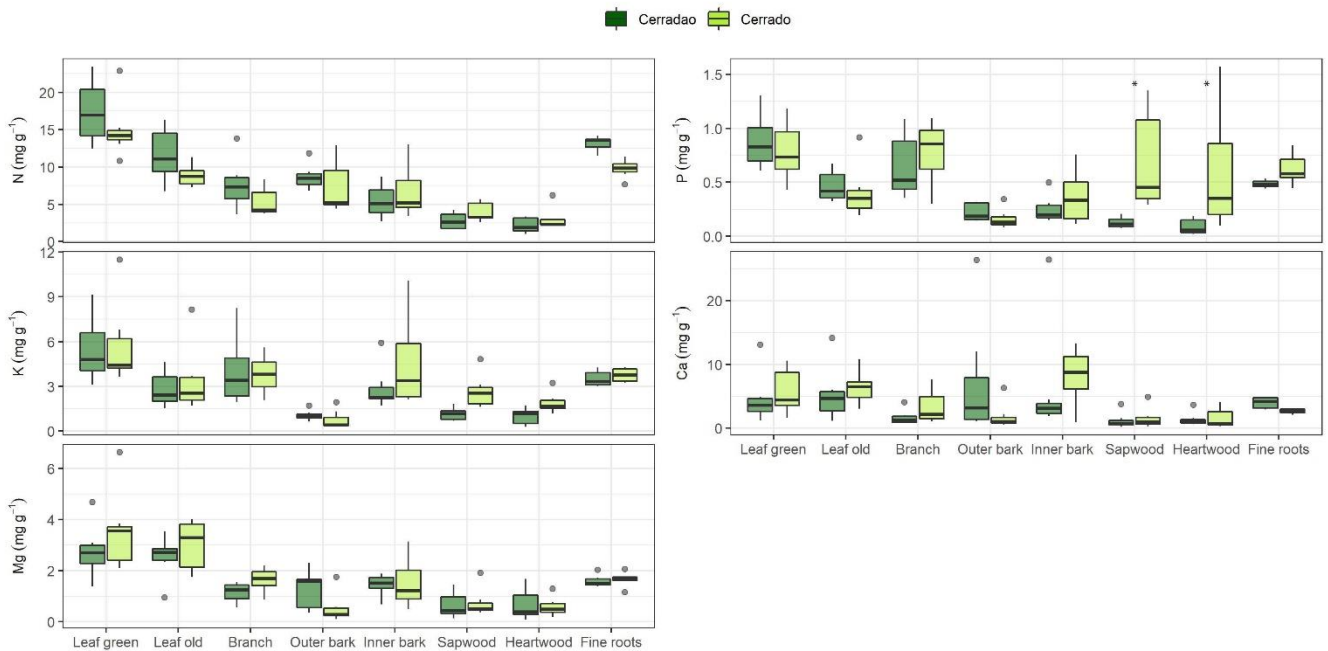
Figure 1: Macronutrient (N, P, K, Ca and Mg) concentrations (%) for different plant organs (leaf, branch, outer bark, inner bark, sapwood, heartwood and fine roots) in cerradão (dark green boxes) and cerrado (light green boxes)

vegetation. The continuous line within the box shows the median, and error bars show 10 and 90 percentiles (n = 7 species per vegetation type). Asterisks (*) represent differences between the two sites (P < 0.05). Species specific concentrations are shown in Figure S1.
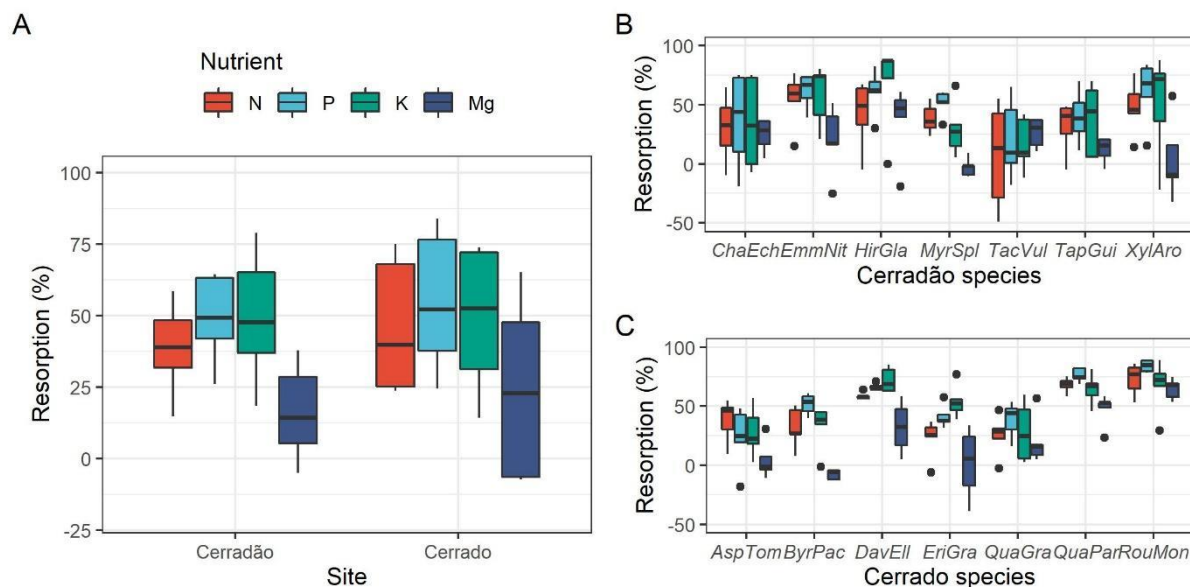
Figure 2: Nutrient (N, P, K, Mg) resorption efficiency (%) averaged for both vegetation types considering the community weighted mean for each species (A) and calculated for each of the species representing the transition forest (cerradão, B), savanna (cerrado, C). The continuous line within the box shows the median, and error bars show 10 and 90 percentiles (n = 5 individuals per species). Species abbreviation refer to the first three letters of the genera followed by the first three letters of the specific epithet, as follow from left to right: cerradão species (*Chaetocarpus echinocarpus*, *Emmotum nitens*, *Hirtella glandulosa*, *Myrcia splendens*, *Tachigali vulgaris*, *Tapirira guianensis*, *Xylopia aromatica*); and savanna species (*Aspidosperma tomentosum*, *Byrsonima pachyphylla*, *Davilla elliptica*, *Eriotheca gracipiles*, *Qualea grandiflora*, *Qualea parviflora*, *Roupala montana*).

