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Diversidade funcional e estratégias nutricionais de espécies arbustivo-arbóreas de cerrado e floresta estacional

Orientador: Dr. Marco Antônio Batalha

São Carlos

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SUMÁRIO

RESUMO

A fertilidade do solo é um dos principais determinantes das transições abruptas entre o cerrado e a floresta estacional. Uma vez que os fragmentos remanescentes de cerrado estão cercados por matrizes agrícolas e podem ser impactados pela eutrofização, entender em que extensão os solos distrófico do cerrado determinam as estratégias e diversidade vegetal pode nos ajudar a prever os riscos de substituição do cerrado pela vegetação florestal e a evitar a perda de espécies e funções. No primeiro capítulo, comparamos as espécies de cerrado e de floresta estacional em relação às concentrações de nitrogênio e fósforo nas folhas verdes e senescentes e em relação à reabsorção proporcional desses nutrientes. Quantificamos a relação desses traços com outros traços foliares estruturais e com as propriedades do solo de cada ambiente. As variações das concentrações de nitrogênio e fósforo nas folhas verdes e senescentes estiveram mais relacionadas a medidas gerais de fertilidade do solo do que ao nitrogênio e fósforo do solo. No caso eficiência de reabsorção de nutriente, essas relações foram menos claras. Ainda, a relação nitrogênio:fósforo foliar foi menor entre as espécies de cerrado, apesar de os solos de cerrado e floresta não diferirem em relação ao nitrogênio e ao fósforo. No segundo capítulo, testamos se o cerrado e a floresta estacional foram montados por regras diferentes, apesar da proximidade física que possuem. Calculamos a distância filogenética-funcional entre os pares das espécies presentes em cada comunidade. Testamos se essas distâncias estavam relacionadas às propriedades do solo de cada ambiente. As regras de assembleias não diferiram do cerrado para a floresta estacional, e a fertilidade do solo determinou as diferenças funcionais entre ambos os tipos vegetacionais, apesar de não ser o único fator estruturando suas comunidades. No terceiro capítulo, estudamos padrões nos traços químicos e estruturais das folhas verdes das espécies de cerrado e de floresta, suas respostas à fertilidade do solo e seus efeitos sobre as taxas de decomposição. Apesar de um forte impacto da taxonomia na variação dos traços foliares, o solo exerceu um controle importante nos traços e nas estratégias das espécies do cerrado e da floresta por meio de múltiplos elementos. Contudo, o efeito dos traços e estratégias sobre o funcionamento das comunidades foi menos evidente.

Palavras-chave: filtro ambiental, florestas tropicais, reabsorção, regras de assembleia, savanas

ABSTRACT

Soil fertility is one of the main determinants of the abrupt boundaries between the cerrado and the seasonal forest. Given that the remaining patches of cerrado are surrounded by agricultural matrices and may be impacted by eutrophication, understanding whether the dystrophic soils of cerrado drive plant strategies and diversity might help us predict the risk of cerrado replacement by forest vegetation and avoid loss of species and functions. In the first chapter, we compared cerrado and seasonal forest species in terms of nitrogen and phosphorus concentration in green and senesced leaves and resorption efficiencies. We quantified the relationships among these traits, with other key leaf traits, and with soil features. Nitrogen and phosphorus concentration in green and senesced leaves were more strongly related to generalised measures of soil fertility than to soil total nitrogen and available phosphorus, but this pattern was not so clear for resorption efficiencies. Besides, leaf nitrogen:phosphorus ratio was lower in cerrado, despite the lack of difference in soil nitrogen and phosphorus between both vegetation types. In the second chapter, we tested whether cerrado and seasonal forest communities were assembled by different processes, despite their physical proximity. We calculated the pairwise functional-phylogenetic distances in cerrado and seasonal forest communities. We tested whether these distances were related to soil properties in each environment. Cerrado and seasonal forest were not assembled by different rules, and soil fertility determined the functional differences between both vegetation types, even though it was not the only force shaping the communities. In the third chapter, we studied patterns in chemical and structural traits in green leaves of cerrado and forest species, in their response to soil fertility, and in their effect on litter decomposition rates. Despite the large effect of taxonomy, soil exerted strong effect through multiple-element control over species functional traits and strategies. The effect of such different strategies on functioning, however, was less prominent.

Keywords: environmental filter, tropical forest, resorption, assembly rules, savannas

I - INTRODUÇÃO GERAL

Introdução geral

Em geral, as savanas ocorrem em locais cujas condições climáticas atuais suportariam florestas (Cole 1986). Ao redor do mundo, formações savânicas e florestais estão em contato, como estados alternados ou fixos (Staver et al. 2011). Muitos fatores, como o fogo e as disponibilidades de luz, nutrientes e água, foram postulados para explicar a ocorrência de savanas e florestas, bem como a localização das transições abruptas entre elas (Sarmiento 1984, Cole 1986, Viani et al. 2011). Apesar de esses postulados terem sido testados de maneira independente, a maioria dos autores (por exemplo, Sarmiento e Monasterio 1975) concordam que diferentes fatores podem interagir e coatuar, contribuindo para a origem e manutenção das savanas. A topografia, a drenagem, a herbivoria, o solo e o fogo agem em conjunto como determinantes principais dos limites entre florestas e savanas (Murphy e Bowman 2012). Especificamente em relação aos atributos do solo, sabe-se que a pobreza nutricional das savanas está fortemente associada aos processos geomorfogênicos e pedogênicos que ocorrem em escalas de paisagem, sendo independente da cobertura vegetal (Sarmiento 1984). Todavia, o oligotrofismo que predomina nessas regiões desestabiliza o equilíbrio entre florestas e savanas e, em geral, favorece estas em detrimento daquelas (Sarmiento 1984). Assim, enquanto as florestas ocorrem tanto em solos ricos quanto em pobres, as savanas tendem a ocorrer em solos pobres em nutrientes minerais (Sarmiento e Monasterio 1975, Bond 2010).

O nitrogênio é um recurso essencial para as plantas e costuma ser importante e limitante nas comunidades terrestres, relacionando-se aos padrões de produtividade primária (Templer et al. 2012). Além de apresentar uma ciclagem vulnerável a pequenos distúrbios (Sarmiento 1984), o nitrogênio constitui moléculas doadoras de elétrons e ácidos nucleicos e atua em processos respiratórios e fotossintéticos (Epstein e Bloom 2005). Consequentemente, o nitrogênio é o elemento mineral em maior demanda para os vegetais, e sua deficiência pode ser drástica para o desenvolvimento, sobrevivência e defesa dos mesmos (Epstein e Bloom 2005). Contudo, o fósforo é igualmente importante na maioria dos processos fisiológicos vegetais e pode ser também um fator limitante. Em comunidades antigas, cujos solos foram amplamente lixiviados, o fósforo tende a se tornar o recurso mais limitante, restringindo processos biológicos, especialmente para organismos de crescimento rápido (Matzek e Vitousek 2009), e atuando na regulação do ciclo do nitrogênio (Vitousek e Farrington 1997). Ainda que em menor extensão, o nitrogênio e outros elementos também podem ser vulneráveis à lixiviação nesses ambientes (Vergutz et al. 2012). Logo, as espécies adaptadas a solos inférteis tendem a apresentar estratégias para diminuir suas perdas nutricionais (Vergutz et al. 2012).

Considerado um dos 25 pontos quentes de conservação mundial da biodiversidade (Myers et al. 2000), o cerrado brasileiro ocupava originalmente cerca de dois milhões de km^2 (Ratter et al. 1997). Nos últimos 35 anos, mais de dois terços das áreas originais de cerrado foram perdidos para a agricultura (Cavalcanti e Joly 2002). Caso sua atual taxa de destruição seja mantida, estima-se que o cerrado esteja extinto em 2030 (Machado et al. 2004). Apesar da sua alta diversidade, do seu alto grau de endemismo e do seu estado de conservação ameaçado, o cerrado permanece 'esquecido' (Marris 2005). A vegetação do cerrado não é fisionomicamente uniforme, indo de uma formação campestre a outra florestal, mas com a maioria de suas fisionomias dentro da definição de 'savana tropical' (Bourlière e Hadley 1983, Coutinho 1990). O tipo de solo predominante no cerrado são os latossolos, provavelmente os solos mais antigos, originados no Terciário (Gottsberger e Silberbauer-Gottsberger 2006). Apesar de esses solos terem características físicas adequadas para o estabelecimento das plantas devido à estabilidade de agregação, eles são muito pobres em nutrientes, especialmente fósforo e cálcio (Motta et al. 2002), e estão sujeitos a longos períodos de lixiviação e ferralização (Buringh 1970). Além do estresse hídrico e do fogo, a fertilidade do solo determina a variação fisionômica do cerrado: quanto mais fértil é o solo, maior a produtividade do componente arbóreo (Goodland 1971, Gottsberger e Silberbauer-Gottsberger 2006). Assim, a vegetação do cerrado tende a predominar sob condições de solos pobres e bem drenados e a ser substituída por floresta estacional com o aumento da disponibilidade de água e fertilidade do solo (Oliveira-Filho e Ratter 2002, Ruggiero et al. 2002).

Nas savanas, o nitrogênio é crítico para o crescimento vegetal (Lüttge 1997) e sua ciclagem é vulnerável, com baixas taxas de reciclagem, dependendo de condições ambientais bem definidas (Sarmiento 1984). Entretanto, o fósforo é também importante e pouco disponível no cerrado, limitando o crescimento vegetal e, como consequência, afetando a distribuição das fronteiras entre cerrado e floresta (Haridasan 2008, Resende et al. 2011). No componente herbáceo-subarbustivo do cerrado, por exemplo, o aumento na disponibilidade de nutrientes, especialmente de fósforo, influencia drasticamente a diversidade e funcionamento da comunidade, propiciando a colonização de gramíneas invasoras, com a concomitante redução da diversidade de espécies herbáceas e subarbustivas (Bustamante et al. 2012).

Sendo a disponibilidade de nutrientes um dos principais atributos do solo relacionados à presença e predominância de savanas ou florestas (Sarmiento e Monasterio 1975), as espécies que ocorrem em florestas e as que ocorrem em savanas podem apresentar diferentes mecanismos adaptativos para lidar com ambientes distróficos (Sarmiento 1984). Apesar de muito ter sido discutido sobre a pobreza em nutrientes dos solos de cerrado, pouco se sabe sobre as estratégias das espécies de cerrado para superar esse problema (Haridasan 2008). As espécies de solos pobres, como os do cerrado, tendem a desenvolver estratégias para maximizar aquisição e minimizar as perdas nutricionais (Aerts and Chapin 2000, Kozovitz et al. 2007, Nardoto et al. 2006). Folhas duras, coriáceas e tecidos longevos são bons exemplos de traços ligados à conservação de recursos, porque eles tornam as plantas capazes de extender o tempo de residência dos nutrientes em suas biomassas, reduzindo a dependência de recursos do solo (Aerts e Chapin 2000, Wright e Westoby 2003). Uma outra maneira de aumentar a conservação de recursos e diminuir a dependência dos recursos do solo é pela reabsorção de nutrientes antes da senescência foliar (Aerts e Chapin 2000, Wright e Westoby 2003). Além disso, a toxicidade do alumínio deve influenciar o gradiente fisionômico do cerrado, pela densidade e altura da vegetação, pelo aspecto retorcido das árvores e arbustos e pelas folhas duras e coriáceas (Gottsberger e Silberbauer-Gottsberger 2006). A toxicidade por alumínio pode levar à variação fisionômica diretamente, afetando os sistemas radiculares, ou indiretamente, diminuindo a disponibilidade de nutrientes no solo, especialmente o fósforo (Haridasan 1982, Lambers et al. 2008). Esperamos, pois, encontrar maiores taxa de reabsorção de nitrogênio e fósforo, bem como um conjunto de atributos relacionados à estratégia de conservação de recursos entre as espécies de cerrado (altos valores de massa por área foliar, alta densidade de tecidos, baixas concentrações de fósforo e nitrogênio foliares, alta longevidade foliar, baixa área foliar específica). Por outro lado, esperamos encontrar um padrão oposto, que caracteriza uma estratégia "aquisitiva" (Craine 2009), entre as espécies de floresta.

Embora todas as plantas utilizem os mesmos recursos-chave, elas não são unidades equivalentes, pois cada uma exibe uma combinação diferente de atributos biológicos (Westoby et al. 2002). Esses atributos, geralmente tratados como traços funcionais, influenciam o estabelecimento, a sobrevivência e o valor adaptativo das plantas (Reich et al. 2003). Os traços funcionais afetam a assimilação e uso de recursos e nutrientes, resultando em diferenças no crescimento, reprodução, defesa e tolerância a estresse entre os organismos (Ackerly et al. 2000). Portanto, a combinação de traços de uma espécie determina seu desempenho e, sob restrições ambientais específicas, os traços e as espécies serão filtrados pelo ambiente de acordo com o desempenho de cada espécie (Webb et al. 2010). Uma vez que a disponibilidade de recurso influencia a similaridade entre as espécies coocorrentes (Inouye e Tilman 1995, Brauer et al. 2012), a fertilidade do solo pode ser um filtro ambiental crucial, contribuindo para a pouca similaridade na composição de espécies entre o cerrado e a floresta (Hoffmann e Franco 2008). Todavia, restrições ambientais, como infertilidade do solo ou fogo, também podem promover diversificação ao limitarem a similaridade entre espécies e forçarem o preenchimento de um espaço de nicho com pouca competição (Grime 2006, Simon et al. 2009). De acordo com a teoria de similaridade limitante (Diamond 1975, Pacala e Tilman 1994), a competição por recursos geralmente resulta em divergência dos traços, o que permite uma coexistência estável entre os organismos. Nesse caso, espera-se que as espécies coexistentes tenham atributos funcionais distintos, por meio dos quais os recursos são capturados e explorados de diferentes modos, reduzindo as chances de exclusão competitiva (Grime 2006). Esperamos, pois, que os solos distróficos do cerrado atuem tanto como filtro ambiental, quanto como promotor da divergência dos traços por causa da similaridade limitante (Grime 2006).

Sabendo que as estratégias de nutrição mineral das plantas são fortemente associadas às propriedades dos solos em paisagens antigas e inférteis (Lambers et al. 2010) e que a produtividade vegetal pode ser limitada pelo fósforo nas savanas tropicais (Resende et al. 2011), queremos testar se o solo infértil do cerrado determina as estratégias de nutrição mineral e a diversidade vegetal. No capítulo um, utilizamos as concentrações de nitrogênio e fósforo em folhas verdes e senescentes, calculamos as taxas de reabsorção de nitrogênio e fósforo e medimos três traços foliares estruturais fundamentais: área foliar específica, dureza e conteúdo de matéria seca foliar. Relacionamos os traços nutricionais e os traços estruturais das folhas entre si e com as as características nutricionais do solo, comparando o cerrado com a floresta estacional. No segundo capítulo, calculamos as distâncias filogenética-funcionais entre pares de espécies do cerrado e da floresta estacional a partir dos seguintes traços: altura, área basal, tortuosidade, área foliar específica, conteúdo de matéria seca foliar e tamanho da folha. Utilizamos a distância par-a-par das espécies e os dados de nutrientes do solo para testar se as comunidades de cerrado e de floresta estacional possuem diferentes regras de montagem, apesar da proximidade física entre elas. No terceiro capítulo, analisamos os dados de diversos nutrientes foliares, os nutrientes do solo e a taxa de decomposição por parcela para comparar o cerrado e a floresta estacional em relação aos seus traços químicos, particionando as propriedades químicas foliares entre os componentes taxonômico, ambiental e sistemático. Nele, estudamos como os traços químicos e a área foliar específica das espécies arbustivo-arbóreas respondem às propriedades do solo e os seus efeitos sobre as taxas de decomposição.

Apresentamos a tese com os três capítulos no formato de artigo científicos. Como uma regra comum nas revistas em que foram ou serão submetidos é a redação do manuscrito em inglês, nossos capítulos foram escritos nesse idioma. O primeiro capítulo foi aceito na revista *Plant and Soil* e está disponível desde fevereiro de 2016 eletronicamente. O segundo capítulo foi submetido para a *Journal of Plant Ecology.* O terceiro capítulo foi submetido para a revista *Plant Ecology* após a defesa da tese.

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II - Capítulo 1

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Relationships between soil nutrient status and nutrient-related leaf traits in Brazilian cerrado and seasonal forest communities

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Abstract

Aims: In Brazil, cerrado and seasonal forest occur in close proximity but on soils with very different chemistry and texture. We aimed to compare species from these two vegetation types in terms of leaf N and P concentrations (of green and senesced leaves) and proportional nutrient resorption, quantifying the relationships among these traits, with other key leaf traits, and with soil properties.

Methods: We collected topsoil at 100 25 m^2 sample plots in south-eastern Brazil and measured leaf traits of 89 woody species occurring therein, expressing them as community-weighted means. Soil nutrient status was indexed using eight standard variables.

Results: In terms of properties such as pH, clay content, and cation exchange capacity, cerrado soils were deemed as being less “fertile” than forest soils, yet cerrado and forest sites did not differ in soil total N or available P (which themselves were negatively correlated). On average, forest species showed higher proportional P resorption but lower N resorption. Leaves with higher nutrient concentrations were less scleromorphic.

Conclusion: In Brazilian cerrado and forests, variation in green- and senesced-leaf nutrients was better aligned with generalised measures of soil fertility than to total N or available P and showed far more clear patterns than nutrient resorption efficiencies.

Key words: nitrogen, phosphorus, resorption, savanna, senescence, and tropical forest.

Introduction

Savannas and tropical forests, two of the major biomes in the world, together cover *ca*. 30% of the world's land surface (Scholes and Hall 1996) and are often in contact, being at steady or alternating states through time (Staver et al. 2011). Although the distribution of major biomes is predominantly shaped by climate, savannas tend to occur where forests could also be supported by current climatic conditions (Cole 1986). Savannas and tropical forests are commonly found forming abrupt transitions, for example in Africa (Schwartz et al. 1996), Asia (Puyravaud et al. 1994), Oceania (Ibanez et al. 2013), and South America (Viani et al. 2014). In such transitions, in a matter of a few meters, one can move from a savanna, by definition with shrubs and trees distributed among an almost continuous grass layer, to a forest with densely distributed tall trees and a thin herbaceous layer (Furley 1999; Warman et al. 2013). Topography, fire, soil features, and water availability are considered the main determinants of forest-savanna boundaries around the world, acting as a set of environmental filters (Murphy and Bowman 2012). Although there is no simple deterministic explanation for the limits of savannas around the world, impoverished soils and lower effective rainfall (the balance between annual precipitation and potential evapotranspiration) are thought to be the predominant filters in South American savannas (Lehmann et al. 2011).

The Central Plateau of Brazil is covered mostly by "cerrado", a physiognomic gradient that embraces grassland (the "campo limpo" formation), savannas ("campo sujo", "campo cerrado", and "cerrado *sensu stricto*" formations), and the sclerophyllous forest "*cerradão*" (Coutinho 1990). Very often, the cerrado occurs with patches of semi-deciduous seasonal forest scattered throughout (Coutinho 1990) and the boundaries between these two different vegetation types are primarily associated with soil fertility and water availability (Goodland and Pollard 1973; Ruggiero et al. 2002). In general, cerrado is found on nutrient-poor, aluminium-rich and very sandy soils, whereas seasonal forest is found on higher-nutrient soils derived either from richer sandstones or volcanic rocks, usually with clay content about 50% higher (Ruggiero et al. 2002; Durigan and Ratter 2006). Since soil features may change at distances as small as 1 m (Souza and Martins 2004), soil fertility may also be responsible for the abrupt transitions between savannas and tropical forests. Despite being spatially close, few species are shared between the two vegetation types. Furthermore, cerrado and forest species have been shown to differ in patterns of biomass allocation, growth rates, seedling light and water requirements, and fire-resistance traits (Hoffmann and Franco 2003; Hoffmann et al. 2004, 2005, 2012; Rossatto et al. 2009; Viani et al. 2011a).

Soil nutrient status can be an important driver of plant functional traits and strategies (Reich et al. 2003; Lambers et al. 2010). Species adapted to low nutrient soils tend to develop strategies that enhance nutrient acquisition. For instance, they may have higher root mass relative to shoot mass than species from higher-nutrient situations, devote more photosynthate to mycorrhizal partners, or – in families such as Proteaceae and Cyperaceae – develop specialised cluster roots which exude organic compounds (e.g. carboxylates) that solubilise recalcitrant soil nutrients, especially inorganic P (Chapin 1980; Lambers et al. 2008a). Species typical of nutrient-poor soils also display traits that enhance resource conservation, such as deploying physically robust (scleromorphic), long-lived leaves, and drawing nutrients down to particularly low levels prior to leaf fall – properties with direct consequences for extending nutrient residence times in biomass, hence decreasing reliance on soil-derived nutrients (Aerts and Chapin 1999; Wright and Westoby 2003). Nutrient resorption, the withdrawal of nutrients from aging tissues for transport to and re-use in developing tissues, plays an important role in community functioning and nutrient cycling (Aerts 1996). On average, plants resorb around 50% of leaf nitrogen and phosphorus, although there is wide variation among species (Aerts and Chapin 1999; Vergutz et al. 2012). Besides percentage resorption (resorption “efficiency”), a second and perhaps more ecologically-relevant index of resorption is the degree to which nutrients are reduced prior to leaf fall; i.e., the residual nutrient concentration in senesced leaves (Killingbeck 1996; sometimes called resorption “proficiency”). Judged by this index, species on low-nutrient soils rely more heavily on resorption than species from higher-nutrient soils, whereas they may or may not show any mean difference in proportional resorption efficiency (Wright and Westoby 2003).