3.2 Nutrient demand and partition

Cerradão yielded higher NPP for canopy (cerradão: 4.78 ± 0.12 and cerrado: 2.38 ± 0.08 Mg C ha^{-1} year^{-1}; P < 0.001) but similar NPP values for wood (cerradão: 2.77 ± 0.58 and cerrado: 2.79 ± 0.45 Mg C ha^{-1} year^{-1}; P = 0.111) and fine roots NPP (cerradão: 2.96 ± 0.76 and cerrado: 3.63 ± 0.81 Mg C ha^{-1} year^{-1}; P = 0.954, Fig. 3a, Table S2) components. In agreement with our expectations, nutrient demand was generally higher for cerradão species for all nutrients except for nutrient demand for the wood component, especially for phosphorus, which was 4-fold higher in the cerrado plot, but also for N and K (Fig. 3).
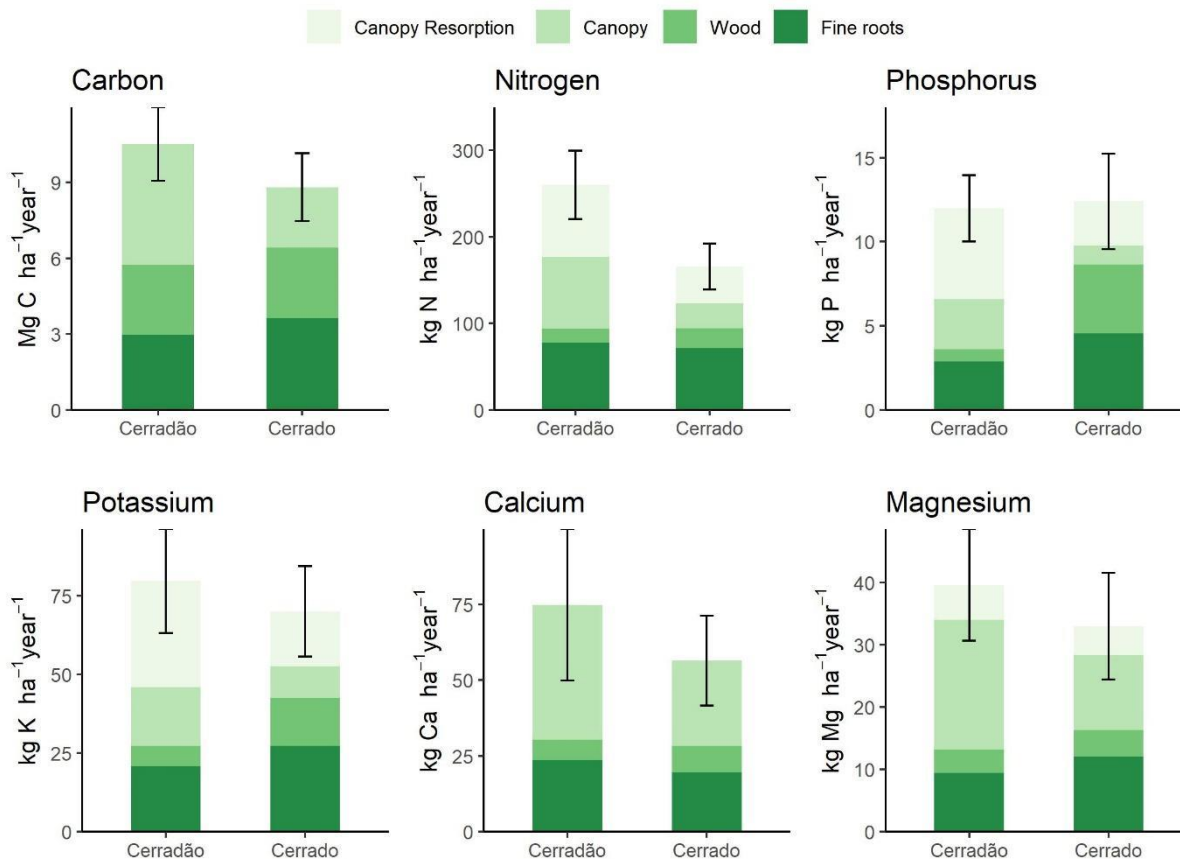
Figure 3: Net primary productivity (NPP, Mg C ha-1 year-1), and nutrient demands (N, P, K, Ca and Mg) partitioned into biomass components: canopy demand met by resorption (canopy resorption), canopy demand met by new uptake (canopy), wood and fine roots in cerradão (transition forest) and typical cerrado (savanna). Error bars indicate ± SE for all components pulled together (see Table S2 for comparison test results and Table 2 for individual values and errors).

Nutrient demand in the cerradão was predominantly allocated to canopy, with nutrient demand met by resorption corresponding to generally ~ 50% of the total canopy demand, while less than 35% of the N, P, K, Ca and Mg were allocated to the wood or fine roots (Table 2). For the cerrado, proportional allocation of nutrients was more equally partitioned across the different organs. For instance, in the cerrado, root nutrient demand was similar to total canopy nutrient demand for all nutrients, while P demand to the wood component corresponded to ~ 50% of the total phosphorus demand. In contrast, cerradão proportionally demanded more nutrients to the canopy, while cerrado proportionally demanded more N, P and K, Ca and Mg to the wood and fine roots (Table 2).

Table 2. The total (mean ± SE, kg ha^{-1} year^{-1}) and proportional (%) partitioning of nutrient demand between canopy, wood and fine roots, together with the component of overall nutrient demand met via resorption from senescent leaves, for transitional forest (*cerradão*) and savanna (*cerrado*) sites.

Nutrient	Cerradão				Cerrado			
	Canopy		Wood	Fine root	Canopy		Wood	Fine root
	Total mean ± SE (%)	Resorption mean ± SE (%)	mean ± SE (%)	mean ± SE (%)	Total mean ± SE (%)	Resorption mean ± SE (%)	mean ± SE (%)	mean ± SE (%)
N	166.52 ± 25.83 (63.98)	83.09 ± 16.59 (49.90)	15.93 ± 3.52 (6.12)	77.83 ± 10.32 (29.90)	71.29 ± 13.67 (43.00)	42.35 ± 10.23 (59.41)	23.51 ± 3.94 (14.18)	70.99 ± 8.93 (42.82)
P	8.37 ± 1.43 (69.97)	5.41 ± 1.05 (64.55)	0.73 ± 0.17 (6.11)	2.86 ± 0.38 (23.93)	3.75 ± 0.86 (30.25)	2.63 ± 0.67 (70.02)	4.11 ± 1.27 (33.14)	4.53 ± 0.69 (36.60)
K	52.29 ± 12.18 (65.68)	33.64 ± 8.76 (64.35)	6.55 ± 1.31 (8.22)	20.77 ± 3.04 (26.10)	27.42 ± 7.69 (39.17)	17.38 ± 5.43 (63.40)	6.55 ± 3.27 (21.87)	27.27 ± 3.42 (38.96)
Ca	44.42 ± 17.71 (59.33)	0.00	6.81 ± 3.37 (9.09)	23.64 ± 3.88 (31.58)	28.07 ± 7.88 (49.71)	0.00	8.85 ± 4.37 (15.68)	19.54 ± 2.54 (34.61)
Mg	26.37 ± 6.12 (66.63)	5.55 ± 2.53 (21.05)	3.80 ± 1.53 (9.60)	9.41 ± 1.29 (23.77)	16.65 ± 5.58 (50.48)	4.61 ± 3.07 (27.68)	4.28 ± 1.51 (12.98)	12.05 ± 1.78 (36.54)

250 PUE$_{uptake}$ and KUE$_{uptake}$ were ~45% and ~30% higher for the cerradão plot respectively (P < 0.001 and P = 0.011, respectively; Table S3), while NUE$_{uptake}$ was ~17% higher in the cerrado plot (Fig. 4, non-significant, P = 0.078; Table S3). NUE$_{uptake}$, CaUE$_{uptake}$ and MgUE$_{uptake}$ were similar between cerradão and cerrado (Fig. 4; Table S3). For nitrogen, cerradão uptake was similar with similar resorption factor and lower (~24%) NUE$_{demand}$ (P = 0.012; Table S3), leading to higher N demand compared to the cerrado (Fig. 4). For P, there was a decrease in uptake in the cerradão coupled with an increase in

255 resorption and 24% higher PUE$_{demand}$ (non-significant, P = 0.107; Table S3), leading to little overall change in P demand (Fig. 4). There was little difference in K uptake between the sites but the increased resorption in cerradão supports greater demand (Fig. 4). Comparing cerrado and cerradão plots, \Mg uptake matched demand and there was little adjustment in resorption or nutrient use efficiency (Fig. 4).

260
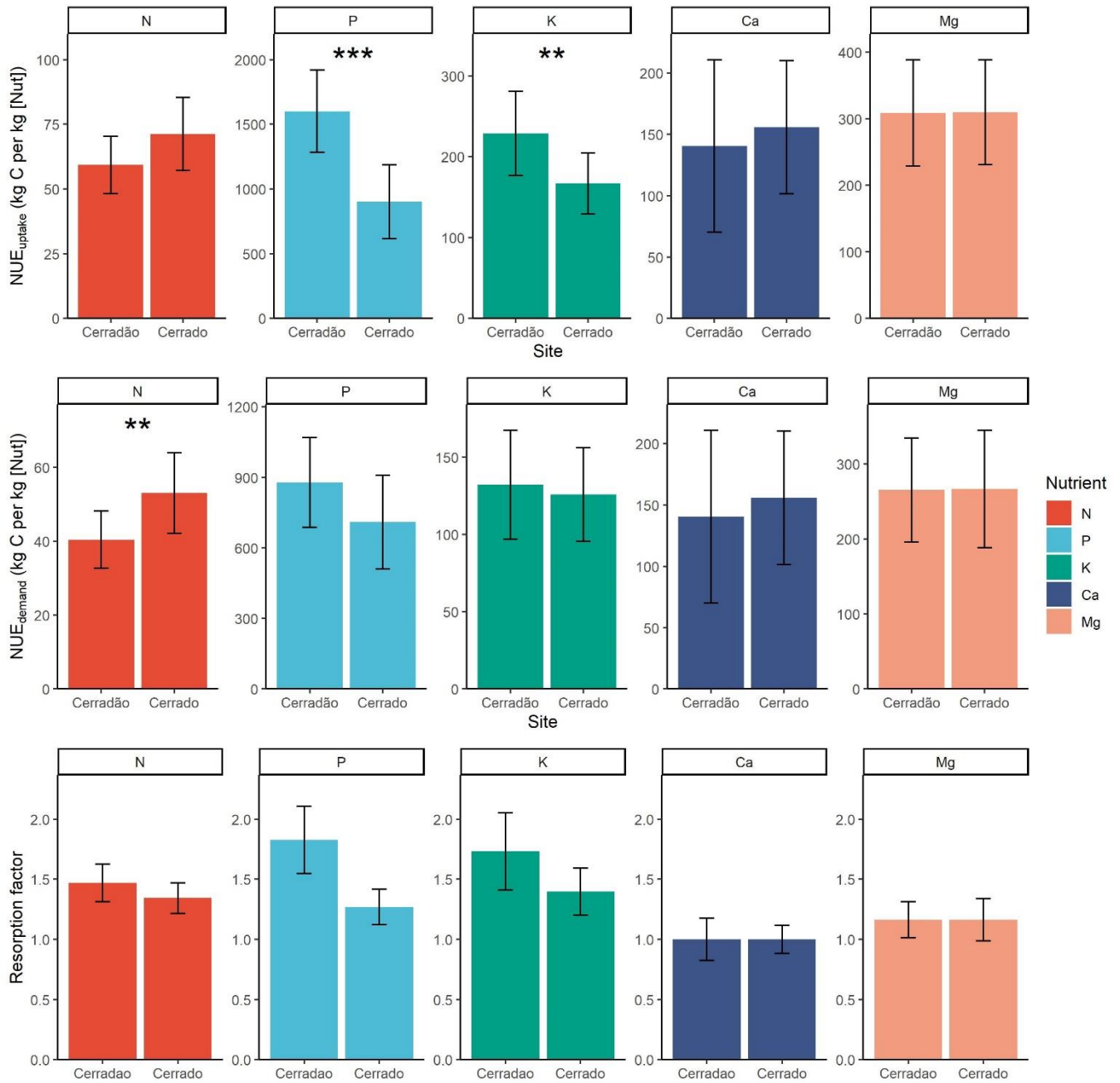
Figure 4: Nutrient uptake efficiency (kg C per kg [Nut]), nutrient use efficiency (kg C per kg [Nut]), resorption factor (i.e., the demand to uptake ratio) in cerradão (transition forest) and typical cerrado (savanna). Error bars indicate ± SE and asterisks show significant differences between sites (z-tests, ** 0.01 < P < 0.05; ***P < 0.001; Table S3).