Both nitrogen and phosphorus limit net primary production and affect community dynamics (Lambers et al. 2008a; Menge et al. 2012). Nitrogen is an essential resource to plants, being part of nucleic acids and all proteins, and thus key to both photosynthesis and respiration (Epstein and Bloom 2005). Consequently, nitrogen is the mineral nutrient that plants need in highest concentrations and its deficiency promotes drastic consequences for plant development, survival, and defence (Epstein and Bloom 2005). After nitrogen, phosphorus is the most limiting nutrient for plant growth. It is a component of key molecules, such as nucleic acids, phospholipids, and adenosine triphosphate, and is involved in controlling key enzyme reactions and in regulating metabolic pathways (Schachtman et al. 1998). On very old soils, phosphorus is often considered at least or even more limiting to productivity than nitrogen (Vitousek et al. 2010).

Despite the recognition that cerrado and seasonal forest species have to cope with somewhat different environmental restrictions (i.e. light, soil fertility and toxicity, susceptibility to fire; Sarmiento 1984), relatively little is known about the ecophysiological underpinnings of their distribution patterns along environmental gradients. This is of particular importance given that cerrado has been losing its cover to crop production and the remaining areas, surrounded by silvicultural-agricultural matrices, suffer from fertilizer impact and susceptibility to eutrophication (Hunke et al. 2015), which, potentially, could lead to its replacement by forest vegetation. Here, we aimed to compare species from cerrado and seasonal forest in terms of leaf N and P concentration and resorption, quantifying the relationships among them, with other key leaf traits, and with soil features. By sampling leaf N and P from green and senesced leaves and several other traits for 89 species from 100 plots across cerrado and seasonal forest in a State reserve in south-eastern Brazil, we tackled the following questions, all considered at the level of community-weighted means:

1. Are green and senesced leaf nutrient concentrations positively and leaf nutrient resorption efficiencies negatively related to soil nutrient status? Since nutrient resorption is expected to be more critical in poorer soils (Aerts and Chapin 1999), promoting higher internal cycling and reducing the dependence of the species on soil nutrients, we expected these relationships to be so.

2. Is specific leaf area positively related and are leaf dry matter content and leaf toughness negatively related to leaf nutrient concentrations? Since the richer in nutrients the leaves, the less scleromorphic they tend to be (Loveless 1961), we expected these relationships to be so.

3. Are the nutrient contents lower and the resorption efficiencies higher in the cerrado than in the seasonal forest? Since cerrado species tend to occur on poorer soils (Ruggiero et al. 2002), we expected them to be.

Methods

Study sites

We carried out this study in the Vaçununga State Park, Santa Rita do Passa Quatro municipality, São Paulo state, south-eastern Brazil (21°36-47’ S and 47°34-41’ W, Ruggiero et al. 2002). The park is at 590-740 m above sea level and under Cwa regional climate, that is, warm temperate, with wet summers and dry winters (Köppen 1931). Annual rainfall is approximately 1,500 mm, concentrated from November to April, and mean annual temperature is around 22°C (Pivello et al. 1998). The park comprises 2,071 ha and is divided into six fragments, one of them covered mostly by cerrado and five covered mostly by semi-deciduous seasonal forest. Soils are mainly Neosols and Latosols according to the Brazilian classification system (Embrapa 2012) or Entisols and Oxisols according to the USDA classification system (Soil Survey Staff 2014). The cerrado occurs on sandy, nutrient-poor, and aluminium-rich soils, whereas the seasonal forest occurs on clayey, nutrient-rich, and aluminium-poor soils (Ruggiero et al. 2002). The park is one of the most important conservation units in the southern portion of the Cerrado domain, harbouring more than 500 plant species (Batalha and Mantovani 2005) and threatened mammals such as the puma and the maned-wolf (Pivello et al. 1998).

We established 100 25 m^2 plots in the three fragments that were accessible to researchers. In these three fragments, 1,192 ha were covered by cerrado and 578 ha, by seasonal forest. We placed the plots using a random stratified sampling (Krebs 1998; Sutherland 2006). The number of plots in each vegetation type was proportional to the area covered by them in the three fragments, that is, 68 plots in the cerrado and 32 plots in the seasonal forest. Most of the 68 plots in cerrado belong to the cerrado *sensu stricto,* with a dominant woody component, interspersed by the herbaceous component (Coutinho 1990). The cerrado we studied had, on average, more individuals and species per m^2 than the seasonal forest (0.59 and 0.32 in cerrado versus 0.29 and 0.20 in the forest). The average sum of basal area per plot was also slightly higher in cerrado than in forest (1208 cm^2 versus 1060 cm^2, respectively), even though the degree of canopy closure is notably lower in cerrado than in the seasonal forest (Fig 1). Here, our focus was just on the woody component of both vegetation types, that is, on the trees and shrubs.

Leaf and soil properties

In each plot, we sampled all the individuals belonging to the woody layer, defined as those woody individuals with stem diameter at the soil level equal to or greater than 3 cm (SMA 1997). We identified the individuals to species level, comparing the collected material to vouchers lodged at the Botanical Institute of São Paulo herbarium or using identification keys based on vegetative characters (Batalha et al. 1998; Batalha and Mantovani 1999). In the cerrado we sampled 1,012 individuals belonging to 70 species whereas in the seasonal forest we sampled 233 individuals belonging to 65 species (Appendix 1). Overall we sampled 128 species (seven being common to both vegetation types), on average sampling 8 species per 25m^2 plot (Appendix 1). We randomly selected 5-10 individuals to sample of each species. For a small number of species we also sampled individuals outside but near to the plots, in order to reach the minimum five samples. We collected data on nutrient content for 89 species (Appendix 2), accounting for 1,164 individuals in the sample or 94% of the total.

Senesced leaves were sampled at the beginning of the dry season, from May to June 2013. Senesced leaves were sampled via a gentle flicking of the branch or twig, since leaves without abscission layer are not removed by this procedure (Wright and Westoby 2003). For each species and depending on the number of individuals presenting senesced leaves, we collected from two to seven samples, each one with enough leaves to obtain 2 g when dried. We placed each sample in paper bags and, later, oven-dried them at 70°C for 72 hours prior to determination of nitrogen and phosphorus concentrations, respectively, by Kjeldahl (Bradstreet 1965) and nitric-perchloric acid digestion (Grimshaw 1987) methods, run at the Luiz de Queiroz College of Agriculture, University of São Paulo.

In the wet season, from October 2013 to April 2014, we collected five green leaves from the selected individuals. We placed the leaves in plastic bags inside an insulated box and took them to the laboratory, where we measured three functional traits (Pérez-Harguindeguy et al. 2013): specific leaf area, leaf dry matter content, and leaf toughness. We scanned the leaves and calculated their areas with ImageJ software (Rasband 2014). We also weighed the leaves on an analytical balance to 0.001g to obtain their fresh masses. Then, we placed the leaves in paper bags, oven-dried them at 70°C for 72 hours, and weighed them again to obtain their dry masses. We divided leaf area by dry mass to obtain specific leaf area and dry mass by fresh mass to obtain leaf dry matter content. As an index of leaf toughness, we measured force to punch on fresh leaves, with a dynamometer, punching at both sides of the midrib and recording the force necessary to penetrate it. Nitrogen and phosphorus concentrations were determined for dried samples at the Luiz de Queiroz College of Agriculture.

In each plot, we collected a composite soil sample to 5 cm deep, after removal of the organic layer, by mixing five subsamples, four taken in the corners and one taken in the centre of the plot. We sent the samples to the Luiz de Queiroz College of Agriculture, at the University of São Paulo, for determination of pH, organic matter, total nitrogen, available phosphorus, exchangeable cations (potassium, calcium, magnesium, and aluminium), sum of bases, cation exchange capacity, aluminium saturation, base saturation, and soil texture (sand, silt and clay contents). The pH was determined for a salt solution of $CaCl_2$ to reduce interference of soil electrolyte concentration. Organic matter was determined by organic carbon oxidation with potassium dichromate. Total nitrogen was determined by digestion with sulphuric acid. Available phosphorus was determined by spectrophotometry after anion exchange resin extraction. K^+, Ca^{2+}, Mg^{2+}, and Al^{3+} were extracted with KCl prior to a complexometric determination with EDTA. The sum of bases was obtained by the sum of K, Ca, and Mg. Cation exchange capacity was the sum of bases plus H^+ and Al^{3+} concentrations. Aluminium saturation was determined as percentage of the sum of sum of bases and Al^{3+}. Base saturation was determined as percentage of cation exchange capacity. Sand, silt and clay percentages were determined by granulometric analysis. The chemical and physical analyses were conducted according to prescriptions and protocols described in Silva and Batalha (2008).

Analyses

Average nitrogen and phosphorus concentrations in green and senesced leaves were calculated for each species. Leaf resorption efficiency was calculated as the percentage reduction in leaf nutrient from green to senesced leaves following Killingbeck (1996): $r = 100 * (Cg - Cs)/Cg$, where r is the leaf resorption efficiency, Cg is the nutrient concentration given on mass basis in green leaves and Cs is the nutrient concentration given on mass basis in senesced leaves. Although we were aware that a better estimation of resorption efficiency would be based on leaf area due to leaf mass loss during senescence (van Heerwaarten et al. 2003), it was not possible to obtain it that way. Considering that mass loss during senescence leads to an underestimation in resorption efficiency lower than 10% and that leaf shrinkage causes an underestimation of up to 6% (Vergutz et al. 2012), we believe that our approach is still acceptable. In this study all leaf traits (specific leaf area, leaf dry matter content, leaf toughness, N and P concentrations in senesced and green leaves, and N and P resorption efficiency) were expressed as community-level weighted means, calculated as the sum of the mean trait values of each species present in the community weighted by its respective relative abundance (Garnier et al. 2004). Relative abundance was measured as number of individuals.

With a view to summarising multidimensional variation in soil properties in just a small number of dimensions, from the complete set of soil variables we first identified and excluded eight that were highly correlated with others (Pearson's $r > |0.7|$; cations K^+ Ca^{2+}, Mg^{2+}, as well as potential acidity (referring to cations H^+ and Al^{3+} that are not available in the soil solution), percentage of base saturation, percentage of aluminium saturation, silt, and sand content), leaving as the final set: pH, organic matter, total nitrogen, available phosphorus, exchangeable aluminium, sum of bases, cation exchange capacity, and clay content. Each variable was then standardised by its range and the data matrix summarised with Principal Component Analysis (Jongman et al. 1995), extracting axis scores from the first two components.

Multiple linear regression was used to tackle the first research question outlined in the Introduction (whether leaf nutrient traits covary with soil properties), treating the log-transformed community-weighted mean leaf nutrient concentration or resorption efficiency as response variable and the scores from the first two principal components as explanatory variables. To check whether the inclusion of the second principal component enhanced the explanatory power of the models, we also applied simple linear regressions using the community-weighted mean leaf nutrient concentration and resorption efficiency as response variables and only the scores of the first principal component as explanatory variable. Pearson correlations were used to quantify association between community-weighted mean leaf nutrient concentrations and the scores of each principal component. We analysed the diagnostic graphs (e.g. residuals vs. fitted values and quantile-quantile graphs) to check whether the assumptions of linear models were satisfied.

We used Spearman's rank correlations to answer the second question (whether leaf nutrients and resorption efficiency were related to physical leaf traits), analysing trait-trait relationships across all sites and also for each vegetation type on its own. To answer the third question (whether cerrado and forest species differ in leaf nutrients), we applied two-way analyses of variance, using either leaf nitrogen or leaf phosphorus as response variable and leaf stage (green or senesced) and vegetation type (cerrado or seasonal forest) as factors. We also applied t-tests, using either nitrogen or phosphorus resorption efficiency as response variable and vegetation type as explanatory variable. We carried out all the analyses in R (R Development Core Team 2014), using the FD (Laliberté and Legendre 2010), Hmisc (Harrell Jr and Dupont 2014), and vegan (Oksanen et al. 2013) packages.

Results

Soil differences

The first axis of the principal component analysis (PC1) explained 48% of the variation in the soil matrix, being positively related to pH, organic matter, sum of bases, cation exchange capacity, and clay content (Fig. 2) – that is, to a range of variables indicating generally higher soil fertility. Importantly, neither soil total N nor available P were related to this axis. The second axis, PC2, explained an additional 18% of variation and was most strongly related to total N, exchangeable Al (both positively) and available P (negatively). Some variation in pH, sum of bases, and clay content was also associated with PC2 (Fig. 2; Appendix 3). Cerrado and forest plots were separated along PC1 and in the expected direction, with forest sites on soils with higher pH, higher concentrations of clay and organic matter, and higher cation exchange capacity (Fig. 2). However, they were not clearly separated along PC2. A post-hoc t-test with soil total nitrogen and available phosphorus confirmed the results from the Principal Component Analysis (PC2; Fig. 2): there were no differences between cerrado and forest sites in regard to these soil nutrients ($p = 0.79$ for total N; $p = 0.59$ for available P). Additionally, as a matter of curiosity, we checked whether particular species of cerrado or forest segregated to low and high Al soils within each vegetation type (see Appendix 5).

Soil-trait relationships

Community-mean N and P concentrations in green leaves were positively related to site scores along PC1, but not to scores along PC2 (Table 1). Consequently, the 31% of variation in green-leaf nitrogen explained in a multiple regression was almost all explained by PC1 (partial regression coefficient non-significant for PC2; Table 2). Similarly, the 41 % of variation in green-leaf phosphorus explained in a multiple regression was explained almost exclusively by PC1 (partial regression coefficient non-significant for PC2; Table 2). This pattern is especially notable given that variation in soil N and P was aligned with the second principal component but not the first (Fig. 2).

Community-mean nutrient concentrations in senesced leaves showed a similar pattern in regard to the first principal component (higher residual leaf N and P concentrations on soils with higher pH, cation exchange capacity (CEC), sum of bases (SB), organic matter (OM), and clay content; Fig. 2, Tables 1 and 2). Somewhat different patterning was found in regard to the second principal component. In this case there were significant, negative correlations with both N and P (Table 1), and the partial regression coefficients were also significant (Table 2). For senesced-leaf nitrogen, PC1 and PC2 together explained 41% of variation (35% by PC1 on its own). The negative coefficient along PC2 indicated a tendency for lower senesced-leaf N on higher N soils (i.e., opposite to what might be expected). For senesced-leaf P, the two PC axes together explained 37% of variation (34% by PC1 on its own).

Resorption efficiencies showed far weaker relationships to soil variables than the nutrient concentrations in either green or senesced leaves. Nitrogen resorption efficiency was positively related to PC2 but unrelated to PC1 (Table 1), the two PCs together explaining just 5% variation (Table 2). By contrast, P resorption efficiency was related to the first principal component only, and positively (Table 1), the two PCs together explaining 17% of variation (Table 2). That is, species on soils with higher pH, cation exchange capacity, organic matter, sum of bases and clay content (as judged by PC1) showed higher P resorption efficiency, and species on higher N soils (PC2) showed higher N resorption efficiency.

Community-mean trait-trait relationships

Specific leaf area was positively correlated with N and P concentrations in green and in senesced leaves (all $\rho > 0.39$, $p < 0.05$; Fig. 3), both in analyses of all sites and in analyses restricted to a particular vegetation type. The only exception occurred with phosphorus in green leaves among forest species ($\rho > 0.30$, $p = 0.09$; Fig. 3b). In general, the relationships were stronger when all sites were examined together.

Considering all sites, SLA and P resorption efficiency were correlated ($\rho = 0.65$, $p < 0.001$;

Fig. 3f); however, these traits were unrelated within cerrado and forest considered individually (both $\rho \leq 0.12$). Specific leaf area and N resorption efficiency were unrelated both across all sites and within individual vegetation types (Fig. 3e).

As expected, SLA was negatively correlated with both dry matter content ($\rho = -0.64$, $p < 0.001$) and leaf toughness ($\rho = -0.68$, $p < 0.001$). Consequently, these traits showed broadly similar relationships (but opposite in sign) to leaf nutrient concentrations, at least when considered across all sites (Fig. 3). Leaf DMC was significantly and positively related to N resorption efficiency ($\rho = 0.36$, $p < 0.001$) yet unexpectedly and *negatively* correlated with P resorption efficiency ($\rho = 0.58$, $p < 001$). Leaf toughness was unrelated to N resorption efficiency ($p = 0.24$), but negatively correlated with P resorption efficiency (correlation $\rho = -0.49$, $p < 0.001$). When relationships between leaf dry matter content and N and P in green and senesced leaves were significant across all sites, this was not necessarily the case when cerrado and forest sites were analysed separately. Conversely, the relationships for SLA and leaf toughness were equally significant when cerrado and forest sites were analysed all together, or separately. For leaf dry matter content, then, the differences between the two vegetation types were the main causes for the significant correlation with nutrient concentrations in green and senesced leaves (Fig. 3).

Vegetation type differences

Leaf N concentration was related to vegetation type and leaf stage (two-way ANOVA, $P < 0.001$, $R^2_{adj} = 0.73$; Fig. 4). That is, it was higher in forest than in cerrado sites ($P < 0.001$) and higher in green than in senescent leaves ($P < 0.001$), and there was no significant interaction between vegetation type and leaf stage ($P = 0.57$). Phosphorus concentration was also related to vegetation type and leaf stage ($P < 0.001$, $R^2_{adj} = 0.90$; Fig. 4). It was also higher in forest than in cerrado species ($P < 0.001$) and in green than in senesced leaves ($P < 0.001$). However, in this case, there was a significant interaction between vegetation type and leaf stage ($P < 0.001$), decreasing more from green to senescent leaves in forest species (Fig. 4). Nitrogen resorption efficiency was not significant higher in the cerrado than in the seasonal forest ($P = 0.052$; Fig. 3). Indeed, the entire range of N resorption efficiencies observed across cerrado sites fell within the wider range reported across forest sites. Phosphorus resorption was clearly higher in forest sites (averaging 61.8% versus 52.1% in cerrado; $P < 0.001$; Fig. 4). N:P ratios of green leaves were generally higher in cerrado than in forest (means 23.2 versus 19.5; $P < 0.001$; Fig. 4). For senesced leaves, N:P ratios were lower in cerrado than in forest (means 36.5 versus 40.7; $P = 0.001$; Fig. 4).

Discussion

Although on average cerrado and forest soils did not differ in either total N or available P (in contrast to what has been reported from south-eastern Brazil: Viani et al. 2011b), we still concluded that cerrado sites were less "fertile", in a general sense, as previously found (Furley and Ratter 1988, Ruggiero et al. 2002), cerrado soils were generally more acid, aluminium-rich and sandy than forest soils and generally had lower sum of bases, cation exchange capacity and organic matter content.

Acidity is one of the main determinants of soil fertility across the globe, co-varying (not always linearly) with properties such as cation exchange capacity, N availability and concentrations of exchangeable bases and organic carbon (Maire et al. 2015). When pH is lower, aluminium hydrolyses in the soil solution and trivalent forms (Al^{+3}) appear, which bind to many organic and inorganic ligands and decrease nutrient availability, including that of inorganic phosphate (Delhaize and Ryan 1995, Lambers et al. 2008b). Besides acidity, low clay content and low cation exchange capacity can also contribute to a low diffusion coefficient for inorganic phosphate (Lambers et al. 2008b). That is, in this sense it is possible that P was more difficult to acquire at cerrado sites – in a manner not indexed by measuring P availability. Similarly, although we were only able to measure total nitrogen, we expect that N availability was likely on average lower in cerrado than in forest sites, with low levels of organic matter diminishing N availability and uptake through a reduction in nutrient mineralisation and decomposition rates (Näsholm et al. 2009). It is likely that in these soils a better index of N availability would have been net nitrogen mineralization rate (Schimel and Bennett 2004).

Soil pH and several indices of general fertility (organic matter, sum of bases, cation exchange capacity, and clay content) were related to leaf nutrient concentrations (lower green- and senesced-leaf N and P at lower fertility), yet it was only for senesced leaves that leaf nutrient concentrations were correlated with soil N and P. This was unexpected, green-leaf N and P being generally thought to be patterned in relation to soil N and P (Aerts and Chapin 1999); however, for the reasons outlined above, perhaps there would have been some degree of patterning if we had measured, say, N mineralisation rate rather than total N. Alternatively, since the cost for acquiring nitrogen and phosphorus also relies on other soil features, perhaps N and P concentrations in green leaves are more strongly regulated by soil fertility as a whole than by nitrogen and phosphorus *per se*. Indeed, evidence of multiple element controls on leaf nutrient-related traits have being demonstrated in manipulated (Fujita et al. 2013) and non-manipulated systems (See et al. 2015).

Nitrogen and phosphorus concentrations in senesced leaves, in turn, represent the degree to which nutrients are withdrawn before abscission and, thus, are regulated by a more complex mechanism, which presumably relies on the relative costs of recycling nutrients within the plant versus acquiring them from the soil (Killingbeck 1996; Wright and Westoby 2003). Nevertheless, the fact that senesced-leaf phosphorus was lower at lower soil available phosphorus concentration whereas senesced-leaf nitrogen was *higher* under lower soil total nitrogen concentration suggests that phosphorus is a more limiting resource than nitrogen in both environments, as expected for communities with old and highly weathered soils (Lambers et al. 2008a), and reinforces the possibility that other soil features related to nutrient availability would constitute a better index of nitrogen availability than total nitrogen in these communities.

Contrary to our expectations, nitrogen resorption efficiency was positively correlated with soil nitrogen and did not respond to the other parameters of fertility (i.e., the second principal component was negatively and the first was not correlated to nitrogen resorption efficiency), and phosphorus resorption efficiency did not respond to soil phosphorus but responded positively to the other fertility parameters (i.e., the first principal component was positively and the second was not correlated to phosphorus resorption efficiency). Unclear effects of nutrient supply on resorption efficiency have also been found by previous studies, either manipulative (Aerts 1996; Heerwaarden et al. 2003, Mao et al. 2013) or correlative (Aerts 1996; Wright and Westoby 2003; Vourlitis et al. 2014), despite evidences for the contrary (Hayes et al. 2014, Yuan and Chen 2015).