4 Discussion

Unexpectedly, there was no major difference in cerradão and cerrado species nutrient content in the different plant organs. The only and most remarkable difference was in wood P concentration, where we found a clear trend of all cerrado species allocating very high amounts of P to the sapwood and heartwood. Wood nutrient allocation directly affects nutrient residence time at a whole tree level; nutrients allocated to the canopy lead to larger flux via fast turnover meaning a shorter residence time, compared to nutrients allocated to wood biomass (Tsujii et al., 2020). Our results agree with the current literature suggesting that P in tropical ecosystems is a key limiting nutrient (Malhi et al., 2009; Quesada et al., 2010) and may be affecting transition ecosystem dynamics (Dionizio et al., 2018), suggesting two distinct strategies in the cerrado and cerradão vegetation. In the cerradão, transition forest species may be allocating P to the canopy as an adaptive mechanism to maintain higher photosynthetic rates (Gleason et al., 2009; Reich et al., 2009, Aoyagi and Kitayama, 2016) to support the high net primary productivity in low-P soils. In cerrado, savanna species might allocate P to the wood as a mechanism to extend P residence time in the living biomass (Tsujii et al., 2020).

The strategy of storing P in wood biomass of cerrado species may be important to avoid P loss by recurrent fires. Although soil P may even increase shortly after fire (Schaller et al., 2015), P-binding components in ash may decrease P availability, by forming low soluble P forms that are not readily available for plants (Schaller et al., 2015, Ngoc Nguyen, 2014 #8852). Furthermore, the loss of P stocks after fire because of volatilization remains anecdotal because P has a high volatilisation temperature (above 770C, DeBano, 2000) and Cerrado fires are usually very fast and do not achieve these high temperatures (Miranda et al., 1993). Although some experimental studies comparing the amount of nutrients in the fuel and in the ash after fire found a ~50% reduction of P content (Pivello and Coutinho, 1992; Kauffman et al., 1994), Resende and others (2011) suggested that the decrease in organic-P fraction and P availability in cerrado burned plots compared to unburned plots was probably caused by the decrease of organic inputs through litterfall, rather than a direct effect of fire. In the same study area as ours, de Oliveira and others (2017) have found higher decomposition of the total biomass, and higher nutrients cycling through litterfall in the cerradão compared to cerrado plot. Indeed, Mendes and others (2012) have shown that forest-like vegetation types in the Cerrado biome (cerradão and gallery forests) presented higher microbial biomass and soil biological functioning compared to savannas. Therefore, we suggest that cerradão species may have adopted the strategy of relying on the soil biota activity and higher litterfall production to promote rapid nutrient cycling, whereas cerrado vegetation species may have evolved by natural selection to minimise P loss, by storing P in the wood. Nevertheless, further research in nutrient dynamics in these vegetation types is needed to test this hypothesis.

Nutrient resorption efficiency was also similar between cerrado and cerradão vegetation, and our results are in agreement with the global average range for woody angiosperms (Vergutz et al., 2012). Our fine-scale leaf resorption results are consistent with previous reports suggesting that effective nutrient cycling in the cerradão compensates for the low saturation of exchangeable bases in the soil (de Oliveira et al., 2017).

While the cerradão showed higher total NPP and higher nutrient demand on all elements for canopy production, cerrado vegetation allocated more nutrient to root and wood, demanding a higher amount of most nutrients (particularly P and K) despite showing similar woody NPP. Differences in fine-root nutrient demand between cerrado and cerradão varied by nutrient. The cerrado plot showed similar fine-root NPP to the cerradão and demanded a similar amount of N, Ca and Mg. However, cerrado species demanded more P and K to the fine roots, suggesting that generally cerrado species require more nutrient for fine roots production. Fine roots are an important component of the biomass, reflecting in a higher uptake of limiting nutrients in soil (Loiola et al., 2016), and are essential to overcome the strong water deficit during the dry season in the Cerrado (Oliveira et al., 2005). Therefore, the efficient fine root production in the cerradão vegetation may be an important adaptation to readily absorb water and nutrients during the strongly seasonal rainfall period (February et al., 2013). However, since our sampling strategy may have measured non-target species, such as grasses, our results could be biased.

Ultimately, cerradão species showed higher NUE_{uptake} for both P and K , which may explain how similar soils and the same climate can support forest-like formations. Cerradão vegetation require more N, Ca and Mg, and less P, but adjust the stoichiometry and boost P resorption, leading to similar overall usage of P, while K resorption is increased, which supports greater NPP despite similar net uptake. The relatively similar Ca and Mg NUE_{uptake} between sites suggests that both ecosystems are able to satisfy their Ca and Mg requirements (uptake tracks demand, with only modest adjustments in stoichiometry), whereas P, N and to some extent K, may be more limiting nutrients.