The lack of correlation between resorption efficiency and soil nutrient availability, compared to the very strong relationships between green- and senesced-leaf nutrients and soil properties, suggests that there is no clear control over nutrient resorption efficiency *per se*, but rather that it simply reflects the mathematical difference between the traits under strong selective pressure (i.e., the green- and senesced-leaf nutrient concentrations). That is, despite its importance as the relative degree to which individuals or communities can conserve nutrients (Killingbeck 1996), our understanding of plant ecological strategies as related to nutrient conservation relies far more on residual leaf nutrient concentrations (Chapin 1980; Reich et al. 2003; Wright and Westoby 2003). Besides, plants do have control over the minimum concentrations of nitrogen and phosphorus in their leaves, but not necessarily on the proportional withdrawal before senescence (Aerts and Chapin 1999). As a consequence of the absent correlation between resorption efficiency and soil nutrient availability, N-resorption efficiency did not differ between cerrado and seasonal forest, while P-resorption efficiency was higher in the forest.

Higher-nutrient leaves were less scleromorphic (they had higher specific leaf area, lower dry matter content, and lower toughness; Fig. 2). This was as expected; a long line of literature shows that scleromorphic (thick, hard, long-lived) leaves typically have low nutrient, protein, and chlorophyll concentrations and they also have low water and high fibre, lignin, and cellulose concentrations (Loveless 1961; Turner 1994). Scleromorphism is a common attribute among plants from infertile soils, and has an important ecological implication on the trade-off between plant growth and resource allocation (Wright et al. 2002; Craine 2009). Species typical of high-nutrient soils have seemingly been evolutionarily selected for high specific leaf area, and leaf nitrogen and phosphorus concentrations, presenting an "acquisitive" strategy (Craine 2009). Such species can be thought of as falling towards the "quick-return" end of the leaf economic spectrum, i.e., they have potential to make quicker returns on the carbon and nutrients invested in leaves (e.g. via faster photosynthetic rates) than scleromorphic, "slow-return" species from impoverished soils, which as part of their "conservative" strategy typically have slower rates of photosynthesis and respiration, and longer leaf lifespans, achieved via lower SLA, high leaf dry matter content, and high toughness (Wright et al. 2004). In relation to those concepts, the cerrado species measured here would be considered to have more conservative leaf strategies, and forest species more acquisitive strategies. This broad distinction was supported not only when accounting for leaf nutrient concentrations and scleromorphic traits, but also for N:P ratio (i.e., the higher green-leaf N:P found in cerrado is suggestive of stress-tolerant, conservative strategies as commonly seen in many low-productivity habitats; Grime 1977, Güsewell 2004).

Conclusions

Our results corroborated the idea that proportional resorption efficiency is not clearly responsive to soil nutrient status (Aerts 1996; Wright and Westoby 2003), suggesting that nutrient resorption efficiency may not always be a good predictor of plant strategy in regard to nutrient conservation. More importantly than an efficient nutrient resorption, the degree to which natural selection has acted to minimise nutrient loss in the nutrient-impoverished cerrado was reflected by low leaf nutrient concentrations in senesced leaves and sclerophyllous traits, which presumably lead to longer leaf lifespans. Changes in soil nutrient availability, induced either by land use changes or by climate change, may alter floristic composition in the cerrado and promote shifts in cerrado-forest transitions. Nevertheless, studies on root system, particularly on root strategies and specialisations, and long-term fertilisation experiments with cerrado and forests species might help evaluating more precisely the consequences of a predicted susceptibility to eutrophication in the cerrado (Lambers et al. 2013; Hunke et al. 2015) and the likelihood of replacement by the forest.

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Table 1. Pearson correlation (r) of nitrogen and phosphorus concentration in green and senesced leaves and resorption as function of the scores of the two first ordination axes found in a principal component analysis done on the soil matrix. Significant values in bold for α=0.05.

	Nitrogen			Phosphorus		
	Green	Senesced	Resorption	Green	Senesced	Resorption
PC1	**0.57**	**0.60**	-0.08	**0.65**	**0.59**	**0.42**
PC2	-0.08	**-0.25**	**0.26**	-0.07	**-0.20**	0.06

Table 2. Non-standardised partial regression coefficients and adjusted coefficient of determination (R^2_{adj}) of nitrogen and phosphorus concentration in green and senesced leaves and resorption as function of the scores of the two first ordination axes found in a principal component analysis done on the soil matrix. Significant values in bold for α=0.05.

	Nitrogen			Phosphorus		
	Green	Senesced	Resorption	Green	Senesced	Resorption
PC1	**8.85**	**8.77**	-3.26	**0.77**	**0.24**	**10.77**
PC2	-1.32	**-3.60**	**10.18**	-0.08	**-0.08**	1.66
R^2_{adj}	0.31	0.41	0.053	0.41	0.37	0.17

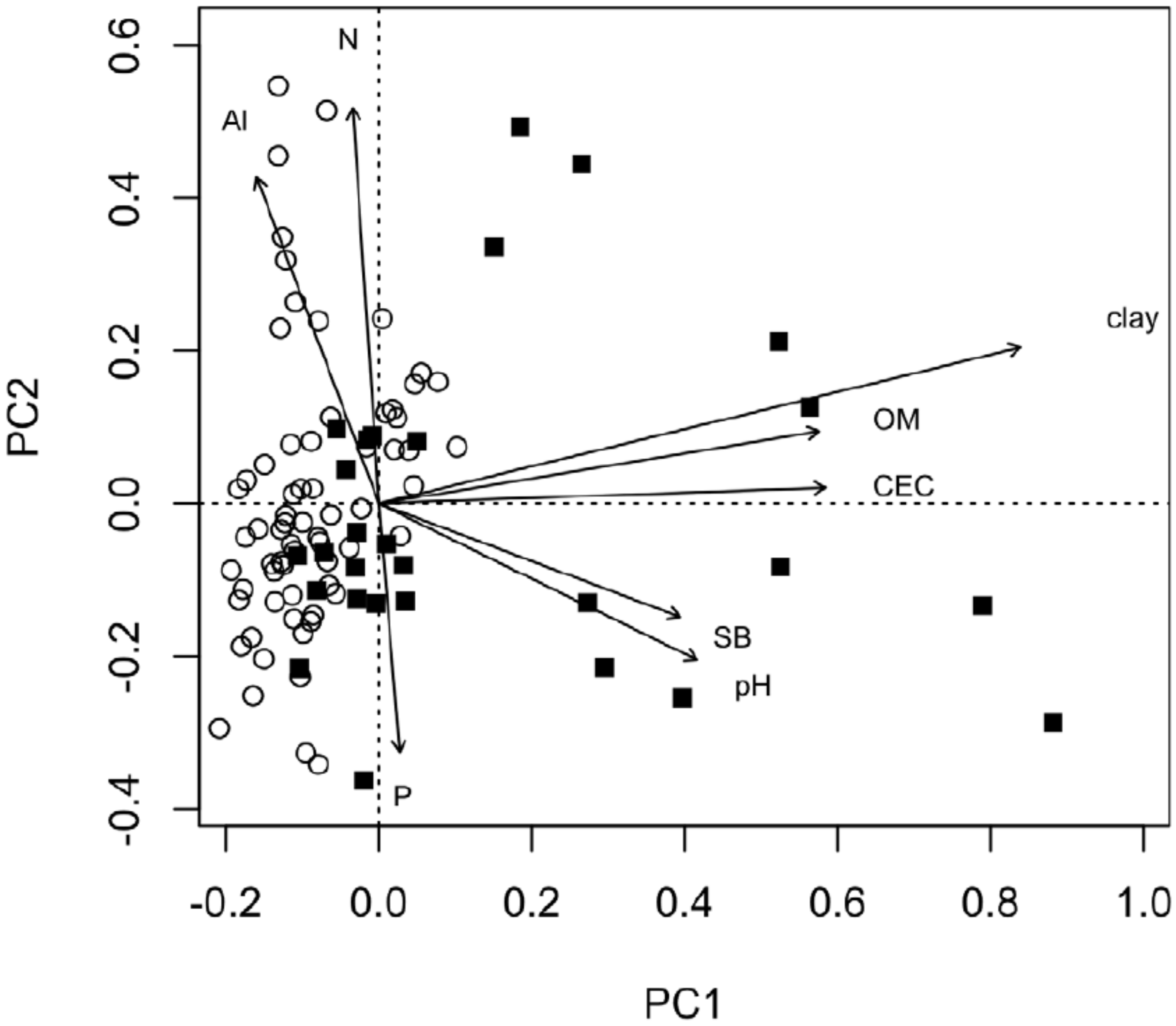
Fig 1 Representative photos of the cerrado (a-c) and seasonal forest vegetation (d-f) sampled in this study. The view from the main access tracks is shown in panels (a) and (d), and images taken from inside study plots are shown in the other panels (b, c, e, and f). Cerrado vegetation typically has a higher density of individuals per unit ground area than the seasonal forest, but a lower degree of canopy closure. The herbaceous layer is more pronounced in the cerrado but, still, the woody component prevails in cerrado *sensu stricto*. Photographs were taken in the Vaçununga State Park (21°36-47' S and 47°34-41' W) in January (a-c) and April (d-f) 2014, during the rainy season. Photographs: Raquel C. Miatto (a-c) and Pavel Dodonov (d-f)

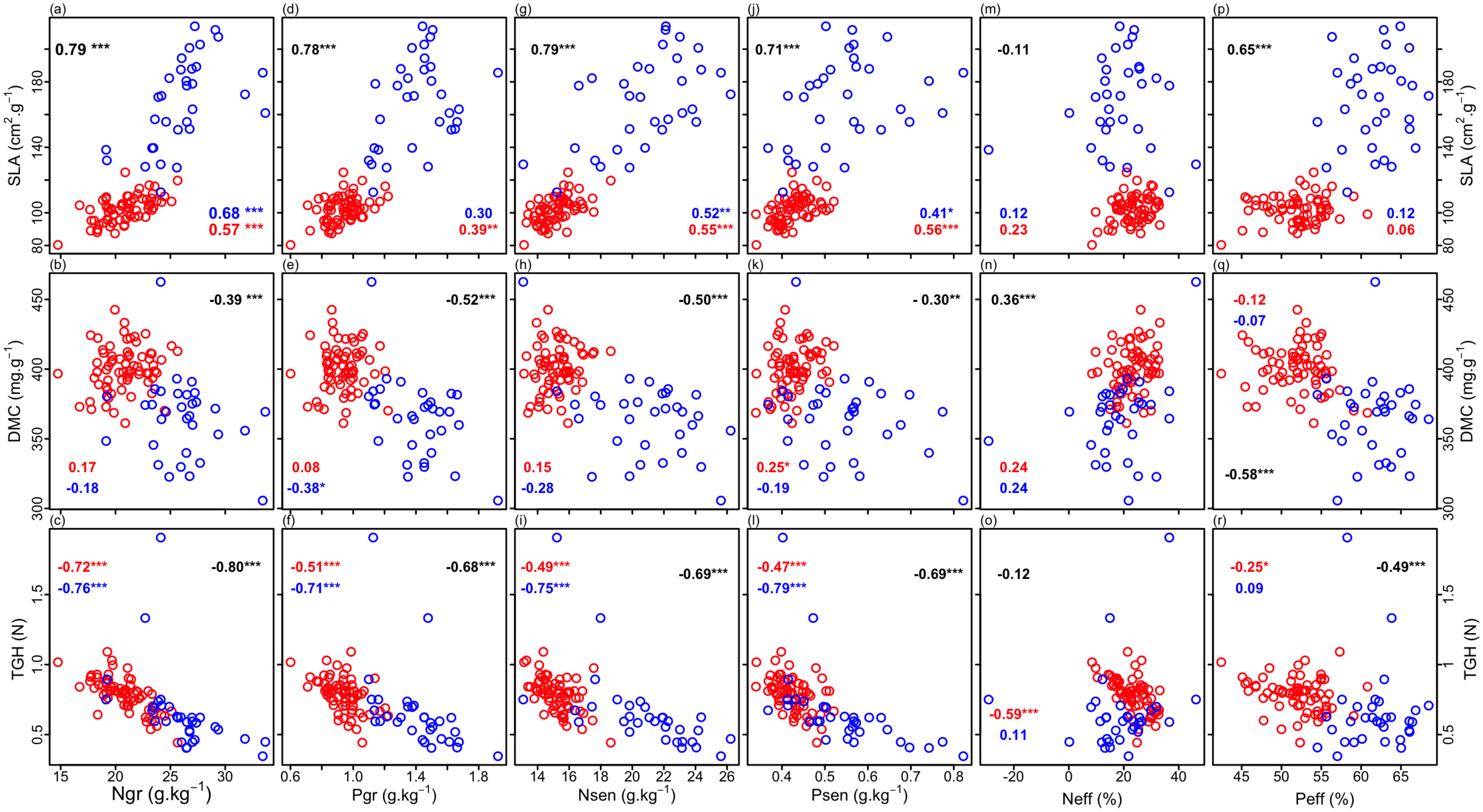
Fig 2 Ordination diagram for the soil matrix in 100 plots in the Vaçununga State Park (21°36-47' S and 47°34-41' W). SB = sum of bases, CEC = cation exchange capacity, OM= organic matter, P = phosphorus, N = nitrogen, Al = aluminium. White circles represent plots in the cerrado and black squares plots in the forest

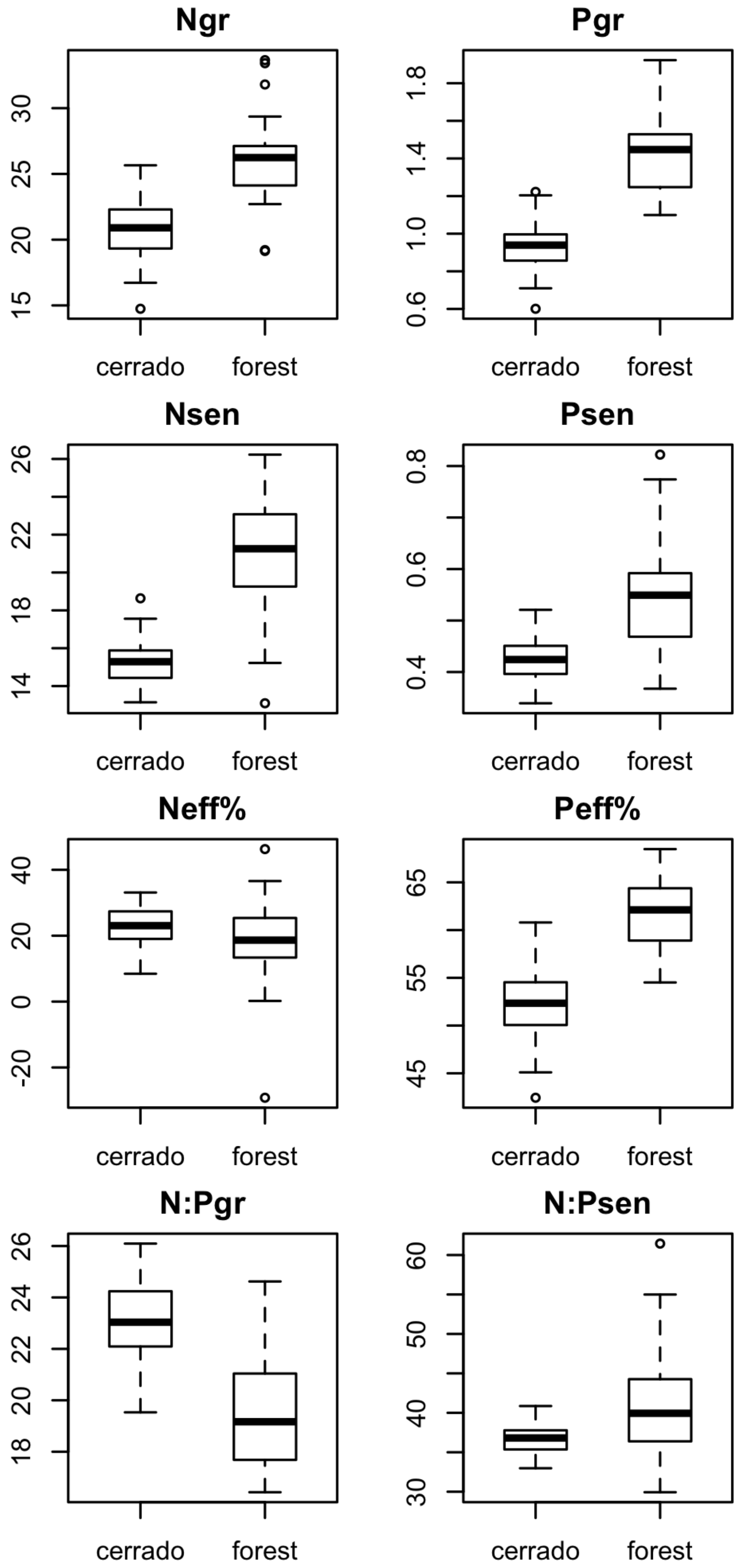
Fig 3 Scatterplots of the relationships between nitrogen concentration in green leaf (N_{gr}; g kg^{-1}) and (a) specific leaf area (SLA; $cm^2 g^{-1}$), (b) leaf dry matter content (DMC, mg g^{-1}), (c) toughness (TGH; N). Between phosphorus concentration in green leaf (P_{gr}; g kg^{-1}) and (d) specific leaf area (SLA), (e) leaf dry matter content (DMC), (f) toughness (TGH; N). Between nitrogen concentration in senesced leaves (N_{sen}; g kg^{-1}) and (g) specific leaf area (SLA), (h) leaf dry matter content (DMC), (i) toughness (TGH). Between phosphorus concentration in senesced concentration in senesced leaves (P_{sen}; g kg^{-1}) and (j) specific leaf area (SLA), (k) leaf dry matter content (DMC), (l) toughness (TGH). Between nitrogen resorption efficiency ($N_{eff\%}$) and (m) specific leaf area (SLA), (n) leaf dry matter content (DMC), (o) toughness (TGH). Between phosphorus resorption efficiency ($P_{eff\%}$) and and (p) specific leaf area (SLA), (q) leaf dry matter content (DMC), (r) toughness (TGH). Cerrado sites are represented by red and forest sites are represented by blue. Spearman's coefficient of correlation in bold and partial Spearman's coefficient coloured accordingly. *** $P < 0.001$. ** $P < 0.01$. * $P < 0.05$

Fig 4 Boxplots of community-weighted untransformed nitrogen and phosphorus concentrations in green (N_{gr}, P_{gr}) and senescent leaves (N_{sen}, P_{sen}), nitrogen and phosphorus resorption efficiencies (NRe, PRe), and nitrogen to phosphorus ratio of green ($N:P_{gr}$) and senesced leaves ($N:P_{sen}$) in cerrado and forest communities in the Vaçununga State Park (21°36-47’ S and 47°34-41’ W)


(a)
(d)
(b)
(e)
(c)
(f)


PC2
0.6
0.4
0.2
0.0
-0.2
-0.4
PC1
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
N
Al
clay
OM
CEC
SB
pH
P


(a)
0.79 ***
0.68 ***
0.57 ***
(d)
0.78***
0.30
0.39**
(g)
0.79***
0.52**
0.55***
(j)
0.71***
0.41*
0.56***
(m)
-0.11
0.12
0.23
(p)
0.65***
0.12
0.06
SLA (cm^2.g^{-1})
80
100
140
180
(b)
-0.39 ***
0.17
-0.18
(e)
-0.52***
0.08
-0.38*
(h)
-0.50***
0.15
-0.28
(k)
- 0.30**
0.25*
-0.19
(n)
0.36***
0.24
0.24
(q)
-0.12
-0.07
-0.58***
DMC (mg.g^{-1})
300
350
400
450
(c)
-0.72***
-0.76***
-0.80***
(f)
-0.51***
-0.71***
-0.68***
(i)
-0.49***
-0.75***
-0.69***
(l)
-0.47***
-0.79***
-0.69***
(o)
-0.12
-0.59***
0.11
(r)
-0.25*
0.09
-0.49***
TGH (N)
0.5
1.0
1.5
1
15
20
25
30
Ngr (g.kg^{-1})
0.6
1.0
1.4
1.8
Pgr (g.kg^{-1})
14
16
18
20
22
24
26
Nsen (g.kg^{-1})
0.4
0.5
0.6
0.7
0.8
Psen (g.kg^{-1})
-20
0
20
40
Neff (%)
45
50
55
60
65
Peff (%)


Ngr
15
20
25
30
cerrado
forest
Pgr
0.6
1.0
1.4
1.8
cerrado
forest
Nsen
14
18
22
26
cerrado
forest
Psen
0.4
0.6
0.8
cerrado
forest
Neff%
-20
0
20
40
cerrado
forest
Peff%
45
55
65
cerrado
forest
N:Pgr
18
20
22
24
26
cerrado
forest
N:Psen
30
40
50
60
cerrado
forest

Appendix 1 Species and number of individuals sampled in cerrado and seasonal forest in the Vaçununga State Park, south-eastern Brazil.

Species	**Vegetation type**	
	Cerrado	**Forest**
Actinostemon concepcionis (Chodat & Hassl.) Hochr.	0	4
Actinostemon klotzschii (Didr.) Pax	0	54
Amaioua guianensis Aubl.	0	2
Anadenanthera peregrina (Benth.) Altschul	28	0
Andira cujabensis Benth.	0	1
Annona coriacea Mart.	15	0
Annona crassiflora Mart.	6	0
Aspidosperma ramiflorum Müll.Arg.	0	2
Aspidosperma tomentosum Mart.	25	0
Astronium graveolens Jacq.	0	10
Bauhinia rufa (Bong.) Steud.	3	0
Blepharocalyx salicifolius (Kunth) O.Berg	0	3
Bowdichia virgilioides Kunth	3	0
Bredemeyera floribunda Willd.	1	0
Brosimum gaudichaudii Trécul	6	0
Brosimum guianense (Aubl.) Huber	0	8
Byrsonima coccolobifolia Kunth	5	0
Byrsonima intermedia A.Juss.	1	0
Byrsonima pachyphylla A.Juss.	1	0
Cabralea canjerana (Vell.) Mart.	0	6
Calyptranthes clusiifolia O.Berg	0	4
Calyptranthes concinna DC	0	2
Campomanesia adamantium (Cambess.) O. Berg	2	0
Cariniana legalis (Mart.) Kuntze	0	1
Caryocar brasiliense Cambess.	11	0
Casearia gossypiosperma Briq.	0	2
Casearia sylvestris Sw.	8	0
Cedrela fissilis Vell.	0	4
Connarus suberosus Planch.	6	0
Copaifera langsdorffii Desf.	21	3

Species	**Vegetation type**	
	Cerrado	**Forest**
Cordiera macrophylla (K.Schum.) Kuntze	0	3
Cordiera sessilis (Vell.) Kuntze	1	0
Couepia grandiflora (Mart. & Zucc.) Benth.	4	0
Couepia sp.	1	0
Coutarea hexandra (Jacq.) K.Schum.	0	1
Croton floribundus Spreng.	0	9
Croton piptocalyx Müll.Arg.	0	1
Dalbergia miscolobium Benth.	8	0
Dimorphandra mollis Benth.	3	0
Diospyros hispida A.DC.	1	0
Diptychandra aurantiaca Tul.	76	0
Duguetia furfuracea (A.St.-Hil.) Saff.	2	0
Duguetia lanceolata A.St.-Hil.	0	4
Esenbeckia febrifuga (A.St.-Hil.) A. Juss. ex Mart.	0	5
Eugenia astringens Cambess.	0	1
Eugenia livida O.Berg	2	0
Eugenia punicifolia (Kunth) DC.	4	0
Galipea jasminiflora (A.St.-Hil.) Engl.	0	2
Guapira noxia (Netto) Lundell	3	0
Guapira opposita (Vell.) Reitz	5	1
Guarea macrophylla Vahl	0	1
Handroanthus ochraceus (Cham.) Mattos	3	0
Hymenaea courbaril L.	0	2
Hymenaea stigonocarpa Mart. ex Hayne	3	0
Ilex cerasifolia Reissek	0	1
Inga vera (DC.) T.D.Penn.	0	1
Ixora venulosa Benth.	0	5
Kielmeyera rubriflora Cambess.	1	0
Lafoensia pacari A.St.-Hil.	3	0
Licania humilis Cham. & Schltdl.	2	0
Machaerium aculeatum Raddi	0	1
Machaerium acutifolium Vogel	1	0
Maprounea guianensis Aubl.	0	3
Matayba elaeagnoides Radlk.	0	2

Species	Vegetation type	
	Cerrado	Forest
Metrodorea nigra A.St.-Hil.	0	6
Miconia albicans (Sw.) Triana	53	0
Miconia cabucu Hoehne	0	1
Miconia latecrenata (DC.) Naudin	0	2
Miconia ligustroides (DC.) Naudin	11	0
Miconia rubiginosa (Bonpl.) DC.	24	0
Miconia stenostachya DC.	4	0
Micrandra elata (Didr.) Müll.Arg.	0	2
Mimosa bimucronata (DC.) Kuntze	0	1
Myrcia bella Cambess.	7	0
Myrcia guianensis (Aubl.) DC.	180	0
Myrcia lasiantha DC.	7	0
Myrcia splendens (Sw.) DC.	0	1
Myrciaria floribunda (H.West ex Willd.) O.Berg	0	3
Nectandra cuspidata Nees	0	3
Neea theifera Oerst.	3	0
Ocotea aciphylla (Nees & Mart.) Mez	0	1
Ocotea corymbosa (Meisn.) Mez	28	1
Ocotea diospyrifolia (Meisn.) Mez	0	4
Ouratea castaneifolia (DC.) Engl.	0	1
Ouratea spectabilis (Mart.) Engl.	10	0
Palicourea rigida Kunth	3	0
Piper amalago L.	0	1
Platypodium elegans Vogel	1	0
Pouteria ramiflora (Mart.) Radlk.	29	0
Pouteria torta (Mart.) Radlk.	3	0
Protium heptaphyllum (Aubl.) Marchand	0	6
Psidium laruotteanum Cambess	3	0
Psychotria vellosiana Benth.	0	2
Pterodon pubescens (Benth.) Benth.	39	1
Qualea dichotoma (Mart.) Warm.	2	0
Qualea grandiflora Mart.	21	0
Qualea multiflora Mart.	22	0
Qualea parviflora Mart.	26	0

Species	**Vegetation type**	
	Cerrado	**Forest**
Roupala montana Aubl.	24	1
Rourea induta Planch.	1	0
Rudgea viburnoides (Cham.) Benth.	1	0
Savia dictyocarpa Müll.Arg.	0	2
Schefflera morototoni (Aubl.) Maguire et al.	0	4
Schefflera vinosa (Cham. & Schltdl.)	19	0
Sebastiania brasiliensis Spreng.	0	1
Seguiera floribunda Benth	0	1
Senegalia polyphylla (DC.) Britton & Rose	0	1
Siparuna guianensis Aubl.	3	16
Strychnos bicolor Progel	1	0
Strychnos brasiliensis Mart.	3	0
Strychnos pseudoquina A.St.-Hil.	1	0
Stryphnodendron polyphyllum Mart.	9	0
Styrax camporum Pohl	1	0
Styrax ferrugineus Nees & Mart.	5	0
Handroanthus heptaphyllus (Vell.) Mattos	0	1
Terminalia glabrescens Mart.	0	1
Terminalia triflora (Griseb.) Lillo	0	1
Tetrastylidium grandifolium (Baill.) Sleumer	0	1
Trichilia catigua A.Juss.	0	1
Trichilia pallida Sw.	0	13
Urtica dioica L.	0	1
Vatairea macrocarpa (Benth.) Ducke	13	0
Virola sebifera Aubl	14	1
Vochysia cinnamomea Pohl	22	0
Vochysia tucanorum Mart.	2	0
Xylopia aromatica (Lam.) Mart.	152	0
Zanthoxylum monogynum A.St.-Hil.	0	1
Zeyheria tuberculosa (Vell.) Bureau ex Verl.	0	1

Appendix 2 Leaf functional traits and nutrient content of species sampled in cerrado and seasonal forest in the Vaçununga State Park, south-eastern Brazil. SLA = specific leaf area ($cm^2 . g^{-1}$), DMC = leaf dry matter content ($mg.g^{-1}$), TGH = leaf toughness (N), NG = nitrogen content in green leaves ($g.kg^{-1}$), NS = nitrogen content in senesced leaves ($g.kg^{-1}$), PG = phosphorus content in green leaves ($g.kg^{-1}$), PS = phosphorus content in senesced leaves, N:P = nitrogen to phosphorus ratio in green leaves.

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Senegalia polyphylla	59.700	455.540	0.156	12.558	NA	1.167	NA	10.761
Actinostemon communis	226.020	389.028	0.485	27.726	22.269	1.437	0.488	19.294
Actinostemon concepciones	208.940	421.949	0.508	25.032	24.640	1.440	NA	17.383
Amaioua guianensis	110.450	399.170	0.538	21.175	21.819	1.057	0.354	20.033
Anadenanthera peregrina	70.530	497.730	0.170	20.353	21.284	1.465	0.578	13.893
Andira cujabensis	125.530	344.356	0.458	12.208	28.378	0.956	0.860	12.770
Annona coriacea	79.970	340.248	2.281	10.816	14.625	1.073	0.392	10.080
Annona crassiflora	104.150	359.092	0.756	14.009	NA	1.176	NA	11.912
Aspidosperma ramiflorum	156.850	344.816	0.895	30.023	29.799	1.314	0.648	22.849
Aspidosperma tometosum	90.660	339.604	0.565	21.602	13.274	1.430	0.304	15.106
Astronium graveolens	119.520	388.485	0.344	23.215	23.170	2.092	0.774	11.097
Bauhinia rufa	90.820	337.234	0.871	24.617	17.900	1.826	0.369	13.481
Blepharocalyx salicifolius	142.850	436.601	0.657	24.010	NA	0.812	NA	29.569
Bowdichia virgilioides	89.570	446.117	0.690	23.646	11.984	1.195	0.289	19.787
Bredemeyera floribunda	163.600	379.870	0.515	18.354	NA	1.217	NA	15.081
Brosimum gaudichaudii	82.460	343.906	0.904	23.497	16.454	1.515	0.403	15.510

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Brosimum guianense	126.950	440.288	0.816	24.364	14.935	1.045	0.354	23.315
Byrsonima coccolobifolia	161.750	358.860	0.556	18.385	14.797	0.821	0.364	22.393
Byrsonima intermedia	114.720	382.917	0.483	20.776	16.030	0.754	0.287	27.554
Byrsonima pachyphylla	73.840	439.694	0.632	11.760	8.596	0.600	0.257	19.600
Cabralea canjerana	129.870	288.738	0.512	25.782	21.392	1.871	0.628	13.780
Calyptranthes clusiifolia	86.390	376.982	1.190	15.418	17.267	0.634	0.446	24.319
Calyptranthes concinna	183.530	208.121	0.920	19.824	NA	1.847	NA	10.733
Campomanesia adamantium	124.210	426.824	0.634	16.954	9.856	0.900	0.339	18.838
Cariniana legalis	138.370	457.208	0.576	24.038	23.534	0.965	0.683	24.910
Caryocar brasiliense	81.470	385.042	0.318	19.748	16.691	0.880	0.415	22.441
Casearia gossypiosperma	199.680	389.744	0.358	26.628	20.888	1.020	0.767	26.106
Casearia sylvestris	168.800	449.170	0.396	25.949	20.184	0.721	0.450	35.990
Cedrela fissilis	131.130	369.499	0.637	20.879	18.662	1.504	0.448	13.882
Connarus suberosus	55.680	481.804	1.869	16.422	23.912	0.812	0.528	20.224
Copaifera langsdorffii (cerrado)	104.950	506.311	0.818	26.396	19.127	1.235	0.581	21.373
Copaifera langsdorffii (forest)	139.010	526.952	0.736	25.564	15.827	1.305	0.578	19.589
Cordiera macrophylla	175.640	273.681	0.567	NA	29.679	NA	0.762	NA
Cordiera sessilis	157.940	274.101	0.676	41.916	NA	1.371	NA	30.573
Couepia grandiflora	75.480	445.178	1.094	21.554	15.431	0.949	0.439	22.712
Couepia sp.	105.350	360.732	0.851	NA	14.091	NA	0.332	NA
Coutarea hexandra	201.100	312.469	0.246	31.850	22.904	1.590	0.723	20.031
Croton floribundus	154.350	299.097	0.312	28.451	23.159	2.101	0.752	13.542

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Croton piptocalyx	159.640	266.048	0.310	NA	24.864	NA	1.219	NA
Dalbergia miscolobium	128.180	358.822	0.456	32.018	19.282	1.023	0.417	31.298
Dimorphandra mollis	92.880	432.145	0.270	32.597	27.020	1.145	0.325	28.469
Diospyros hispida	94.910	327.548	0.497	23.352	NA	1.311	NA	17.812
Diptychandra aurantiaca	133.260	409.852	0.486	30.962	18.566	1.551	0.683	19.963
Duguetia furfuracea	69.190	531.873	1.471	19.250	NA	0.758	NA	25.396
Duguetia lanceolata	128.950	369.196	0.769	28.004	27.300	1.482	0.478	18.896
Esenbeckia febrifuga	207.340	259.885	0.364	40.786	29.267	1.909	0.962	21.365
Eugenia astringens	183.990	400.050	0.836	NA	NA	NA	NA	NA
Eugenia livida	79.060	442.870	1.321	14.672	13.594	0.540	0.422	27.170
Eugenia punicifolia	154.680	311.594	0.853	24.640	15.428	1.063	0.339	23.180
Galipea jasminiflora	173.340	279.251	0.577	26.789	28.280	1.999	NA	13.401
Guapira noxia	126.350	271.043	0.873	42.397	NA	2.190	NA	19.359
Guapira opposita (cerrado)	206.970	266.745	0.706	32.909	28.084	2.159	0.887	15.243
Guapira opposita (forest)	118.130	316.310	0.709	35.000	NA	1.278	NA	27.387
Guarea macrophylla	146.710	277.187	0.707	27.269	NA	1.645	NA	16.577
Handroanthus ochraceus	107.950	381.127	0.684	23.609	20.637	1.400	0.551	16.864
Hymenaea courbaril	126.000	409.872	0.645	19.978	NA	1.048	NA	19.063
Hymenaea stigonocarpa	83.480	450.012	1.145	27.169	14.420	1.069	0.601	25.415
Ilex cerasifolia	201.650	369.693	0.529	23.156	NA	0.726	NA	31.895
Inga vera	71.300	602.109	0.614	NA	22.596	NA	0.163	NA
Ixora venulosa	140.830	386.053	0.918	18.540	14.378	1.020	0.190	18.176

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Kielmeyera rubriflora	141.820	293.782	0.315	11.522	NA	NA	NA	NA
Lafoensia pacari	135.790	411.438	0.377	19.082	15.603	0.905	0.494	21.085
Licania humilis	66.160	521.182	1.766	14.896	13.985	0.681	0.409	21.874
Machaerium aculeatum	179.070	NA	1.070	23.324	NA	1.360	NA	17.150
Machaerium acutifolium	104.740	410.361	0.975	30.618	17.374	1.209	NA	25.325
Maprounea guianensis	187.820	317.312	0.350	26.236	19.628	0.841	0.373	31.196
Matayba elaeagnoides	120.580	347.508	5.557	23.800	NA	1.604	NA	14.838
Metrodorea nigra	176.110	306.773	0.839	30.779	21.966	1.794	0.759	17.157
Miconia albicans	80.750	466.402	0.551	21.753	11.610	0.589	0.311	36.932
Miconia cabucu	171.550	266.637	0.399	27.146	NA	1.029	NA	26.381
Miconia latecrenata	159.520	282.203	0.348	24.906	17.668	0.873	0.462	28.529
Miconia ligustroides	116.870	377.107	0.331	22.798	12.446	0.724	0.354	31.489
Miconia rubiginosa	79.900	471.121	0.590	15.070	13.527	0.522	0.324	28.870
Miconia stenostachya	49.260	511.042	0.744	15.988	15.104	0.606	0.322	26.383
Micrandra elata	174.560	412.721	0.532	30.240	21.663	1.346	0.524	22.467
Mimosa bimucronata	88.660	486.150	0.166	57.890	26.474	1.388	0.587	41.707
Myrcia bella	105.560	415.718	1.134	13.774	10.934	0.587	0.204	23.465
Myrcia splendens	124.350	453.861	0.721	11.928	18.438	0.643	0.583	18.551
Myrcia guianensis	93.450	359.978	1.105	14.930	13.810	0.684	0.342	21.827
Myrcia lasiantha	71.390	439.178	1.537	11.116	10.396	0.510	0.261	21.796
Myrciaria floribunda	184.240	438.350	0.429	26.474	NA	0.993	NA	26.661
Nectandra cuspidata	99.140	445.446	0.643	30.660	11.933	0.873	0.217	35.120

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Neea theifera	184.120	150.352	0.748	43.619	14.840	1.520	0.587	28.697
Ocotea aciphylla	122.790	420.433	0.700	22.428	8.512	1.002	0.366	22.383
Ocotea corymbosa (cerrado)	142.900	370.774	0.667	21.568	15.778	0.873	0.383	24.706
Ocotea corymbosa (forest)	111.61	490.695	0.760	NA	NA	NA	NA	NA
Ocotea diospyrifolia	119.300	435.262	0.922	17.500	17.178	0.933	0.434	18.757
Ouratea castaneifolia	88.770	427.051	1.282	23.310	12.880	0.947	0.490	24.615
Ouratea spectabilis	68.030	407.947	2.275	15.686	9.142	0.872	0.276	17.989
Palicourea rigida	140.970	214.699	0.872	30.226	14.708	1.428	0.428	21.167
Piper amalago	275.000	223.606	0.412	44.912	NA	1.755	NA	25.591
Platypodium elegans	121.640	420.495	0.541	34.076	NA	0.926	NA	36.799
Pouteria ramiflora	91.080	409.007	0.644	18.981	12.993	0.845	0.379	22.463
Pouteria torta	94.410	379.461	0.759	17.164	11.396	0.966	0.325	17.768
Protium heptaphyllum	128.550	342.206	0.589	20.994	11.669	1.263	0.373	16.622
Psidium laruotteanum	57.270	448.036	1.347	12.187	NA	0.540	NA	22.569
Psychotria vellosiana	304.630	299.465	0.354	26.978	NA	1.241	NA	21.739
Pterodon pubescens (cerrado)	119.470	397.181	0.383	30.220	19.256	1.155	0.502	26.165
Pterodon pubescens (forest)	76.090	529.466	0.528	NA	18.830	NA	0.546	NA
Qualea dichotoma	140.140	329.840	0.749	19.118	15.568	0.787	0.474	24.292
Qualea grandiflora	97.080	382.255	0.806	16.920	13.726	0.757	0.392	22.351
Qualea multiflora	141.690	328.261	0.495	22.600	15.428	0.866	0.528	26.097
Qualea parviflora	141.540	380.113	0.496	17.833	17.206	0.736	0.554	24.230
Roupala montana (cerrado)	89.620	411.159	0.862	10.786	8.909	0.447	0.225	24.130

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Roupala montana (forest)	77.300	466.337	1.165	12.600	NA	0.597	NA	21.106
Rourea induta	53.310	506.683	1.905	13.958	NA	0.840	NA	16.617
Rudgea viburnoides	99.330	218.463	0.969	21.252	12.330	1.371	0.510	15.501
Savia dictyocarpa	248.730	373.291	0.359	31.458	22.015	1.438	0.591	21.876
Schefflera morototoni	59.840	377.879	0.589	26.775	14.952	0.988	0.469	27.100
Schefflera vinosa	76.080	421.998	0.733	19.992	16.878	0.982	0.460	20.358
Sebastiania brasiliensis	176.180	464.821	0.661	27.888	23.786	1.112	0.542	25.079
Seguieria floribunda	179.140	281.267	0.571	51.268	NA	1.755	NA	29.213
Siparuna guianensis (cerrado)	151.830	272.107	0.522	35.672	17.024	1.597	0.501	22.337
Siparuna guianensis (forest)	180.040	274.341	0.870	24.181	21.331	1.518	0.406	15.930
Strychnos bicolor	148.340	474.227	0.408	25.368	18.445	0.874	0.374	29.025
Strychnos brasiliensis	151.790	457.869	0.423	24.346	NA	1.161	NA	20.970
Strychnos pseudoquina	86.550	486.510	0.554	19.726	15.582	0.849	NA	23.234
Stryphnodendron polyphyllum	123.710	373.815	0.282	27.647	17.124	1.209	0.371	22.868
Styrax camporum	66.990	422.743	0.917	11.970	10.934	0.574	NA	20.854
Styrax ferrugineus	81.720	489.112	1.513	14.468	10.738	0.658	0.305	21.988
Handroanthus heptaphyllus	81.490	365.493	1.438	NA	15.316	NA	0.542	NA
Terminalia glabrescens	119.300	358.138	0.657	23.072	NA	1.029	NA	22.422
Terminalia triflora	285.250	274.286	0.372	33.040	NA	1.397	NA	23.651
Tetrastylidium grandifolium	151.970	291.841	0.731	17.808	24.724	2.527	0.515	7.047
Trichilia catigua	126.130	160.059	0.468	18.886	NA	1.232	NA	15.330
Trichilia pallida	198.920	337.905	0.509	29.146	19.892	1.662	0.718	17.537

Species	**SLA**	**DMC**	**TGH**	**NG**	**NS**	**PG**	**PS**	**N:P**
Urtica dioica	314.820	267.081	0.161	NA	NA	NA	NA	NA
Vatairea macrocarpa	81.710	437.801	1.803	15.212	14.973	0.787	0.384	19.329
Virola sebifera (cerrado)	88.070	388.523	0.712	19.583	20.050	0.814	0.508	24.058
Virola sebifera (forest)	91.200	360.277	0.743	22.526	NA	0.937	NA	24.041
Vochysia cinnamomea	63.840	373.509	1.157	12.267	12.394	0.490	0.341	25.035
Vochysia tucanorum	120.960	265.444	0.911	17.486	14.777	0.789	0.434	22.162
Xylopia aromatica	103.020	422.203	0.679	24.408	14.934	0.996	0.449	24.506
Zanthoxylum monogynum	226.940	310.803	0.438	27.454	21.812	1.195	0.501	22.974
Zeyheria tuberculosa	78.000	441.711	0.539	NA	30.772	NA	0.704	NA

Appendix 3 Mean, standard deviation and range of each soil feature in the cerrado and in the seasonal forest. Clay (g.kg^{-1}), cation exchange capacity (CEC, mmol.kg^{-1}), organic matter (OM, mmol.kg^{-1}), pH, and sum of bases (SB, mmol.kg^{-1}), available phosphorus (P, mg.kg^{-1}), total nitrogen (N, mg.kg^{-1}), Aluminium (Al, mmol.kg^{-1}), Cations K^+ (K, mmol.kg^{-1}), Ca^{2+} (Ca, mmol.kg^{-1}), Mg^+ (Mg, mmol.kg^{-1}), as well as potential acidity (H.Al, mmol.kg^{-1}), percentage of base saturation (V, %), percentage of aluminium saturation (m, %), silt, and sand proportions (1:1000).