In particular, the high P-use efficiency (PUE) exhibited for both cerradão and cerrado vegetation is an expected adaptation for dealing with low-P soils, and extending P residence time is an adaptive trait to increase PUE. Indeed, in Bornean and Australian low-P tropical forest species, P residence time in aboveground component was shown to increase with P deficiency (Paoli et al., 2005; Gleason et al., 2009; Tsujii et al., 2020). However, direct measurements of nutrient concentrations and stocks in wood and fine roots are scarce in tropical forests (Johnson et al, 2001; Feldpausch et al., 2004; Li et al., 2010; Heineman et al., 2016), or limited to a single nutrient (Imai, et el., 2010; Tsujii et al. 2020).

The lower N use efficiency and the higher P and K use efficiencies in the cerradão suggests that differences in tree community composition and the species-specific functional traits may considerably influence nutrient cycling. For example, *Tachigali vulgaris*, which contributes to ~20% basal area in the cerradão), was described as a key N-fixing species (de Castro et al., 1998) that promotes tree encroachment, by increasing enriched litterfall production and facilitating growth and development of other tree species (Morandi et al., 2016; de Oliveira et al., 2017). Indeed, the increased N uptake in the cerradão allows for a reduced NUE meaning more N in stoichiometry. However, it is important to note that our results are based on two plots, and there may be potential misinterpretation due to any particularity of these studied sites. Even though we examined the only Cerrado and Cerradão established sites with intensive monthly data collection and monitoring, our findings would obviously benefit from further testing with more savanna and transition forest sites.

5 Conclusion

By using the direct relationship between nutrient stoichiometry and NPP for different biomass components, we showed that cerrado vegetation is less efficient in fine root and wood production, requiring more nutrients per unit of NPP compared to the cerradão. Ultimately, we also report the different strategies in P use between cerrado and cerradão that may reflect savanna vegetation adaptation to the indirect effects of fire in the soil biota, which is a recurrent disturbance that increases the risk of losing P. With the increasing fire frequency associated with extreme drought events due to climate change, cerradão vegetation, which strongly rely on rapid nutrient cycling, may suffer further P limitation.

6 Author contribution

MCS, IO and YM conceived the idea, questions and hypotheses; IO and YM secured funding for research; MCS, IO, BSM, BHMJr and YM developed study design and methodology; MCS, RF and KSP collected the data; MCS and SR analysed the data; MCS led the writing of the manuscript, and all authors critically contributed to the drafts and gave final approval for publication.

7 Competing interests

The authors declare that they have no conflict of interest.

8 Acknowledgments

We thank NERC (Natural Environmental Research Council) BIO-RED (#ACR00460) for funding this research. We also thank Camila Borges Silva, Halina Jancoski, Edmar Almeida and Igor Araújo for the valuable help during fieldwork. MCS is supported by a postdoctoral fellowship from CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), Brazil. YM is supported by the Jackson Foundation.

9 References

Aerts, R. and Chapin, F. S.: The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns, Adv. Ecol. Res., 30, 1-67, https://doi.org/10.1016/S0065-2504(08)60016-1, 1999.

Aoyagi, R. and Kitayama, K.: Nutrient allocation among plant organs across 13 tree species in three Bornean rain forests with contrasting nutrient availabilities, J Plant Res, 129, 675-684, 10.1007/s10265-016-0826-z, 2016.

Aragão, L., Malhi, Y., Metcalfe, D., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., Almeida, S., Costa, A., Salinas, N., and Phillips, O. L.: Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils, Biogeosciences, 6, 2759-2778, https://doi.org/10.5194/bg-6-2759-2009, 2009.

355 Biot, Y., Higuchi, N., Minette, L., dos Santos, J., and Ribeiro, R. J.: Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira, Acta Amazon, 28, 153-166, https://doi.org/10.1590/1809-43921998282166, 1998.

Bond, W. J.: Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis, Plant Soil, 334, 47-60, https://doi.org/10.1007/s11104-010-0440-0, 2010.

360 Bridgham, S.D., Pastor, J., McClaugherty, C.A. and Richardson, C.J., Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. Am Nat, 145, 1-21. https://doi.org/10.1086/285725, 1995.

Bucci, S. J., Scholz, F. G., Goldstein, G., Meinzer, F. C., Franco, A. C., Campanello, P. I., Villalobos-Vega, R., Bustamante, M., and Miralles-Wilhelm, F.: Nutrient availability constrains the hydraulic architecture and water relations of savannah

365 trees, Plant Cell Environ, 29, 2153-2167, 10.1111/j.1365-3040.2006.01591.x, 2006.

Bustamante, M. M., de Brito, D. Q., Kozovits, A. R., Luedemann, G., de Mello, T. R., de Siqueira Pinto, A., Munhoz, C. B., and Takahashi, F. S.: Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado), Plant Ecol, 213, 795-808, https://doi.org/10.1007/s11258-012-0042-4, 2012.

Case, M. F. and Staver, A. C.: Fire prevents woody encroachment only at higher-than-historical frequencies in a South

370 African savanna, J Appl Ecol, 54, 955-962, https://doi.org/10.1111/1365-2664.12805, 2017.

Chapin III, F. S.: The mineral nutrition of wild plants, Annu Rev Ecol Evol Syst, 11, 233-260, https://doi.org/10.1146/annurev.es.11.110180.001313, 1980.

Chapin III, F. S., Schulze, E. D., and Mooney, H. A.: The ecology and economics of storage in plants, Annu Rev Ecol Evol Syst, 21, 423-447, https://doi.org/10.1146/annurev.es.21.110190.002231, 1990.

375 Chapin III, F. S., Vitousek, P. M., and Van Cleve, K.: The nature of nutrient limitation in plant communities, Am. Nat., 127, 48-58, https://doi.org/10.1086/284466, 1986.

Cole, M. M.: The savannas, Prog Phys Geogr, 11, 334-355, https://doi.org/10.1177/030913338701100302, 1986.

Coley, P. D., Bryant, J. P., and Chapin III, F. S.: Resource availability and plant antiherbivore defense, Science(Washington), 230, 895-899, 10.1126/science.230.4728.895, 1985.

380 Craine, J. M., Morrow, C., and Stock, W. D.: Nutrient concentration ratios and co-limitation in South African grasslands, New Phytol., 179, 829-836, 10.1111/j.1469-8137.2008.02513.x, 2008.

de Castro, A. W. V., de Farias, N., Tomé, J., and Cavalcante, E. d. S.: Efeito do espaçamento na produtividade de biomassa de taxi-branco (*Sclerolobium paniculatum* Vogel), Acta Amazon, 28, 141-141, https://doi.org/10.1590/1809-43921998282146, 1998.

385 de Oliveira, B., Junior, B. H. M., Mews, H. A., Valadão, M. B. X., and Marimon, B. S.: Unraveling the ecosystem functions in the Amazonia–Cerrado transition: evidence of hyperdynamic nutrient cycling, Plant Ecol, 218, 225-239, 10.1007/s11258-016-0681-y, 2017.

DeBano, L. F.: The role of fire and soil heating on water repellency in wildland environments: a review, J Hydrol, 231, 195-206, https://doi.org/10.1016/S0022-1694(00)00194-3, 2000.

390 Dionizio, E. A., Costa, M. H., Castanho, A. D., Pires, G. F., Marimon, B. S., Hur Marimon-Junior, B., Lenza, E., Pimenta, F. M., Yang, X., and Jain, A. K.: Influence of climate variability, fire and phosphorus limitation on vegetation structure and dynamics of the Amazon–Cerrado border, Biogeosciences, 15, 919-936, https://doi.org/10.5194/bg-15-919-2018, 2018.

Durigan, G. and Ratter, J.: Successional changes in cerrado and cerrado/forest ecotonal vegetation in western Sao Paulo State, Brazil, 1962–2000, Edinb J Bot, 63, 119-130, https://doi.org/10.1017/S0960428606000357, 2006.

395 EMBRAPA Empresa Brasileira de Pesquisa Agropecuária (1997) Manual de métodos de análise de solo. Centro Nacional de Pesquisa de Solos, Rio de Janeiro

February, E., Cook, G., and Richards, A. E.: Root dynamics influence tree–grass coexistence in an Australian savanna, Austral Ecol, 38, 66-75, https://doi.org/10.1111/j.1442-9993.2012.02376.x, 2013.

Feldpausch, T. R., Rondon, M. A., Fernandes, E. C., Riha, S. J., and Wandelli, E.: Carbon and nutrient accumulation in 400 secondary forests regenerating on pastures in central Amazonia, Ecol Appl, 14, 164-176, https://doi.org/10.1890/01-6015, 2004.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., Chapin III, F. S., Ciais, P., Malhi, Y., and Obersteiner, M.: Nutrient availability as the key regulator of global forest carbon balance, Nat Clim Change, 4, 471, https://doi.org/10.1038/nclimate2177, 2014.

405 Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., and Graves, S.: Package 'car', Vienna: R Foundation for Statistical Computing, 16, 2012.

Gleason, S. M., Read, J., Ares, A., and Metcalfe, D. J.: Phosphorus economics of tropical rainforest species and stands across soil contrasts in Queensland, Australia: understanding the effects of soil specialization and trait plasticity, Funct Ecol, 23, 1157-1166, https://doi.org/10.1111/j.1365-2435.2009.01575.x, 2009.

410 Grime, J. P.: Plant strategies, vegetation processes, and ecosystem properties, John Wiley & Sons, England, 2006.

Haridasan, M.: Nutritional adaptations of native plants of the cerrado biome in acid soils, Braz J Plant Physiol, 20, 183-195, https://doi.org/10.1590/S1677-04202008000300003, 2008.

Heineman, K. D., Turner, B. L., and Dalling, J. W.: Variation in wood nutrients along a tropical soil fertility gradient, New Phytol, 211, 440-454, https://doi.org/10.1111/nph.13904, 2016.

415 Hendricks, J. J., Nadelhoffer, K. J., and Aber, J. D.: Assessing the role of fine roots in carbon and nutrient cycling, Trends Ecol Evol, 8, 174-178, https://doi.org/10.1016/0169-5347(93)90143-D, 1993.

Hoffmann, W. A., Orthen, B., and Nascimento, P. K. V. d.: Comparative fire ecology of tropical savanna and forest trees, Funct Ecol, 17, 720-726, https://doi.org/10.1111/j.1365-2435.2003.00796.x, 2003.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C., Lau, O. L., Haridasan, M., and Franco, A. C.:
Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes, Ecol Lett, 15, 759-768, https://doi.org/10.1111/j.1461-0248.2012.01789.x, 2012.

Hughes, I. and Hase, T.: Measurements and their uncertainties: a practical guide to modern error analysis, Oxford University Press, New York, 2010.

Imai, N., Kitayama, K., and Titin, J. Distribution of phosphorus in an above-to below-ground profile in a Bornean tropical rain forest. J Trop Ecol, 26, 627–636. Retrieved from https://doi.org/10.1017/S0266467410000350, 2010.

Jackson, R., Canadell, J., Ehleringer, J. R., Mooney, H., Sala, O., and Schulze, E.: A global analysis of root distributions for terrestrial biomes, Oecologia, 108, 389-411, https://doi.org/10.1007/BF00333714, 1996.

Jarek, S. and Jarek, M. S.: Package 'mvnormtest', 2009.

Johnson, C. M., Vieira, I. C. ., Zarin, D. J., Frizano, J., and Johnson, A. H. Carbon and nutrient storage in primary and secondary forests in eastern Amazônia. For Ecol Managt, 147, 245–252, https://doi.org/10.1016/S0378-1127(00)00466-7, 2001,

Kauffman, J. B., Cummings, D., and Ward, D.: Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado, J Ecol, 82, 519-531, https://doi.org/10.2307/226126,1 1994.

Killingbeck, K.T. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology, 77, 1716-1727, https://doi.org/10.2307/2265777, 1996.

Lehmann, C. E., Archibald, S. A., Hoffmann, W. A., and Bond, W. J.: Deciphering the distribution of the savanna biome, New Phytol, 191, 197-209, https://doi.org/10.1111/j.1469-8137.2011.03689.x, 2011.