	Cerrado		Seasonal Forest	
Soil feature (unit)	**mean ± sd**	**range**	**mean ± sd**	**range**
Clay	89.25 ± 30.73	38 - 151	225.94 ± 115.25	100 - 443
CEC	47.38 ± 9.60	28.6 - 82.7	68.5 ± 28.95	31.7 - 155.4
OM	20.37 ± 4.58	8 - 31	24.37 ± 9.21	13 - 46
pH	3.94 ± 0.12	3.7-4.2	4.25 ± 0.44	3.7 - 5.8
SB	1.71 ± 0.37	1.5 - 4.5	17.41 ± 23.57	3.1 - 124
P	2.30 ± 0.69	1.51 - 500	2.38 ± 0.63	1.44 - 4.47
N	1144.11 ± 546.21	651 - 3199	1167.72 ± 308.23	770 - 1960
Al	12.05 ± 2.18	7.50 - 19.21	10.07 ± 5.12	0.01 - 21.08
K	0.45 ± 0.09	0.27 – 0.71	1.36 ± 0.76	0.64 - 3.85
Ca	0.58 ± 0.30	0.55 – 3.02	7.97 ± 8.57	0.99 – 37.05
Mg	0.67 ± 0.12	0.54 – 1.27	5.44 ± 5.96	1.45 – 27.70
H.Al	45.67 ± 9.54	27.01 – 81.10	51.09 ± 16.98	26.14 – 84.52
V	3.66 ± 0.91	2 - 9	21.41 ± 15.61	6 - 80
M	87.41 ± 2.85	71 - 92	47.84 ± 24.04	0 - 84
Silt	22.29 ± 6..40	11 - 39	28.78 ± 18.11	11-96
Sand	88.40 ± 31.39	819 - 944	731.87 ± 136.89	471 - 883

Appendix 4 Loadings of each soil variable on the first two principal components. Clay, cation exchange capacity (CEC), organic matter (OM), pH, and sum of bases (SB) contributed more strongly to PC1. Available phosphorus (P), total nitrogen (N), and aluminium contributed more strongly to PC2.

Soil variable	**PC1**	**PC2**
Clay	**0.637**	0.250
CEC	**0.444**	0.026
OM	**0.438**	0.116
pH	**0.316**	-0.250
SB	**0.299**	-0.181
P	0.021	**-0.397**
N	-0.026	**0.632**
Al	-0.122	**0.521**

Appendix 5. Average soil aluminium concentration of species sampled in cerrado and seasonal forest in the Vaçununga State Park, south-eastern Brazil. We calculated the mean Al concentration across all sites where the species occurred within each vegetation type. We expected cerrado species, or at least some families, to be more associated with high Al sites and forest species to be more associated with low Al sites. Unexpectedly, forest species can occupy, on average, sites with higher Al concentration and there is no pattern of aggregation, in terms of species relatedness, towards high or low Al sites in both vegetation types. Species occurring in both vegetation types, highlighted in bold, tend to be plastic: whereas some were more associated with high Al sites in the forest, others were more associated with high Al sites in the cerrado. Perhaps the soil Al concentration is not a good predictor of either cerrado or forest species preferences or floristic distinctiveness in regards do high or low Al soils. Perhaps what really matters is the difference in species tolerance against the toxic forms of aluminium that are predominant under the more acid soils of cerrado. Although cerrado soils had higher Al concentrations than the forest (Appendix 3), some forest plots had surprising high Al concentrations. Some of the high Al species in the forest were rare species (Appendix 1) occurring incidentally in these uncommon high Al plots.

Cerrado			Seasonal Forest		
Species	Family	Al (mmol.kg^{-1})	Species	Family	Al (mmol.kg^{-1})
Eugenia livida	Myrtaceae	15.696	***Ocotea corymbosa***	**Lauraceae**	21.084
Vochysia tucanorum	Vochysiaceae	14.993	*Psychotria vellosiana*	Rubiaceae	18.741
Bowdichia virgilioides	Fabaceae	14.056	*Matayba elaeagnoides*	Sapindaceae	18.273
Byrsonima intermedia	Malpighiaceae	13.587	*Cabralea canjerana*	Meliaceae	17.804
Byrsonima pachyphylla	Malpighiaceae	13.587	*Nectandra cuspidate*	Lauraceae	17.648
Guapira noxia	Nyctaginaceae	13.431	*Brosimum guianense*	Moraceae	17.336
Psidium laruotteanum	Myrtaceae	13.119	*Handroanthus heptaphyllus*	Bignoniaceae	16.867
Strychnos pseudoquina	Loganiaceae	13.119	*Urtica dioica*	Urticaceae	16.867
Qualea grandiflora	Vochysiaceae	13.091	*Tetrastylidium grandifolium*	Olacaceae	15.461
Casearia sylvestris	Salicaceae	12.963	*Protium heptaphyllum*	Burseraceae	15.087
Caryocar brasiliense	Caryocaraceae	12.906	*Inga vera*	Fabaceae	14.524
Dalbergia miscolobium	Fabaceae	12.826	*Maprounea guianensis*	Euphorbiaceae	13.900
Annona coriacea	Annonaceae	12.728	*Schefflera morototoni*	Araliaceae	13.119
Ocotea corymbosa	**Lauraceae**	12.717	*Trichilia pallida*	Meliaceae	12.885
Dimorphandra mollis	Fabaceae	12.650	*Cariniana legalis*	Lecythidaceae	12.650
Lafoensia pacari	Lythraceae	12.650	***Copaifera langsdorffii***	**Fabaceae**	12.650
Ocotea aciphylla	Lauraceae	12.650	*Amaioua guianensis*	Rubiaceae	12.416
Pouteria ramiflora	Sapotaceae	12.583	*Calyptranthes concinna*	Myrtaceae	12.182
Hymenaea stigonocarpa	Fabaceae	12.338	*Croton piptocalyx*	Euphorbiaceae	12.182
Pouteria torta	Sapotaceae	12.338	*Miconia cabucu*	Melastomataceae	12.182
Anadenanthera peregrina	Fabaceae	12.204	*Ocotea diospyrifolia*	Lauraceae	12.182
Diptychandra aurantiaca	Fabaceae	12.182	*Zeyheria tuberculosa*	Bignoniaceae	12.182
Licania humilis	Chrysobalanaceae	12.182	***Siparuna guianensis***	**Siparunaceae**	12.006
Virola sebifera	**Myristicaceae**	12.182	*Andira cujabensis*	Fabaceae	11.713
Xylopia aromatic	Annonaceae	12.174	*Guarea macrophylla*	Meliaceae	11.713
Miconia albicans	Melastomataceae	12.079	*Ouratea spectabilis*	Ochnaceae	11.573
Myrcia guianensis	Myrtaceae	12.020	*Ixora venulosa*	Rubiaceae	11.362
Stryphnodendron polyphyllum	Fabaceae	12.006	*Micrandra elata*	Euphorbiaceae	11.245
Connarus suberosus	Connaraceae	11.947	*Myrcia splendens*	Myrtaceae	10.776
Vochysia cinnamomea	Vochysiaceae	11.901	*Myrciaria floribunda*	Myrtaceae	10.776
Schefflera vinosa	Araliaceae	11.854	*Croton floribundus*	Euphorbiaceae	10.642
Pterodon pubescens	**Fabaceae**	11.850	*Calyptranthes clusiifolia*	Myrtaceae	10.308
Roupala Montana	**Proteaceae**	11.838	*Miconia latecrenata*	Melastomataceae	10.073
Bauhinia rufa	Fabaceae	11.713	***Roupala montana***	**Proteaceae**	9.839
Diospyros hispida	Ebenaceae	11.713	*Cordiera macrophylla*	Rubiaceae	9.371
Rudgea viburnoides	Rubiaceae	11.713	***Guapira opposita***	**Nyctaginaceae**	9.371
Styrax ferrugineus	Styracaceae	11.713	*Ilex cerasifolia*	Aquifoliaceae	9.371
Miconia ligustroides	Melastomataceae	11.666	*Ouratea castaneifolia*	Lauraceae	9.371
Vatairea macrocarpa	Fabaceae	11.666	*Astronium graveolens*	Anacardiaceae	8.695
Myrcia lasiantha	Myrtaceae	11.619	*Actinostemon klotzschii*	Euphorbiaceae	8.680
Palicourea rigida	Rubiaceae	11.557	*Duguetia lanceolata*	Annonaceae	8.551
Qualea multiflora	Vochysiaceae	11.548	*Actinostemon concepcionis*	Euphorbiaceae	8.433

Cerrado			**Seasonal Forest**		
Species	Family	Al (mmol.kg^{-1})	Species	Family	Al (mmol.kg^{-1})
Qualea parviflora	Vochysiaceae	11.548	*Casearia gossypiosperma*	Salicaceae	8.433
Qualea dichotoma	Vochysiaceae	11.479	*Blepharocalyx salicifolius*	Myrtaceae	7.496
Copaifera langsdorffii	**Fabaceae**	11.432	*Eugenia astringens*	Myrtaceae	7.496
Miconia rubiginosa	Melastomataceae	11.417	***Pterodon pubescens***	**Fabaceae**	7.496
Couepia sp	Chrysobalanaceae	11.245	*Trichilia catigua*	Meliaceae	7.496
Campomanesia adamantium	Myrtaceae	11.245	*Savia dictyocarpa*	Phyllanthaceae	7.028
Platypodium elegans	Fabaceae	11.245	*Terminalia glabrescens*	Combretaceae	6.091
Aspidosperma tometosum	Apocynaceae	11.186	***Virola sebifera***	**Myristicaceae**	6.091
Myrcia bella	Myrtaceae	11.167	*Esenbeckia febrifuga*	Rutaceae	5.935
Byrsonima coccolobifolia	Malpighiaceae	11.151	*Aspidosperma ramiflorum*	Apocynaceae	5.857
Couepia grandiflora	Chrysobalanaceae	11.088	*Coutarea hexandra*	Rubiaceae	4.685
Eugenia punicifolia	Myrtaceae	11.010	*Machaerium aculeatum*	Fabaceae	4.685
Guapira opposita	**Nyctaginaceae**	10.964	*Cedrela fissilis*	Meliaceae	4.456
Annona crassiflora	Annonaceae	10.870	*Senegalia polyphylla*	Fabaceae	4.217
Cordiera sessilis	Rubiaceae	10.776	*Galipea jasminiflora*	Rutaceae	4.217
Machaerium acutifolium	Fabaceae	10.776	*Mimosa bimucronata*	Fabaceae	4.217
Siparuna guianensis	**Siparunaceae**	10.776	*Piper amalago*	Piperaceae	4.217
Bredemeyera floribunda	Polygalaceae	10.308	*Metrodorea nigra*	Rutaceae	3.868
Brosimum gaudichaudii	Moraceae	10.308	*Hymenaea courbaril*	Fabaceae	3.514
Miconia stenostachya	Melastomataceae	10.308	*Seguieria floribunda*	Phytolaccaceae	3.280
Neea theifera	Nyctaginaceae	10.308	*Terminalia triflora*	Combretaceae	0.937
Rourea induta	Connaraceae	10.308	*Zanthoxylum monogynum*	Rutaceae	0.937
Strychnos bicolor	Loganiaceae	10.308	*Sebastiania brasiliensis*	Euphorbiaceae	0.010
Styrax camporum	Styracaceae	10.308			
Handroanthus ochraceus	Bignoniaceae	10.151			
Strychnos brasiliensis	Loganiaceae	9.605			
Duguetia furfuracea	Annonaceae	8.902			
Kielmeyera rubriflora	Calophyllaceae	8.433			

III - Capítulo 2

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Are the cerrado and seasonal forest woody floras assembled by different processes despite their spatial proximity?

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Abstract

Aims

The Brazilian cerrado occupies areas that could be occupied by seasonal forest. Soil is one of the main determinants of cerrado and forest prevalence. We tested whether cerrado and seasonal forest woody floras were assembled by different processes despite their spatial proximity and whether the species pairwise functional-phylogenetic distances were related to soil features. We expected that cerrado nutrient-poor soil would promote trait clustering and that functional-phylogenetic distances would increase towards richer soils.

Methods

In 100 5 x 5 m plots distributed along cerrado and seasonal forest patches in southern Brazil, we sampled 127 species with diameter at soil height ≥ 3cm and measured seven of their functional traits (plant height, basal area, tortuosity, leaf size, specific leaf area, leaf dry matter content, leaf toughness). We also sampled soil at 0-5 cm deep in each plot and had their chemical and physical properties determined. We constructed the phylogenetic tree and calculated the pairwise mean functional-phylogenetic distances (MFPD), an approach that accounts for functional and phylogenetic information both separately and combined. We applied a canonical correspondence analysis, using the community and soil matrices. Then, we related the MFPD to soil properties by applying an analysis of covariance. We compared MFPD between cerrado and forest species with a Mann-Whitney test.

Important findings

Phylogenetic distances were higher than functional ones in both cerrado and seasonal forest communities, suggesting trait convergence in both environments. Irrespectively of the importance given to functional or phylogenetic information, most of the communities in the cerrado and in the seasonal forest lied within the null expectation, implying that multiple assembly processes can occur simultaneously along the gradient of soil fertility. Nevertheless, MFPD was related to soil fertility when only functional distances were considered. In this case, MFPD was lower in cerrado than in the forest, indicating that soil fertility shaped plant traits, with the low-nutrient soils in the cerrado constraining the range of variation in these traits. Accounting for several important traits simultaneously along the phylogenetic distances, we found largely similar sorting mechanisms occurring in cerrado and seasonal forest despite strong evidence for abiotic environmental filtering in the cerrado versus biotic filtering in the seasonal forest. Even not being the only ecological force structuring these communities, soil nutrient status has an important role in maintaining the functional distinctiveness of the two vegetation types.

Key words: competition, functional traits, environmental filter, nutrient limitation, phylogeny, savanna.

Introduction

Assembly rules are any constraint on species coexistence that determines whether species from a regional pool will colonise, survive, and interact to form local communities (Götzenberguer *et al.* 2012, HilleRisLambers *et al.* 2012). Since local communities are determined by a cumulative effect of dispersal and chance restrictions coupled with environmental filtering and biotic interactions (Götzenberguer et al. 2012, HilleRisLambers *et al.* 2012), assembly rules embrace not only the ecological processes that directly influence structure and diversity of communities, but also the biogeographic processes that cause variation on the regional pool (Kraft and Ackerly 2014). By assessing assembly, it is possible to predict community dynamics and the consequences of species loss (Götzenberguer *et al.* 2012, Kraft and Ackerly 2014). Hence, it is an essential tool for biodiversity conservation and restoration ecology (Keddy 1992, Keddy 1999, Hulvey and Aigner 2014).

After the acknowledgement that diversity patterns cannot be reduced to a species list and the concomitant advances in phylogenetic and functional diversities, studies of assembly rules have been boosted (HilleRisLambers *et al.* 2012, Swenson 2013). On the one hand, phylogenetic diversity gives information of species similarity and unmeasured traits, enabling estimations of the evolutionary history to species distributions (Swenson 2013); on the other hand, functional diversity can give a more accurate information on species similarities based on direct morphological or physiological characteristics, allowing the identification of ecological strategies (Swenson 2013). Given the advantages of both methods and considering that important traits can be overlooked and uninformative traits can be included (Cadotte *et al.* 2013), an ideal and more efficient way to assess plant community assembly is to combine the best properties of both approaches, reducing their undesirable properties (Swenson 2013). In this sense, a new approach for quantifying biodiversity by weighting the independent contribution of functional and phylogenetic distances in a single measure was proposed by Cadotte *et al.* (2013). The so-called "functional-phylogenetic distance" can be considered both "a phylogenetic distance that takes trait convergence or divergence into account" and "a functional distance that accounts for information from unmeasured, phylogenetically correlated traits" (Cadotte *et al.* 2013).

Abrupt transitions between the cerrado and the semi-deciduous seasonal forest are common in Brazil (Ratter et al. 1997, Durigan and Ratter 2006, Hoffmann *et al.* 2012, Dantas *et al.* 2013, Viani *et al.* 2014). In southern Brasil, the semi-deciduous seasonal forest often occurs adjoining the cerrado (Durigan and Ratter 2006, Viani *et al.* 2014). Despite occurring under the same climate, having a rich flora, and being spatially close, few species are shared between them, suggesting that abiotic and biotic restrictions might be limiting their similarity, regardless of dispersal events (Ai *et al.* 2012). Studying assembly rules at both sides of the cerrado-forest boundary may give important insights into the processes maintaining high diversity levels and almost no overlap in species composition in these two vegetation types, despite their physical proximity, and might help defining conservation goals.

One of the main factors pointed out as the cause for the maintenance of cerrado and seasonal forest different floras is soil fertility (Ruggiero *et al.* 2002, Durigan and Ratter 2006). According to the habitat-filtering theory (Keddy 1992), low fertility may be a key environmental filter, selecting from the species pool those that have suitable traits to cope with local restrictions and forcing species to converge towards the "most suitable" values for traits. According to the limiting similarity theory (Diamond 1975, Pacala and Tilman 1994), competition for resources usually results in trait divergence, which enables the stable coexistence among organisms. In this case, co-existing species are expected to have different functional attributes whereby resources are captured and exploited in different ways, reducing the chances of competitive exclusion (Grime 2006). Thus, at the same time that soil fertility may be a key environmental filter, contributing to the lack of similarity in species composition between the cerrado and the forest (Hoffmann and Franco 2008), it can also promote diversification, by limiting the similarity among its species or by the filling of a low competition niche space (Grime 2006, Simon *et al.* 2009, Katabuchi *et al.* 2011).

Nonetheless, in nutrient-poor soils, species tend to converge towards a retentive strategy, whereas, in nutrient-rich soils, species seem to have a mixture of strategies in regards to nutrient acquisition (Ordoñez *et al.* 2009, Mason *et al.* 2012). Considering that soil is one of the main factors influencing cerrado-forest prevalence, filtering out species from the regional pool or promoting diversity, we aimed to answer the following questions: (1) Do functional traits present positive phylogenetic signal? In the cerrado, phylogenetically autocorrelated traits have been found (Batalha *et al.* 2011); (2) Are functional-phylogenetic distances lower in the cerrado than in the forest? If cerrado communities are mainly assembled by environmental filtering, given that their nutrient-poor soils promote trait clustering (Batalha *et al.* 2011), and if forest communities are mainly assembled by limiting similarity, given that they are subject to a more competitive environment (Viani *et al.* 2011), we expect them to be so; (3) Are functional-phylogenetic distances related to soil features? Since soil is an important factor influencing cerrado-forest prevalence (Ruggiero *et al.* 2002), we expect functional-phylogenetic distances to increase towards richer soils.

Methods

We carried out this study in Vaçununga State Park, located in Santa Rita do Passa Quatro municipality, south-eastern Brazil (21°36-47’ S and 47°34-41’ W). The park is at 590-740 m above sea level. Regional climate is classified as Cwa (Köppen 1931), with wet summers (from October to April) and dry winters (May to September). Mean annual temperature is about 21.5°C and annual rainfall lies around 1,499 mm (Pivello et al. 1998). The park comprises 2,071 ha divided into six fragments: one mainly covered by cerrado and five mainly covered by semi-deciduous seasonal forest. Soils are mainly Neosols and Latosols, according to the Brazilian classification system (Embrapa 2012), or Entisols and Oxisols, according to the USDA classification system (Soil Survey Staff 2014). We established 100 25 m^2 plots in the three fragments that were accessible to researchers by using a random stratified sampling (Krebs 1998; Sutherland 2006). The number of plots in each vegetation type was proportional to the area covered by them in the three fragments, that is, 68 plots in the cerrado, representing its 1,192 ha, and 32 plots in the seasonal forest, representing its 578 ha.

In each plot, we collected soil samples at 0-5 cm deep and sent them to the Luiz de Queiroz College of Agriculture, at the University of São Paulo, for determination of pH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, calcium, magnesium, and aluminium, sum of bases, base saturation, aluminium saturation, cation exchange capacity, and sand, silt, and clay content, following procedures described in Silva and Batalha (2008). We also sampled all the individuals belonging to the woody layer, that is, those woody individuals with stem diameter at the soil level equal to or higher than 3 cm (SMA 1997). We identified the individuals to species level, comparing the collected material to vouchers lodged at the Botanical Institute of São Paulo herbarium or using identification keys based on vegetative characters (Batalha *et al.* 1998; Batalha and Mantovani 1999). Then, we randomly selected 5-10 individuals of each species to be sampled. For species with less than five individuals, we made an additional effort, looking for other individuals close to the plots and trying to reach five individuals per species.

For each individual, we measured: height, basal area, and tortuosity (Table 1). We considered as plant height the shortest distance between the highest photosynthetic tissue in the canopy and the ground level, corresponding to the top of the general canopy of the plant, discounting any exceptional branches (Pérez-Haguindeguy *et al.* 2013). To measure this distance, we used a Hastings-M 50 telescopic ruler. To calculate basal area, we measured the individuals perimeter at soil height with a tape measure. We considered each branch sprouting from the ground as a different individual. To estimate plant tortuosity, we measured the height and the length of the trunk up to the first bifurcation with a tape measure. Then, we calculated tortuosity as 1 - (height/length). Thus, tortuosity varied from zero to one, and the higher the value, the more twisted the plant.

Additionally, we collected five green leaves from the selected individuals. We placed the leaves in plastic bags, put them in a thermal box, and took them to the laboratory, where we measured four functional traits (Pérez-Harguindeguy *et al.* 2013): leaf size, specific leaf area, leaf dry matter content, and leaf toughness (Table 1). We scanned the leaves and calculated their areas with the ImageJ software (Rasband 2014). We also weighed the leaves in an analytical balance to 0.001 g to obtain their fresh masses. Then, we placed the leaves in paper bags, oven-dried them at 70°C for 72 hours, and weighed them again to obtain their dry masses. We divided leaf area by dry mass to obtain specific leaf area and dry mass by fresh mass to obtain leaf dry matter content. As a surrogate for leaf toughness, we measured the force to punch, punching with a dynamometer at both sides of the midrib and recording the force necessary to penetrate the leaf.