Li, A., Guo, D., Wang, Z., and Liu, H.: Nitrogen and phosphorus allocation in leaves, twigs, and fine roots across 49 temperate, subtropical and tropical tree species: a hierarchical pattern, Funct Ecol, 24, 224-232, https://doi.org/10.1111/j.1365-2435.2009.01603.x, 2010.

Loiola, P. P., Carvalho, G. H., and Batalha, M. A.: Disentangling the roles of resource availability and disturbance in fine and coarse root biomass in savanna, Austral Ecol, 41, 255-262, https://doi.org/10.1111/aec.12306, 2016.

Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., and Phillips, O. L.: ForestPlots. net: a web application and research tool to manage and analyse tropical forest plot data, J Veg Sci, 22, 610-613, https://doi.org/10.1111/j.1654-1103.2011.01312.x, 2011.

Malhi, Y.: The productivity, metabolism and carbon cycle of tropical forest vegetation, J Ecol, 100, 65-75, https://doi.org/10.1111/j.1365-2745.2011.01916.x, 2012.

Malhi, Y., Doughty, C., and Galbraith, D.: The allocation of ecosystem net primary productivity in tropical forests, Philos Trans R Soc B: Biol Sci, 366, 3225-3245, https://doi.org/10.1098/rstb.2011.0062, 2011.

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E., Rifai, S. W., Oliveras, I., Shenkin, A., Aguirre-Gutiérrez, J., and Dahlsjö, C. A.: The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics, Biol Conserv, 253, 108889, https://doi.org/10.1016/j.biocon.2020.108889, 2021.

Marimon-Junior, B. H. and Haridasan, M.: Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado *sensu stricto* em áreas adjacentes sobre solo distrófico no leste de Mato Grosso, Brasil, Acta Bot. Brasilica, 19, 913-

455   926, https://doi.org/10.1590/S0102-33062005000400026, 2005.

Marimon, B., Lima, E. D. S., Duarte, T., Chieregatto, L., and Ratter, J.: Observations on the vegetation of northeastern Mato Grosso, Brazil. IV. An analysis of the Cerrado–Amazonian Forest ecotone, Edinb J Bot, 63, 323-341, https://doi.org/10.1017/S0960428606000576, 2006.

McCormack, M. L., Adams, T. S., Smithwick, E. A., and Eissenstat, D. M.: Predicting fine root lifespan from plant

460   functional traits in temperate trees, New Phytol, 195, 823-831, https://doi.org/10.1111/j.1469-8137.2012.04198.x, 2012.

Mendes, I., Fernandes, M. F., Chaer, G. M., and dos Reis Junior, F. B.: Biological functioning of Brazilian Cerrado soils under different vegetation types, Plant Soil, 359, 183-195, https://doi.org/10.1007/s11104-012-1195-6, 2012.

Miranda, A. C., Miranda, H. S., Dias, I. d. F. O., and de Souza Dias, B. F.: Soil and air temperatures during prescribed cerated fires in Central Brazil, J Trop Ecol, 9, 313-320, https://doi.org/10.1017/S0266467400007367, 1993.

465   Moles, A. T., Peco, B., Wallis, I. R., Foley, W. J., Poore, A. G., Seabloom, E. W., Vesk, P. A., Bisigato, A. J., Cella-Pizarro, L., and Clark, C. J.: Correlations between physical and chemical defences in plants: tradeoffs, syndromes, or just many different ways to skin a herbivorous cat?, New Phytol, 198, 252-263, https://doi.org/10.1111/nph.12116, 2013.

Morandi, P., Marimon-Junior, B., De Oliveira, E., Reis, S., Valadão, M. X., Forsthofer, M., Passos, F., and Marimon, B.: Vegetation succession in the Cerrado–Amazonian forest transition zone of Mato Grosso state, Brazil, Edinb J Bot, 73, 83-93,

470   https://doi.org/10.1017/S096042861500027X, 2016.

Muscarella, R., and Uriarte, M. Do community-weighted mean functional traits reflect optimal strategies? Proc R Society B, 283. 20152434, .https://doi.org/10.1098/ rspb.2015.2434, 2016.

Nardoto, G. B., da Cunha Bustamante, M. M., Pinto, A. S., and Klink, C. A.: Nutrient use efficiency at ecosystem and species level in savanna areas of Central Brazil and impacts of fire, J Trop Ecol, 22, 191–201, 10.1017/s0266467405002865,

475   2006.

Oliveira, R., Bezerra, L., Davidson, E., Pinto, F., Klink, C., Nepstad, D., and Moreira, A.: Deep root function in soil water dynamics in cerrado savannas of central Brazil, Funct Ecol, 19, 574-581, https://doi.org/10.1111/j.1365-2435.2005.01003.x, 2005.

Oliveras, I. and Malhi, Y.: Many shades of green: the dynamic tropical forest–savannah transition zones, Phil. Trans. R. Soc.

480   B, 371, 20150308, https://doi.org/10.1098/rstb.2015.0308, 2016.

Paiva, A. O., Rezende, A. V., and Pereira, R. S.: Estoque de carbono em cerrado sensu stricto do Distrito Federal, Rev Árvore, 35, https://doi.org/10.1590/S0100-67622011000300015, 2011.

Paoli, G. D., Curran, L. M., and Zak, D. R. Phosphorus efficiency of Bornean rainforest productivity: Evidence against the unimodal efficiency hypothesis. Ecology, 86, 1548–1561. https://doi.org/10.1890/04-1126, 2005.

485 Peixoto, K. d. S., Marimon-Junior, B. H., Cavalheiro, K. A., Silva, N. A., das Neves, E. C., Freitag, R., Mews, H. A., and Valadão, M. B. X.: Assessing the effects of rainfall reduction on litterfall and the litter layer in phytophysiognomies of the Amazonia–Cerrado transition, Braz J Bot, 41, 589-600, https://doi.org/10.1007/s40415-018-0443-2, 2018.

Peixoto, K. S., Marimon-Junior, B. H., Marimon, B. S., Elias, F., de Farias, J., Freitag, R., Mews, H. A., das Neves, E. C., Prestes, N. C. C., and Malhi, Y.: Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and

490 CO2 soil efflux in cerradão forest undergoing ecological succession, Acta Oecol, 82, 23-31, https://doi.org/10.1016/j.actao.2017.05.005, 2017.

Pellegrini, A. F.: Nutrient limitation in tropical savannas across multiple scales and mechanisms, Ecology, 97, 313-324, https://doi.org/10.1890/15-0869.1, 2016.

Phillips, O., Baker, T., Feldspauch, T., and Brienen, R.: Field manual for plot establishment and remeasurement

495 (RAINFOR), Amazon Forest Inventory Network, Sixth Framework Programme (2002–2006), 10.13140/RG.2.1.1735.7202, 2002.

Pivello, V. R. and Coutinho, L. M.: Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna), J Trop Ecol, 8, 487-497, https://doi.org/10.1017/S0266467400006829, 1992.

Quesada, C., Lloyd, J., Schwarz, M., Baker, T., Phillips, O. L., Patiño, S., Czimczik, C., Hodnett, M., Herrera, R., and

500 Arneth, A.: Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties, Biogeosci Discuss, 6, 3993-4057, 10.5194/bgd-6-3993-2009, 2009.

Quesada, C., Lloyd, J., Schwarz, M., Patino, S., Baker, T., Czimczik, C., Fyllas, N., Martinelli, L., Nardoto, G., and Schmerler, J.: Variations in chemical and physical properties of Amazon forest soils in relation to their genesis, Biogeosciences, 7, 1515-1541, https://doi.org/10.5194/bg-7-1515-2010, 2010.

505 Ratter, J. A., Richards, P., Argent, G., and Gifford, D.: Observations on the vegetation of northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo Expedition area, Philos Trans R Soc B: Biol Sci, 266, 449-492, https://doi.org/10.1098/rstb.1973.0053, 1973.

Reich, P. and Schoettle, A.: Role of phosphorus and nitrogen in photosynthetic and whole plant carbon gain and nutrient use efficiency in eastern white pine, Oecologia, 77, 25-33, 10.1007/BF00380920, 1988.

510 Reich, P. B., Oleksyn, J., and Wright, I. J.: Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species, Oecologia, 160, 207-212, 10.1007/s00442-009-1291-3, 2009.

Resende, J. C. F., Markewitz, D., Klink, C. A., da Cunha Bustamante, M. M., and Davidson, E. A.: Phosphorus cycling in a small watershed in the Brazilian Cerrado: impacts of frequent burning, Biogeochemistry, 105, 105-118, 10.1007/s10533-010-9531-5, 2011.

515 Ribeiro, J. F. and Walter, B. M. T.: Fitofisionomias do bioma Cerrado, in: Sano, S. M.; Almeida, S. P. de (Ed.). Cerrado: ambiente e flora. Embrapa Cerrados, Planaltina, Brazil, 1998.

Rosan, T. M., Aragão, L. E., Oliveras, I., Phillips, O. L., Malhi, Y., Gloor, E., and Wagner, F. H.: Extensive 21st-century woody encroachment in South America's savanna, Geophys. Res. Lett., 46, 6594-6603, 10.1029/2019GL082327, 2019.

Schaller, J., Tischer, A., Struyf, E., Bremer, M., Belmonte, D. U., and Potthast, K.: Fire enhances phosphorus availability in
520   topsoils depending on binding properties, Ecology, 96, 1598-1606, https://doi.org/10.1890/14-1311.1, 2015.

Silva, L. C., Hoffmann, W. A., Rossatto, D. R., Haridasan, M., Franco, A. C., and Horwath, W. R.: Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil, Plant Soil, 373, 829-842, 10.1007/s11104-013-1822-x, 2013.

Solbrig, O. T.: The diversity of the savanna ecosystem, in: Biodiversity and savanna ecosystem processes, edited by: Solbrig
525   O. T., Medina J. F., and Silva, J. F., Springer, Berlin, Heidelberg, 1-27, https://doi.org/10.1007/978-3-642-78969-4, 1996.

R Core Team: R: a language and environment for statistical computing [Internet]. 2018. R Foundation for Statistical Computing, Vienna, Austria, Available from: http://www.r-project. org, 2019.

Tsujii, Y., Aiba, S. i., and Kitayama, K.: Phosphorus allocation to and resorption from leaves regulate the residence time of phosphorus in above-ground forest biomass on Mount Kinabalu, Borneo, Funct Ecol, 34, 1702-1712,
530   https://doi.org/10.1111/1365-2435.13574, 2020.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., and Jackson, R. B.: Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants, Ecol Monogr, 82, 205-220, https://doi.org/10.1890/11-0416.1, 2012.

Viani, R. A., Rodrigues, R. R., Dawson, T. E., and Oliveira, R. S.: Savanna soil fertility limits growth but not survival of tropical forest tree seedlings, Plant Soil, 349, 341-353, 10.1007/s11104-011-0879-7, 2011.

535   Vitousek, P.: Nutrient cycling and nutrient use efficiency, Am Nat, 114, 553-572, https://doi.org/10.1086/283931, 1982.

Vitousek, P. M.: Litterfall, nutrient cycling, and nutrient limitation in tropical forests, Ecology, 65, 285-298, https://doi.org/10.2307/1939481, 1984.

Vitousek, P. and Sanford R. Nutrient cycling in moist tropical forest. Ann Rev Ecol Syst 17: 137-167. https://doi.org/10.1146/annurev.es.17.110186.001033, 1986.

540   Wang, L., D'Odorico, P., O'Halloran, L. R., Caylor, K., and Macko, S.: Combined effects of soil moisture and nitrogen availability variations on grass productivity in African savannas, Plant Soil, 328, 95-108, 10.1007/s11104-009-0085-z, 2010.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., and Wall, D. H.: Ecological linkages between aboveground and belowground biota, Science, 304, 1629-1633, 10.1126/science.1094875, 2004.

Wright, I. and Westoby, M.: Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species,
545   Funct Ecol, 17, 10-19, https://doi.org/10.1046/j.1365-2435.2003.00694.x, 2003.