After measuring each trait, we standardised each trait to zero mean and unit variance, and obtained a functional distance matrix using Euclidean distances. We also built a phylogenetic tree, using Bell (2010) as reference. We improved tree resolution by consulting recent phylogenies of some clades, such as Fabaceae (Simon et al. 2009), Malpighiales (Wurdack and Davis 2009), and Myrtaceae (Costa 2009). After building the phylogenetic tree, we obtained a phylogenetic distance matrix using cophenetic distances.

To answer the first question, we tested whether there was a positive or a negative phylogenetic signal in each functional trait using Blomberg's K statistic (Blomberg et al. 2003). To answer the second question, we computed the functional-phylogenetic distance matrix, using the functional and phylogenetic matrices and the weighting parameters a and p (Cadotte et al. 2013). The weighting parameter a goes from zero to one and adjusts the contribution of functional and phylogenetic distances: when it is close to zero, more importance is given to functional distances; when it is close to one, more importance is given to pylogenetic distances (Cadotte et al. 2013). The weighting parameter p is used to meet the mathematical restrictions of a distance metric and has to equal or exceed one (Cadotte et al. 2013). We calculated mean functional-phylogenetic distances for each community, setting the parameter *a* to 0 (only functional distances were considered), 0.5 (functional and phylogenetic distances were given the same weight), and 1 (only phylogenetic distances were considered). To compare the mean values between the cerrado and the seasonal forest when *a* was 0, 0.5, and 1, we applied Mann-Whitney tests (Zar 1999).

We tested whether communities were under or overdispersed, plotting mean functional-phylogenetic distances against the weighting parameter *a*. We compared the observed curved with those originated from a null distribution based on 4,999 randomisations. The community was considered overdispersed when the observed curve was above the 0.975 quantile of the distribution and underdispersed when below the 0.025 quantile (Cadotte et al. 2013). We also plotted mean pairwise functional-phylogenetic distances against species richness (Cadotte *et al.* 2013), comparing the observed values with a null distribution generated with 4,999 randomisations. The community was underdispersed when the observed curve was below the 2.5 percentile of the distribution and overdispersed when above the 97.5 percentile. We used this procedure three times, setting *a* to 0, 0.5, and 1 and, thus, giving progressively more importance to phylogenetic distances.

To answer the third question, we applied a canonical correspondence analysis (Jongman *et al.* 1995), using the community and the soil matrices. Then, we applied an analysis of covariance using mean functional-phylogenetic distances as the response variable and the scores of the first two canonical axes, vegetation type, and the interaction terms as explanatory variables. We repeated this procedure, varying the phylogenetic-weighting parameter a from 0 to 1 and recording each time the value of the adjusted coefficient of determination (Cadotte *et al.* 2013). We conducted all analyses in R (R Development Core Team 2014), using the "ade4" (Dray and Dufour 2007) and "vegan" (Oksanen et al. 2013) packages, as well as the functions provided by Cadotte et al. (2013).

Results

We sampled 69 species belonging to 28 families in the cerrado and 65 species belonging to 30 families in the semi-deciduous seasonal forest. Since there were seven species common to both vegetation types, overall we found 127 species, for which we measured the functional traits (Appendix 1) and obtained the phylogenetic tree (Appendix 2). We found values for Blomberg's K always lower than one, even though they were significantly lower only for leaf toughness and specific leaf area (Table 2).

Mean functional-phylogenetic distances were lower in the cerrado than in the forest when only functional distances were considered (P < 0.001; Table 3) and when phylogenetic and functional distances were given equal weight (P = 0.022; Table 3), but not when only phylogenetic distances were considered (P = 0.130; Table 3). Phylogenetic distances were higher than functional distances, providing signatures that pairwise evolutionary relationships were convergent. As a consequence, curves of functional-phylogenetic distances as a function of the weighting parameter a were always increasing (Figure 1, Appendix 3). Among the 68 communities in the cerrado, eight were underdispersed at least for some values of a, whereas the other 60 were always within the null distribution (Figures 1 and 2, Appendix 3). Among the 32 communities in the seasonal forest, three were underdispersed and three were overdispersed at least for some values of *a*, whereas the other 26 were always within the null distribution (Figures 1 and 2, Appendix 3). We highlighted three communities in each vegetation type with different patterns (Figure 1) and presented the patterns across all communities (Appendix 3). When plotting mean functional-phylogenetic distances against species richness, most of the communities lay within the null distribution (Figure 2). When *a* was set to 0, six cerrado communities were underdispersed and one forest community was overdispersed (Figure 2a). When *a* was set to 0.5, 10 cerrado and one forest communities were underdispersed and one forest community was overdispersed (Figure 2b). When *a* was set to 1, five cerrado communities and two forest community were underdispersed (Figure 2c).

The canonical correspondence analysis separated cerrado and forest communities in two axes of fertility, with cerrado communities restricted to more impoverished soils. The first and the second axis eigenvalues were 0.769 and 0.524, respectively. These axes accounted, together, for only 6.9% of the explanation, but they were still significant ($p = 0.001$ in both cases). Whereas the first axis was related to pH, organic matter, sum of bases, cation exchange capacity, and clay content, the second axis was strongly related to aluminium content (Figure 3). Neither total nitrogen nor available phosphorus were significantly represented by the canonical axes ($p = 0.182$ and $p = 0.180$, respectively).

In the analyses of covariance of mean functional-phylogenetic distances as a function of the first two canonical axes, vegetation type, and the interaction terms, values of the adjusted coefficient of determination were higher when *a* was 0 and lower when *a* was 1, decreasing from 0.17 to 0.11, approximately (Figure 4). Mean functional-phylogenetic distances were related to the first two canonical axes when only functional distances were considered, that is, when *a* was set to 0 (Figure 5, Table 4).

Discussion

Contrary to what we expected, none of the traits were positively autocorrelated in the phylogeny. Instead, basal area, height, tortuosity, and leaf size were not autocorrelated in the phylogeny, whereas specific leaf area and leaf toughness were negatively autocorrelated. Basal area and height are traits that strongly define the α-niche and so are subject to rapid evolutionary rates (Silvertown *et al.* 2006). Leaf size is also a labile trait, with a great diversity among plants (Wright *et al.* 2001). The multiple functions that a leaf performs and the consequent trade-off required for its successful functionality offers more opportunities than constraints for ecological and evolutionary shifts, even though leaves tend to be smaller under harsh conditions (Nicotra *et al.* 2011), such as in low-nutrient soil (Chapin 1980, Fonseca et al. 2000). Tortuosity, in turn, is a trait driven by fire, and since fire in the cerrado tends to promote phenotypic but not phylogenetic underdispersion (Silva and Batalha 2010), it was reasonable that tortuosity was not autocorrelated in the phylogeny.

The negative phylogenetic signal we found for specific leaf area and leaf toughness implied phylogenetic convergence. In this case, phylogenetically distant species were more similar for these traits than they would be if these traits had evolved following a Brownian motion (Blomberg *et al.* 2003). The negative phylogenetic autocorrelation of a trait across the phylogeny is not a common phenomenon (Diniz-Filho *et al.* 2012), but it has been recorded for cerrado plants (Batalha *et al.* 2011). A negative phylogenetic signal can be either the result of an evolutionary divergence induced by character displacement in closely related species due to competition or limiting similarity (Losos 2000, Diniz-Filho *et al.* 2012) or the result of an evolutionary convergence for certain traits that have evolved similarly in distant species experiencing similar environmental restrictions that favoured similar "adaptive solution" (Losos 2011, Conte *et al.* 2012). Adding up to the negative phylogenetic signal, the phylogenetic distances were always higher than the functional ones in both cerrado and seasonal forest communities, as showed by the increasing pattern of the curves, suggesting trait convergence rather than divergence in both environments.

As expected, pairwise functional-phylogenetic distances were lower in the cerrado than in the forest, but only when more importance was given to functional information. Low-nutrient soil may be indeed acting as an environmental filter in the cerrado. In low-nutrient soils, leaves are particularly expensive, and there is an evolutionary pressure towards a slow-growth and a conservative strategy (Craine 2009). Specific leaf area and leaf toughness are traits intensely related to soil nutrient status (Craine 2009). Plants from low-nutrient habitats have low specific leaf area and high toughness, which make them able to optimise carbon gain in regards to transpirational loss and to have a longer leaf-lifespan promoted by structural reinforcement (Givnish 1978, Turner 1994, Craine 2009). Conversely, plants from nutrient-rich habitats tend to have high specific leaf area and low toughness with a consequent quick return of the nutrient invested in the leaf through high photosynthetic rates, fast decomposability, and short leaf lifespan (Wright et al. 2004, Craine 2009). Nevertheless, some degree of mixture of strategies in regards to nutrient use is expected in nutrient-rich soils (Ordoñez *et al.* 2009, Mason *et al.* 2012). Hence, if cerrado species were selected for slow growth or a conservative strategy, the forest species were selected for an acquisitive strategy, but with more diversified traits that reduce niche overlap or improve the species competitive abilities, or both.

When analysing communities that deviated from the null expectation, we found evidence for filtering in cerrado communities, some of which were underdispersed, but not necessarily for limiting similarity in the seasonal forest. Some of the forest communities were also underdispersed at low and intermediate values of a, but some were overdispersed. It was at intermediate values that most of the deviations from the null model occurred both when plotting the pairwise functional phylogenetic distance against the weighting parameter or against species richness, implying that both measured and unmeasured functional traits were informative (Cadotte et al. 2013). When traits are convergent, as for specific leaf area and leaf toughness, and environmental filtering is the main ecological force, simultaneous phylogenetic overdispersion and phenotypic underdispersion are expected to occur (Webb et al. 2002). Conversely, phylogenetic random pattern and phenotypic overdispersion are expected to occur when competitive interactions are the main forces structuring the community (Webb et al. 2002). Hence, when a was set to 1, we should have found overdispersion in cerrado and no deviation from the null model in the forest. Instead, underdispersion occurred in both environments, which could have been caused by unmeasured traits that have some outstanding role into these assemblages (Cadotte et al. 2013).

Despite some evidence for environmental filtering in the cerrado and limiting similarity in the forest, most of the communities in the cerrado and in the seasonal forest lay within the null expectation when plotting pairwise functional phylogenetic distances against the weighting parameter or against species richness. Multiple assembly processes can occur simultaneously along the gradient of soil fertility, with traits being selected differently in both extremes of the gradient (Spasojevic and Suding 2012, Cadotte *et al.* 2013). Even if species were selected for a conservative strategy in the cerrado and for an acquisitive strategy in the forest, after they were able to colonise, establish, and persist in a given habitat, they must also interact with their neighbours, occupying certain niche and developing their competitive abilities (Mayfield and Levine 2010). Thus, at least some traits, those important for alpha niche, will be overdispersed due to limiting similarity (Silvertown *et al.* 2006). In other words, traits can be simultaneously constrained in their range due to soil-nutrient status, especially in cerrado, and become overdispersed within that range due to limiting similarity (Silvertown *et al.* 2006).

Cerrado had poorer sites, as highlighted by the canonical correspondence analysis. The low-nutrient soil in cerrado selected for species with the most advantageous traits to succeed there (Ruggiero *et al.* 2002). Nevertheless, there were no differences in soil total nitrogen and available phosphorus, contrary to what had been found for other sites in south-eastern Brazil (Viani *et al.* 2011). The lack of difference in soil total nitrogen and available phosphorus could be due perhaps to similar nitrogen and phosphorus status of the parent materials and intense losses through deep weathering (Haridasan 2008). Even if soil nutrient status was related to the pairwise functional phylogenetic distances when only functional information was considered, a low percentage of the variation was explained. This result was likely related to the fact that cerrado and seasonal forest were equally constrained by nitrogen and phosphorus. Besides, there was a wide range of pairwise functional phylogenetic distances in the cerrado, even though the soils were equally poor among cerrado communities. Hence, we found, once again, evidence that limiting similarity and environmental filtering are both structuring cerrado communities and that niche partitioning is occurring even though conservative strategies prevail in its low-nutrient soil (Mayfield and Levine 2010). In the forest, however, the more fertile the soils, the higher the functional distances, as expected.

Cerrado and seasonal forest are functionally different (Viani *et al.* 2014, Loiola *et al.* 2015), and although phylogenetic distances were not enough to detect differences between both environments, they cannot be dismissed for better predictions on assemblages of cerrado and forest communities. Soil was an important factor contributing to the differences in both environments, but, apparently, the role of the abiotic-environmental filter, played by soil nutrient-status, is not the single ecological force in the cerrado and the biotic-interaction filter, limiting similarity, also structures communities in that vegetation type. Thus, accounting for several important traits simultaneously along with phylogenetic distances, we found largely similar sorting mechanisms occurring in the cerrado and in the seasonal forest, despite strong evidence for abiotic-environmental filter in cerrado versus biotic-interaction filter in the seasonal forest when a trait by trait approach was used (Viani *et al.* 2011, Vourlitis *et al.* 2014). Nevertheless, regardless of the role of biotic-interaction filter structuring both cerrado and seasonal forest, our results supported that environment does have an important role in maintaining the functional distinctiveness of the two vegetation types and that shifts in the cerrado-forest boundaries can occur in a predicted scenario of eutrophication in the cerrado (Hunke *et al.* 2015).

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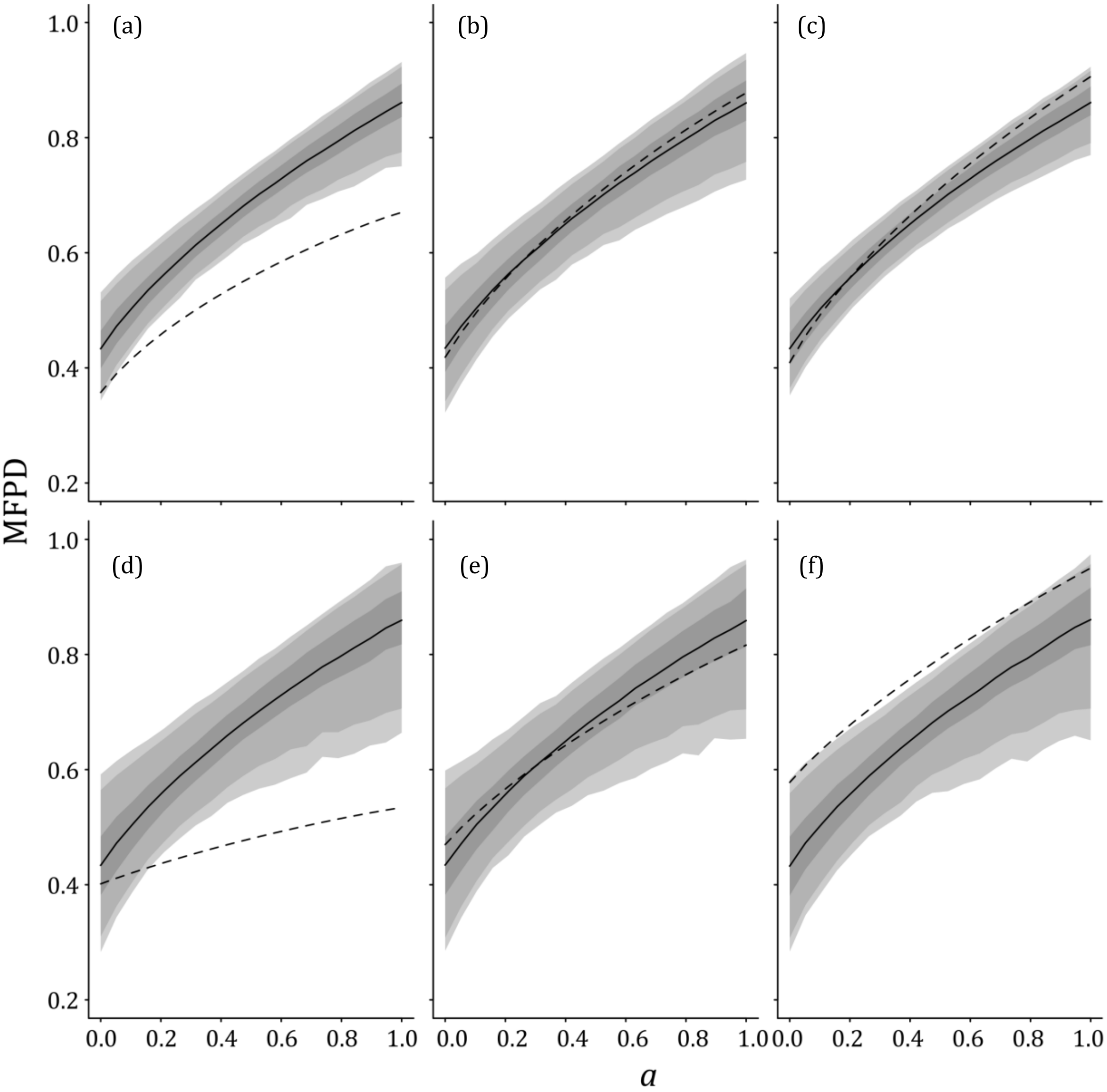
Figure 1. Mean pairwise functional-phylogenetic distances (MFPD) as a function of the weighting parameter a for six communities in the Vaçununga State Park - Brazil (21°41’00’’–21°41’21’’S and 47°34’37’’–47°39’39’’W). (a), (b), and (c) are communities from the cerrado. (d), (e), and (f) are communities from the seasonal forest. Dotted lines represent the observed mean pairwise distances. Dark grey, grey, and light grey shading represents the 50, 90 and 95 confidence intervals of the null distributions. Solid lines represent the average of the null distributions. Species richness are indicated.

Figure 2. Mean pairwise functional-phylogenetic distances (MFPD) as a function of species richness (S) in the 68 communities of cerrado (○) and 32 communities of seasonal forest (■). Dashed lines represent the limits of the null distribution. Different weighting parameters were considered: (a) a-value =0; (b) a -value = 0.5; (c) a-values=1.

Figure 3. Canonical correspondence analysis of the floristic composition of the 68 cerrado (⍰) and 32 seasonal forest (⍰) communities in the Vaçununga State Park (21°36-47’ S and 47°34-41’ W). Soil variables related to both cerrado and seasonal forest communities are indicated. SB = sum of bases, OM = organic matter, CEC = cation exchange capacity, N= total nitrogen, P = available phosphorus, Al = aluminium.

Figure 4. Results of the relationships between MFPD and the first two canonical axes, vegetation types, and the interaction terms as a function of the weighting parameter a. Values are the coefficient of determination of the multiple regression. The maximum R^2_{adj} is obtained at a=0.

Figure 5. MFPD as a function of the first two canonical axes (CCA1 and CCA2) using a-value = 0 (a, b); a-value = 0.5 (c,d); a-value= 1 (e,f) for 100 communities in the Vaçununga State Park - Brazil (21°36-47' S and 47°34-41' W).). White circles represent cerrado communities and grey squares represent seasonal forest communities.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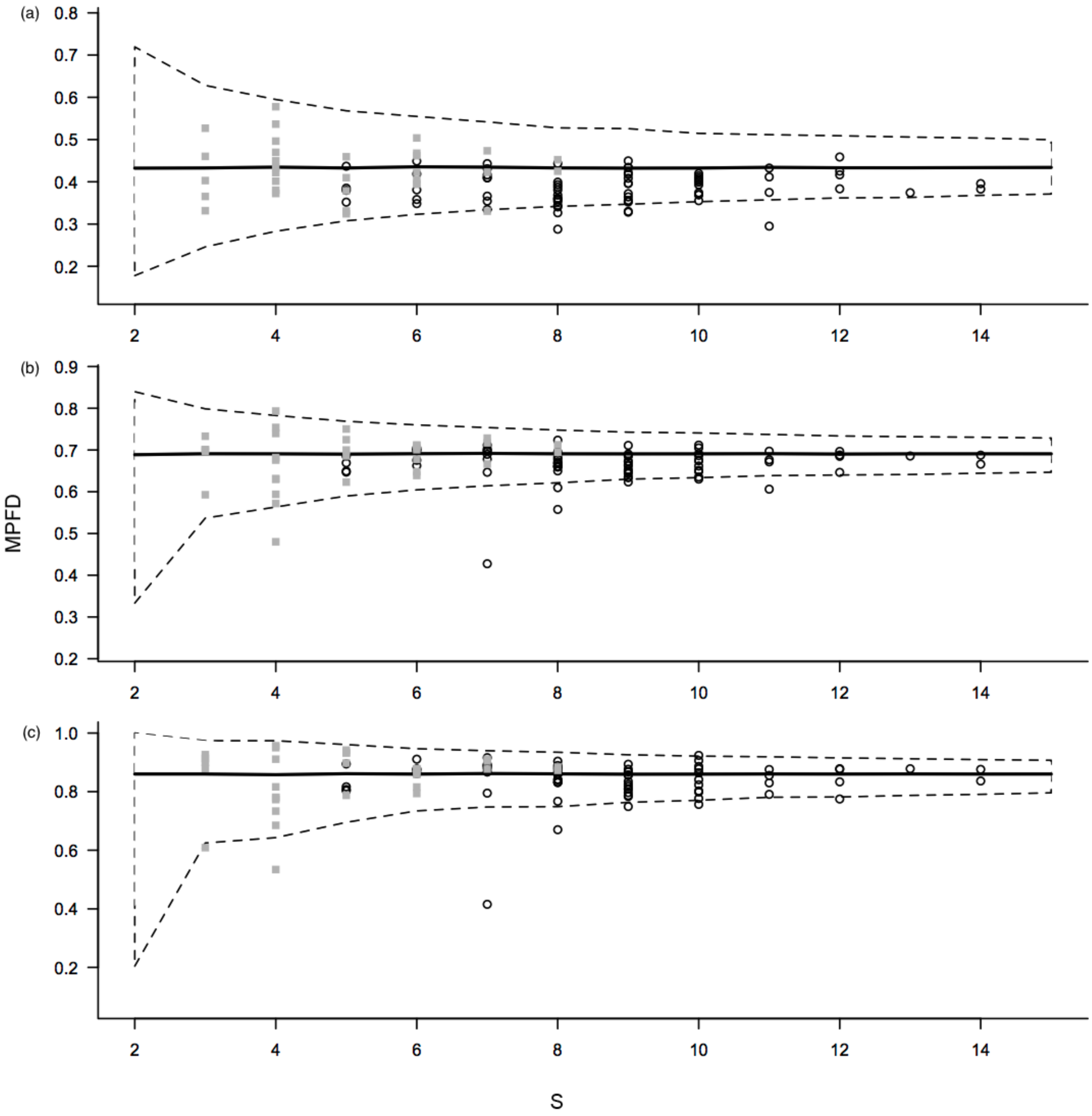
a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14
(b)
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0.8
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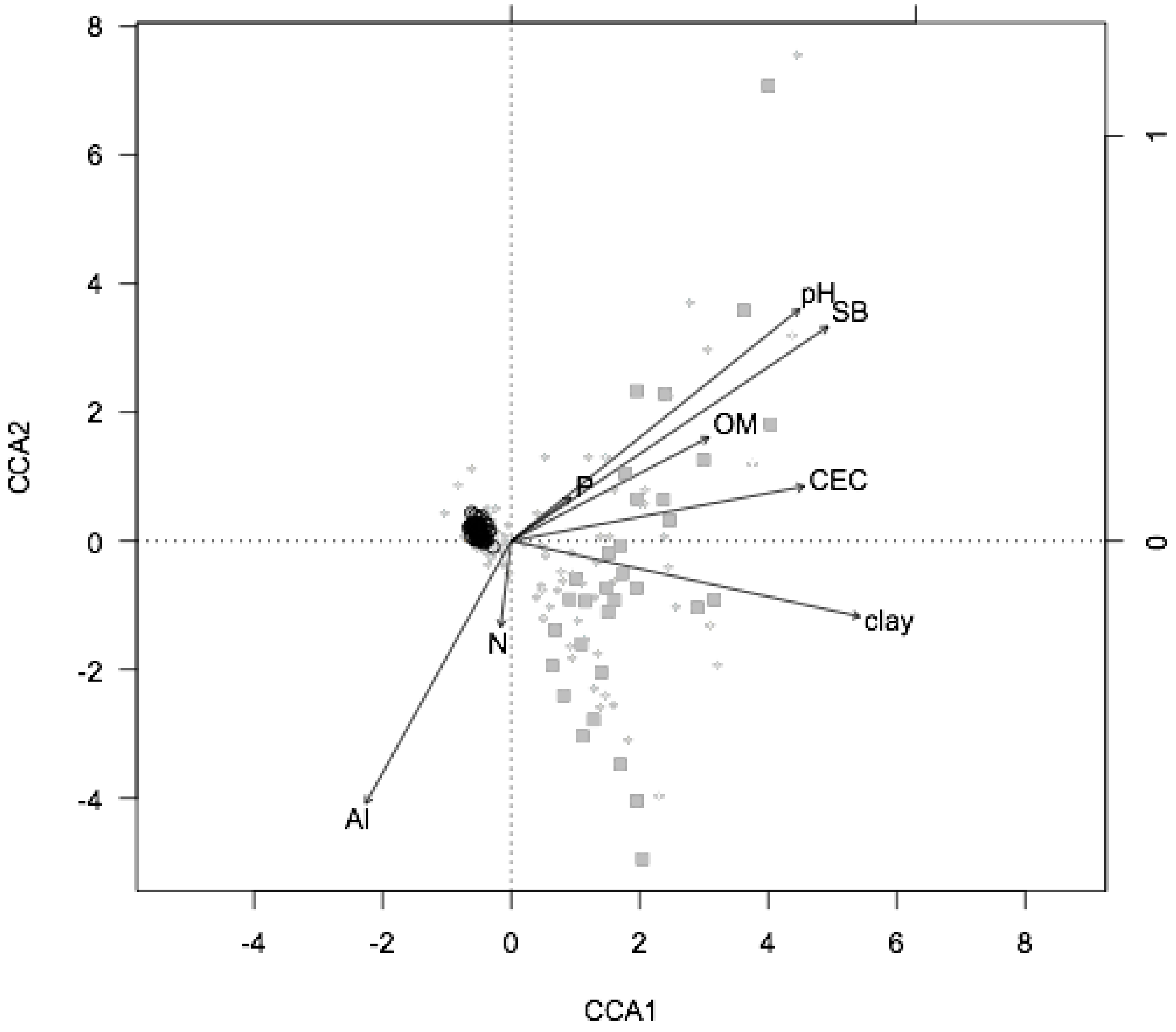
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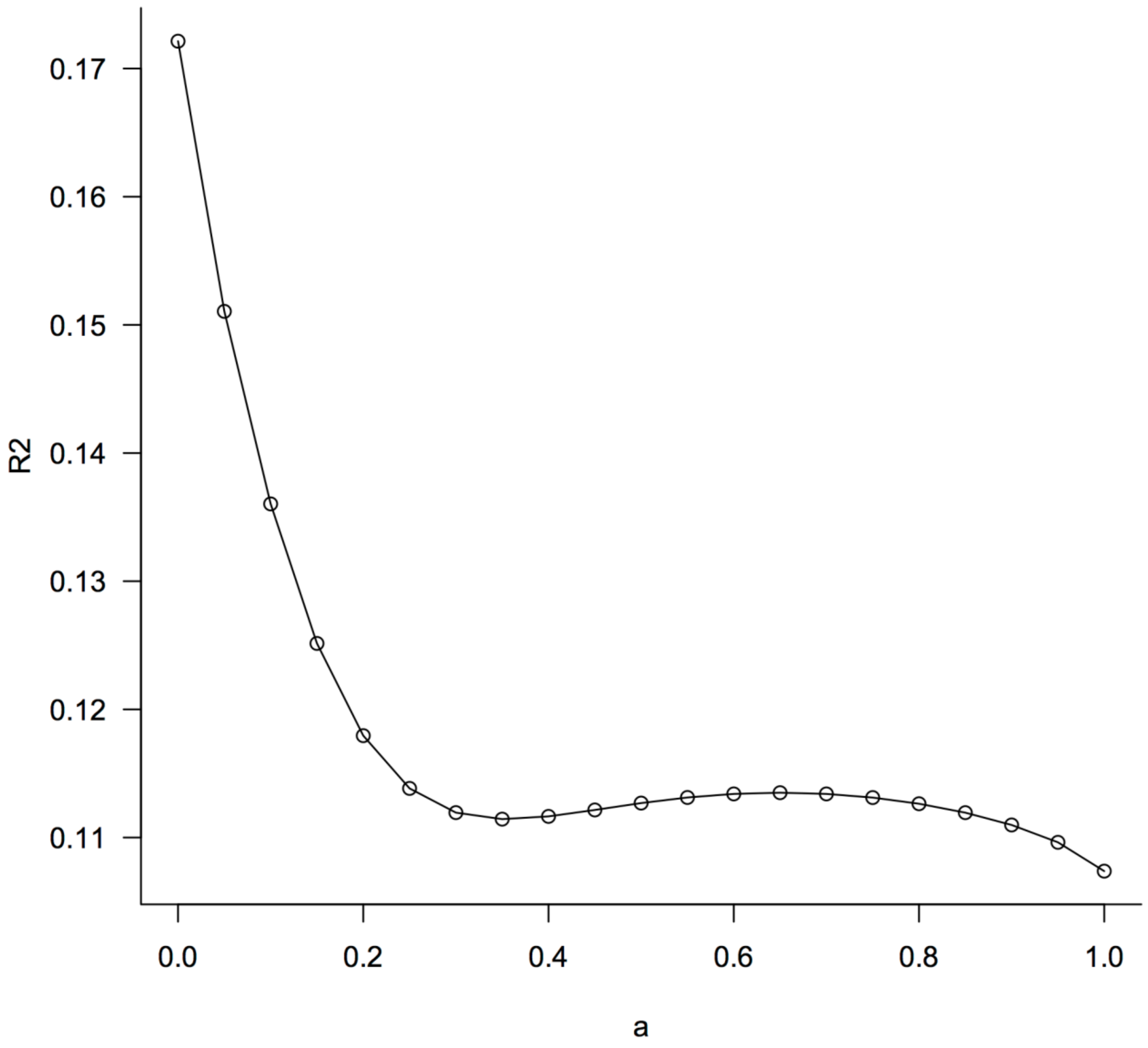
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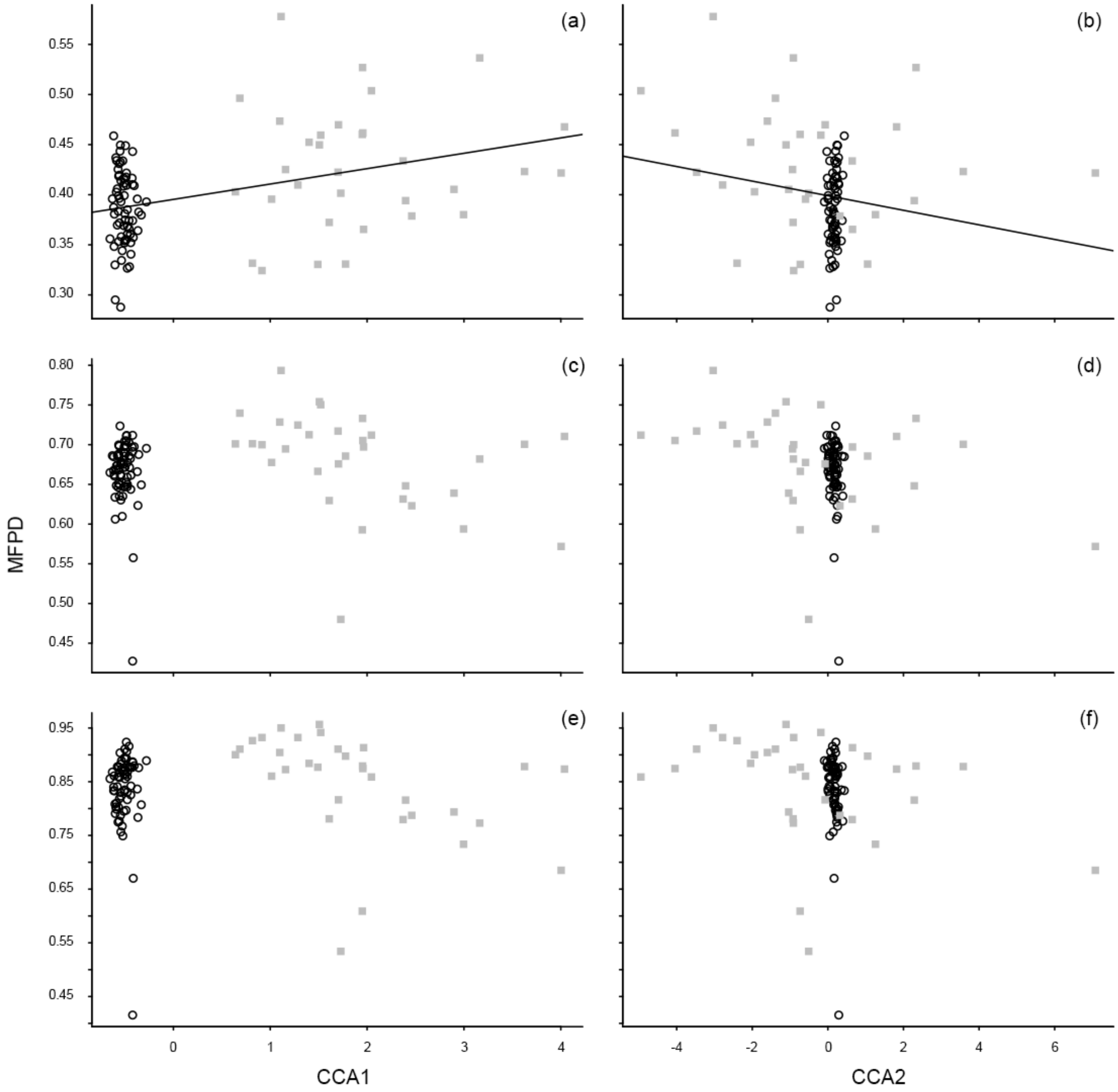
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0.45
0.95
0.85
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0.65
0.55
0.45
MFPD
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1
2
3
4
CCA1
-4
-2
0
2
4
6
CCA2

Table 1. Functional traits and their ecological importance (see Pérez-Haguindeguy et al. 2013 for details).

Functional trait	Unit	Relevance
Basal area	cm	Space occupation, resource occupation, and biomass.
Height	m	Competitive vigour, fecundity, and stress avoidance of stress.
Tortuosity	ratio	Structural reinforcement related to excessive carbon allocation.
Leaf size	cm^2	Leaf energy and water balance, associated with response to resource availability.
Specific leaf area	$cm^2\ g^{-1}$	Resource availability, relative growth rate, and defence.
Leaf dry matter content	$mg\ g^{-1}$	Relative growth rate and litter decomposition.
Leaf toughness	N	Leaf longevity, defence, and carbon allocation.

Table 2. Blomberg’s K (Blomberg et al. 2003) statistics for functional traits.

Functional trait	**K**	**P**
Basal area	0.16	0.303
Height	0.15	0.454
Tortuosity	0.15	0.563
Leaf size	0.12	0.768
Specific leaf area	**0.24**	**0.002**
Leaf dry matter content	0.19	0.075
Leaf toughness	**0.32**	**0.029**

Table 3. Mean functional-phylogenetic distances and standard deviation for three values of the weighting parameter *a*. We used Mann-Whitney test for comparison between the two vegetation types sampled in Vaçununga State Park.

a	**Cerrado**	**Forest**	***P***
0	0.38 ± 0.04	0.43 ± 0.06	< 0.001
0.5	0.67 ± 0.04	0.68 ± 0.06	0.022
1	0.84 ± 0.07	0.84 ± 0.10	0.130

Table 4. P-values of the analyses of covariance between mean pairwise functional-phylogenetic distances as a function of the first two canonical axes (CCA1 and CCA2), vegetation type (type), and the interaction terms when the weighting parameter *a* was set to 0, 0.5, and 1. Significant p-values are in bold.

Term	***a***		
	0	**0.5**	**1**
CCA1	**< 0.001**	0.887	0.387
CCA1	**< 0.001**	0.887	0.387
CCA2	**0.036**	0.103	0.401
Type	0.266	**0.002**	**0.004**
CCA1: Type	0.408	0.785	0.939
CCA2: Type	0.175	**0.034**	**0.011**

Appendix 1. Leaf functional traits of species sampled in cerrado and seasonal forest in the Vaçununga State Park, Brazil (21°36-47' S and 47°34-41' W). BAR = basal area (cm), HEI = height (m), TOR = tortuosity (ratio), TGH = toughness (N), LSZ = leaf size (cm^2), SLA = specific leaf area ($cm^2\ g^{-1}$), DMC = leaf dry matter content ($mg\ g^{-1}$).

Species	Vegetation type	BAR	HEI	TOR	TGH	LSZ	SLA	DMC
Anadenanthera peregrina	Cerrado	1	7.28	0.05	0.17	9	7.05	497.73
Stryphnodendron polyphyllum	Cerrado	61	4.66	0.04	0.28	112	12.37	373.81
Mimosa bimucronata	Forest	38	4.17	0.28	0.17	77	8.87	486.15
Inga vera	Forest	55	15.2	0	0.61	53	7.13	602.11
Senegalia polyphylla	Forest	47	9	0	0.16	10	5.97	455.54
Dimorphandra mollis	Cerrado	74	3	0.04	0.27	104	9.29	432.14
Diptychandra aurantiaca	Cerrado	76	4.12	0.07	0.49	86	13.33	409.85
Machaerium aculeatum	Forest	67	10.5	0	1.07	11	17.91	250.97
Machaerium acutifolium	Cerrado	40	4.62	0.05	0.98	4	10.47	410.36
Platypodium elegans	Cerrado	89	0.55	0.08	0.54	84	12.16	420.49
Dalbergia miscolobium	Cerrado	81	7.44	0.03	0.46	34	12.82	358.82
Andira cujabensis	Forest	95	4.16	0	0.46	62	12.55	344.36
Vatairea macrocarpa	Cerrado	110	3.02	0.04	1.8	21	8.17	437.80
Pterodon pubescens	Both	4	17.6	0.01	0.46	74	9.78	463.32
Bowdichia virgilioides	Cerrado	32	5.44	0.01	0.69	91	8.96	446.12
Hymenaea stigonocarpa	Cerrado	7	4.94	0.04	1.15	46	8.35	450.01
Hymenaea courbaril	Forest	107	7.2	0	0.65	37	12.60	409.87
Copaifera langsdorffii	Both	75	7.75	0.01	0.78	35	12.20	516.63
Bauhinia rufa	Cerrado	99	3.91	0.1	0.87	36	9.08	337.23
Bredemeyera floribunda	Cerrado	12	2.19	0.34	0.52	117	16.36	379.87
Brosimum gaudichaudii	Cerrado	86	4.2	0.04	0.9	6	8.25	343.91
Brosimum guianense	Forest	102	6.25	0.01	0.82	124	12.69	440.29
Urtica dioica	Forest	103	1.53	0.02	0.16	39	31.48	267.08
Actinostemon klotzschii		117	4.21	0.09	0.49	16	22.60	389.03

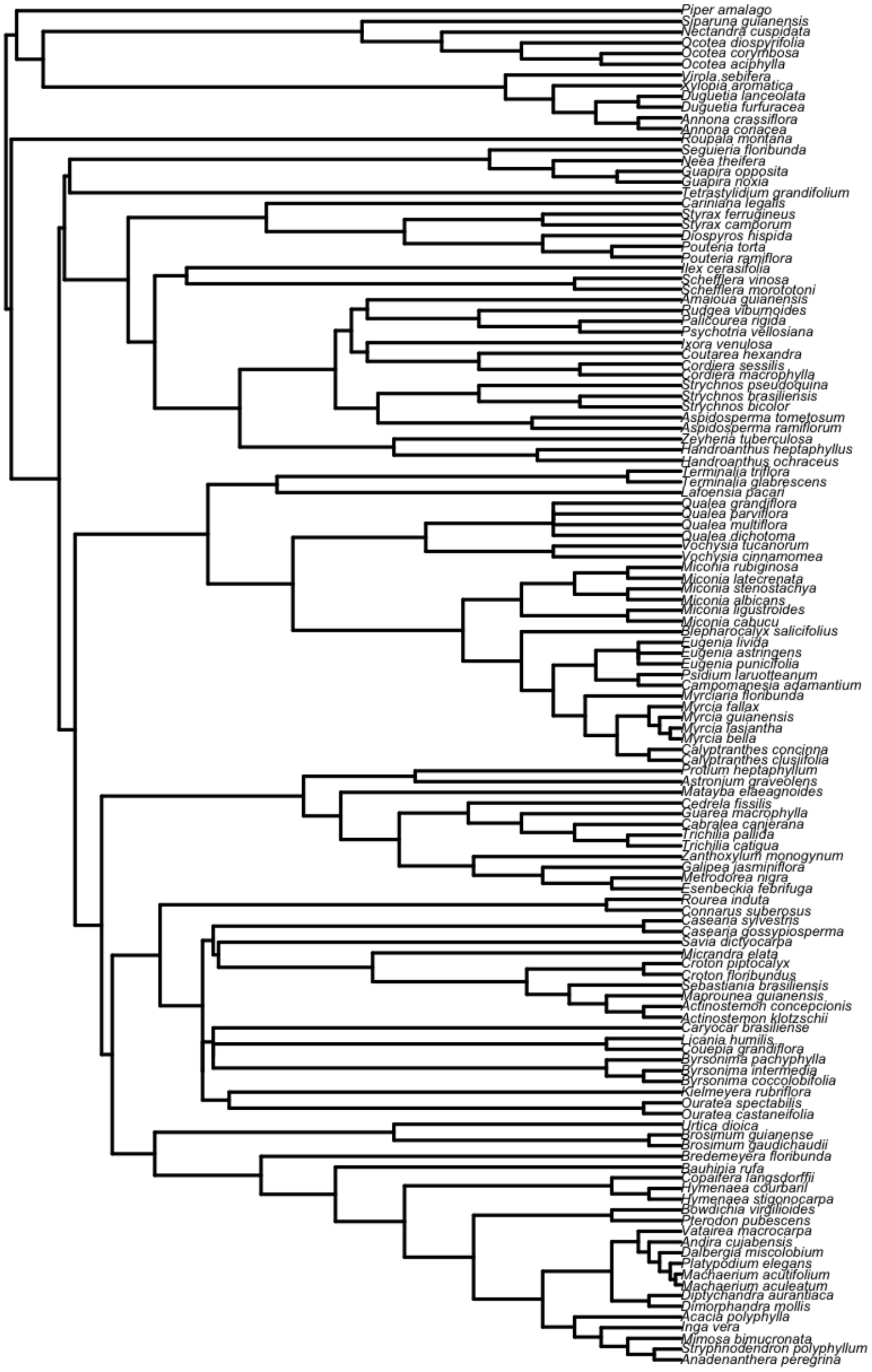
Actinostemon concepcionis	Cerrado	90	3.09	0.16	0.51	20	20.89	421.95
Maprounea guianensis	Forest	36	11.17	0	0.35	99	18.78	317.31
Sebastiania brasiliensis	Forest	8	5.75	0	0.66	113	17.62	464.82
Croton floribundus	Forest	87	8.62	0.04	0.31	13	15.43	299.10
Croton piptocalyx	Forest	114	19.43	0	0.31	81	15.96	266.05
Micrandra elata	Forest	28	10.61	0.01	0.53	63	17.46	412.72
Savia dictyocarpa	Forest	35	7.70	0.01	0.36	5	24.87	373.29
Casearia gossypiosperma	Forest	79	7.63	0	0.36	18	19.97	389.74
Casearia sylvestris	Cerrado	39	5.86	0.04	0.4	126	16.88	449.17
Ouratea castaneifolia	Forest	50	14.8	0	1.28	79	8.88	427.05
Ouratea spectabilis	Cerrado	10	4.91	0.09	2.28	14	6.80	407.95
Kielmeyera rubriflora	Cerrado	48	0.94	0.1	0.32	43	14.18	293.78
Couepia grandiflora	Cerrado	57	4.19	0.11	1.09	97	7.55	445.18
Licania humilis	Cerrado	56	3.52	0.07	1.77	122	6.62	521.18
Byrsonima coccolobifolia	Cerrado	30	3.80	0.07	0.56	103	16.18	358.86
Byrsonima intermedia	Cerrado	14	3.72	0.27	0.48	82	11.47	382.92
Byrsonima pachyphylla	Cerrado	23	3.8	0.26	0.63	48	7.38	439.69
Caryocar brasiliense	Cerrado	62	5.68	0.03	0.32	121	8.15	385.04
Connarus suberosus	Cerrado	100	2.16	0.06	1.87	42	5.57	481.80
Rourea induta	Cerrado	85	1.58	0.14	1.91	93	5.33	506.68
Esenbeckia febrifuga	Forest	73	4.05	0.19	0.36	102	20.73	259.89
Metrodorea nigra	Forest	58	5.42	0.03	0.84	54	17.61	306.77
Galipea jasminiflora	Forest	31	4.47	0.05	0.58	68	17.33	279.25
Zanthoxylum monogynum	Forest	37	17.8	0	0.44	109	22.69	310.8
Trichilia catigua	Forest	2	4.96	0.14	0.47	55	12.61	160.06
Trichilia pallida	Forest	63	7.60	0.06	0.51	72	19.89	337.91
Cabralea canjerana	Forest	96	6.81	0.03	0.51	107	12.99	288.74
Guarea macrophylla	Forest	105	7.32	0.02	0.71	115	14.67	277.19
Cedrela fissilis	Forest	108	7.43	0	0.64	17	13.11	369.50
Matayba elaeagnoides	Forest	88	5.33	0.25	5.56	45	12.06	347.51
Astronium graveolens	Forest	72	10.02	0.1	0.34	88	11.95	388.49
Protium heptaphyllum	Forest	21	9.78	0	0.59	12	12.85	342.21

Calyptranthes clusiifolia	Forest	106	5.46	0.03	1.19	66	8.64	376.98
Calyptranthes concinna	Forest	4	3.22	0.09	0.92	87	18.35	208.12
Myrcia bella	Cerrado	45	1.92	0.08	1.13	111	10.56	415.72
Myrcia lasiantha	Cerrado	77	2.11	0.13	1.54	47	7.14	439.18
Myrcia guianensis	Cerrado	101	2.49	0.13	1.1	105	9.34	359.98
Myrcia splendens	Forest	51	6.42	0.02	0.72	57	12.44	453.86
Myrciaria floribunda	Forest	54	4.12	0.04	0.43	71	18.42	438.35
Campomanesia adamantium	Cerrado	20	2.63	0.04	0.63	25	12.42	426.82
Psidium laruotteanum	Cerrado	113	2.4	0.07	1.35	123	5.73	448.04
Eugenia astringens	Forest	42	10.79	0	0.84	100	18.40	400.05
Eugenia livida	Cerrado	9	1.46	0.08	1.32	89	7.91	442.87
Eugenia punicifolia	Cerrado	71	3.46	0.06	0.85	101	15.47	311.59
Blepharocalyx salicifolius	Forest	109	5.15	0.04	0.66	49	14.28	436.6
Miconia cabucu	Forest	13	4.81	0.06	0.4	40	17.16	266.64
Miconia ligustroides	Cerrado	64	1.89	0.11	0.33	3	11.69	377.11
Miconia albicans	Cerrado	34	2.14	0.14	0.55	96	8.07	466.40
Miconia stenostachya	Cerrado	15	2.91	0.15	0.74	20	4.93	511.04
Miconia latecrenata	Forest	60	7.90	0.01	0.35	120	15.95	282.2
Miconia rubiginosa	Cerrado	111	2.33	0.07	0.59	27	7.99	471.12
Vochysia cinnamomea	Cerrado	91	4.00	0.12	1.16	26	6.38	373.51
Vochysia tucanorum	Cerrado	97	2.07	0.09	0.91	61	12.10	265.44
Qualea dichotoma	Cerrado	53	2.57	0.04	0.75	92	14.01	329.84
Qualea grandiflora	Cerrado	115	6.40	0.03	0.81	85	9.71	382.25
Qualea multiflora	Cerrado	11	4.98	0.05	0.49	110	14.17	328.26
Qualea parviflora	Cerrado	112	3.63	0.07	0.5	19	14.15	380.11
Lafoensia pacari	Cerrado	33	1.99	0.11	0.38	90	13.58	411.44
Terminalia glabrescens	Forest	19	7.09	0	0.66	118	11.93	358.14
Terminalia triflora	Forest	83	4.92	0.01	0.37	108	28.52	274.29
Handroanthus ochraceus	Cerrado	90	1.13	0.11	0.68	75	10.80	381.13
Handroanthus heptaphyllus	Forest	111	11.8	0	1.44	23	8.15	365.49
Zeyheria tuberculosa	Forest	23	11.1	0	0.54	32	7.8	441.71
Aspidosperma ramiflorum	Forest	90	5.17	0.06	0.9	15	15.69	344.82

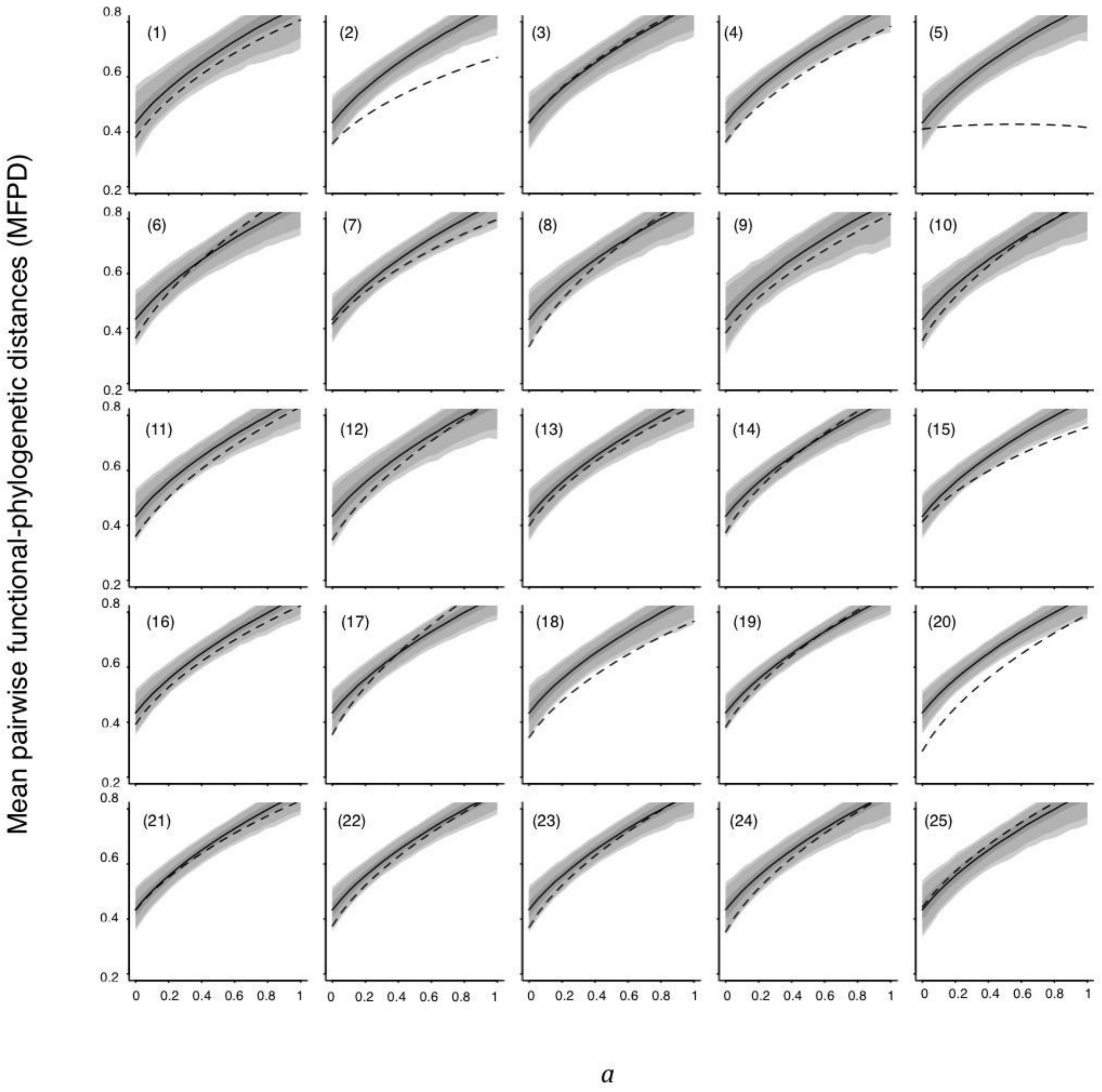
Aspidosperma tometosum	Cerrado	16	2.79	0.04	0.56	106	9.07	339.6
Strychnos bicolor	Cerrado	82	3.26	0.09	0.41	70	14.83	474.23
Strychnos brasiliensis	Cerrado	23	2.38	0.24	0.42	52	15.18	457.87
Strychnos pseudoquina	Cerrado	50	2.6	0.24	0.55	50	8.66	486.51
Cordiera macrophylla	Forest	6	4.05	0.04	0.57	69	17.56	273.68
Cordiera sessilis	Cerrado	78	1.94	0.05	0.68	51	15.79	274.1
Coutarea hexandra	Forest	17	15.7	0.05	0.25	64	20.11	312.47
Ixora venulosa	Forest	69	7.11	0.22	0.92	8	14.08	386.05
Psychotria vellosiana	Forest	22	2.35	0.14	0.35	98	30.46	299.47
Palicourea rigida	Cerrado	41	1.55	0.22	0.87	28	14.10	214.7
Rudgea viburnoides	Cerrado	46	2.50	0	0.97	1	9.93	218.46
Amaioua guianensis	Forest	65	7.85	0	0.54	33	11.05	399.17
Schefflera morototoni	Forest	4	10.01	0	0.59	78	5.98	377.88
Schefflera vinosa	Cerrado	44	2.13	0.25	0.73	116	7.61	422.00
Ilex cerasifolia	Forest	70	4.77	0.05	0.53	30	20.16	369.69
Pouteria ramiflora	Cerrado	43	5.72	0.06	0.64	119	9.11	409.01
Pouteria torta	Cerrado	66	4.97	0.01	0.76	114	9.44	379.46
Diospyros hispida	Cerrado	68	2.91	0.04	0.5	24	9.49	327.55
Styrax camporum	Cerrado	49	3.35	0.06	0.92	59	6.70	422.74
Styrax ferrugineus	Cerrado	94	3.61	0.04	1.51	76	8.17	489.11
Cariniana legalis	Forest	80	4.29	0	0.58	22	13.84	457.21
Tetrastylidium grandifolium	Forest	5	7.12	0	0.73	65	15.2	291.84
Guapira noxia	Cerrado	84	2.44	0.04	0.87	41	12.64	271.04
Guapira opposita	Both	92	4.01	0.07	0.71	29	16.26	291.53
Neea theifera	Cerrado	27	2.84	0.12	0.75	60	18.41	150.35
Seguieria floribunda	Forest	76	4.95	0.08	0.57	7	17.91	281.27
Roupala montana	Both	98	2.11	0.06	1.16	67	7.73	466.34
Annona coriacea	Cerrado	116	3.54	0.09	2.28	95	8.00	340.25
Annona crassiflora	Cerrado	93	4.56	0.04	0.76	2	10.42	359.09
Duguetia furfuracea	Cerrado	25	1.91	0.72	1.47	58	6.92	531.87
Duguetia lanceolata	Forest	59	10.56	0	0.77	31	12.9	369.20
Xylopia aromatica	Cerrado	52	5.47	0.01	0.68	44	10.3	422.20

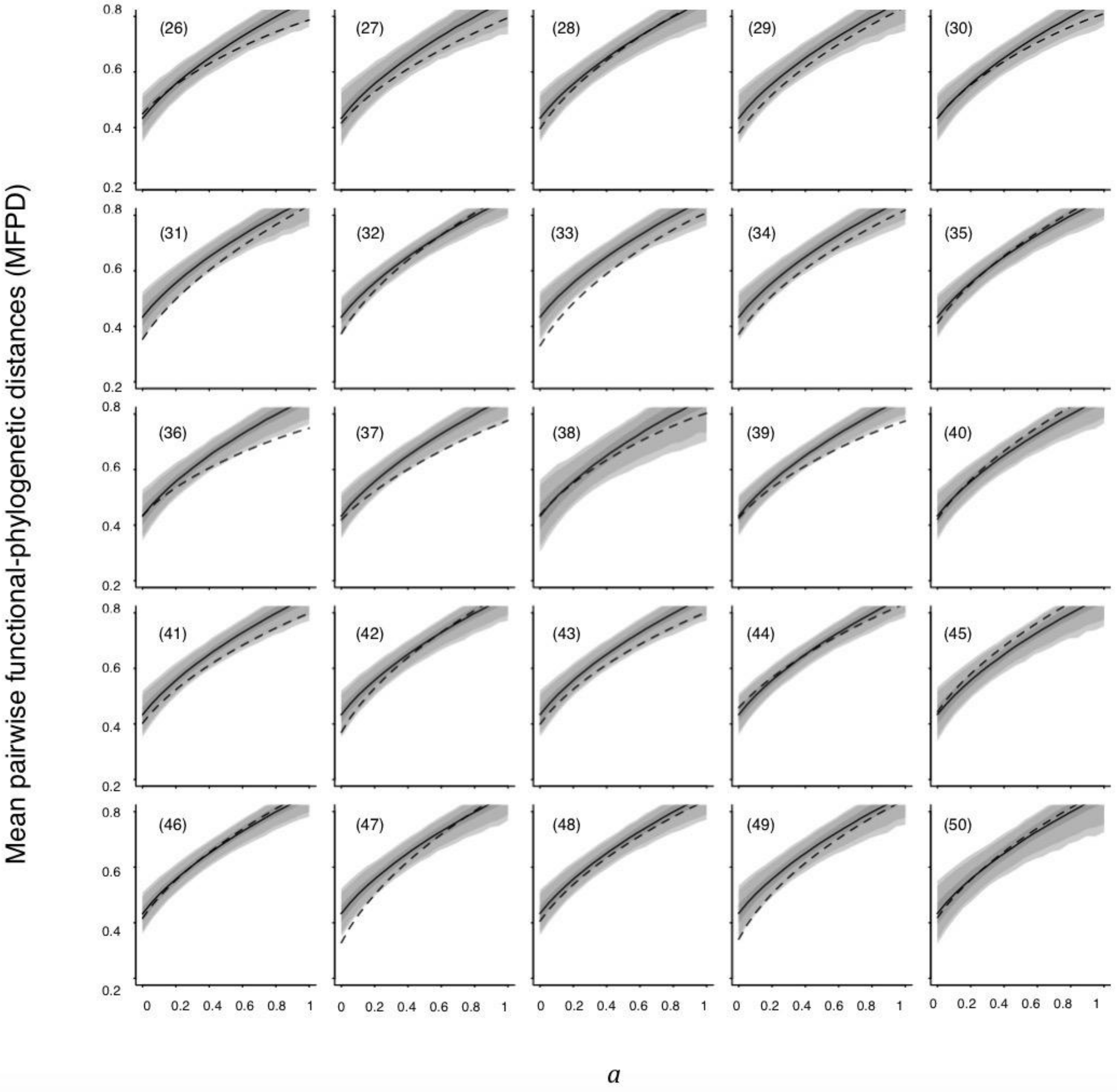
Virola sebifera	Both	18	7.33	0	0.73	83	8.96	374.40
Ocotea aciphylla	Forest	104	9.3	0	0.7	56	12.28	420.43
Ocotea corymbosa	Both	26	8.47	0.01	0.71	38	12.65	430.73
Ocotea diospyrifolia	Forest	3	7.66	0.02	0.92	125	11.93	435.26
Nectandra cuspidata	Forest	29	14.87	0	0.64	94	9.91	445.45
Siparuna guianensis	Both	76	4.58	0.03	0.7	73	16.59	273.22
Piper amalago	Forest	24	4.39	0.14	0.41	80	27.5	223.61

Appendix 2. Phylogenetic tree of the species found in 100 communities in the Vaçununga State Park - Brazil (21°36-47' S and 47°34-41' W).



Appendix 3. Mean pairwise functional-phylogenetic distances (MPFD) of the communities 1 to 25, 26 to 50, 51 to 68, and 69 to 100 as a function of the weighting parameter *a* in the Vaçununga State Park (21°36-47’ S and 47°34-41’ W). The dotted lines show the observed mean pairwise distances. The dark grey, grey, and light grey polygons represent, respectively, the 50%, 90%, and 95% confidence intervals of the null distributions, with their averages indicated by the solid lines.




Mean pairwise functional-phylogenetic distances (MFPD)
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1
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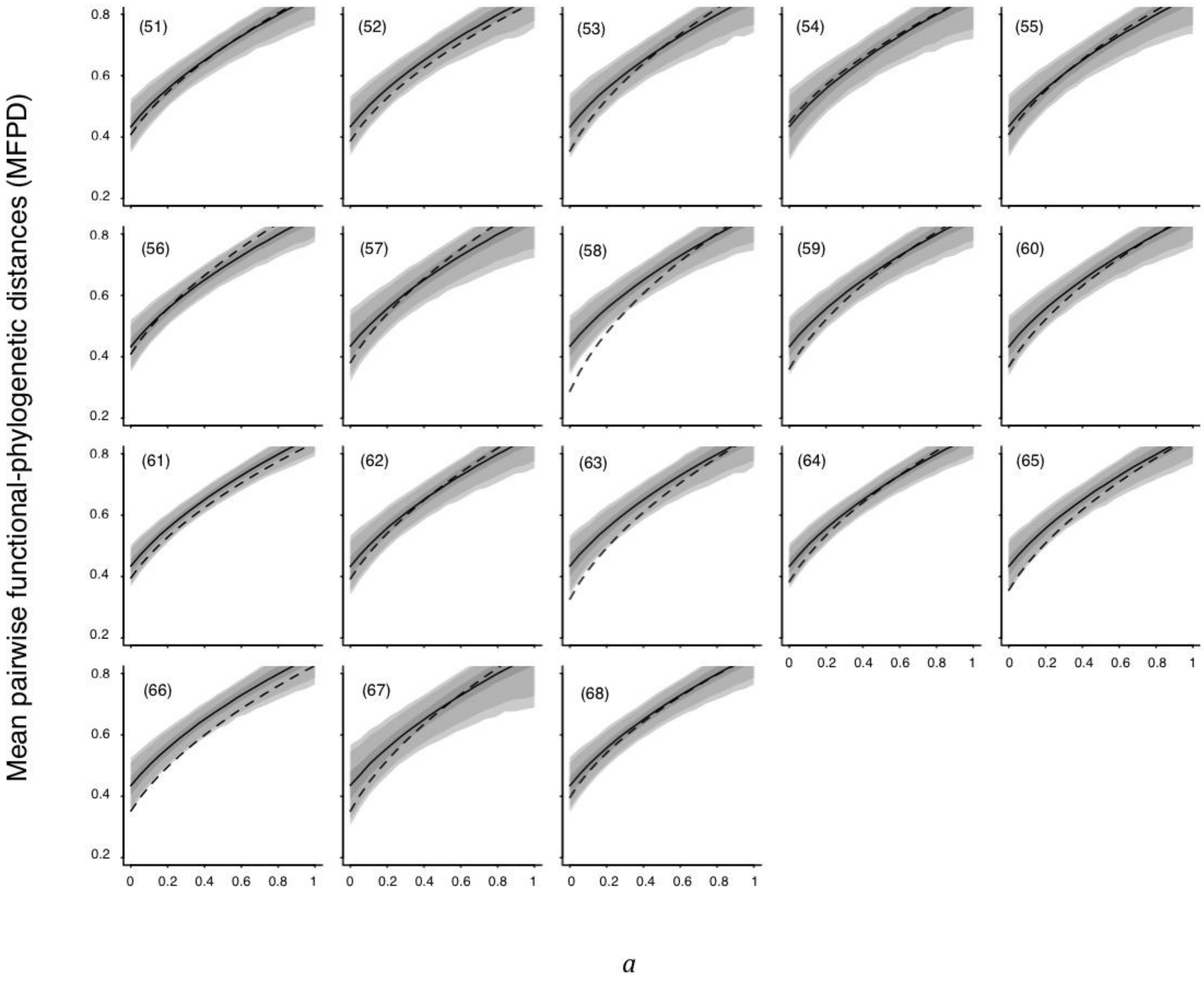
Mean pairwise functional-phylogenetic distances (MFPD)
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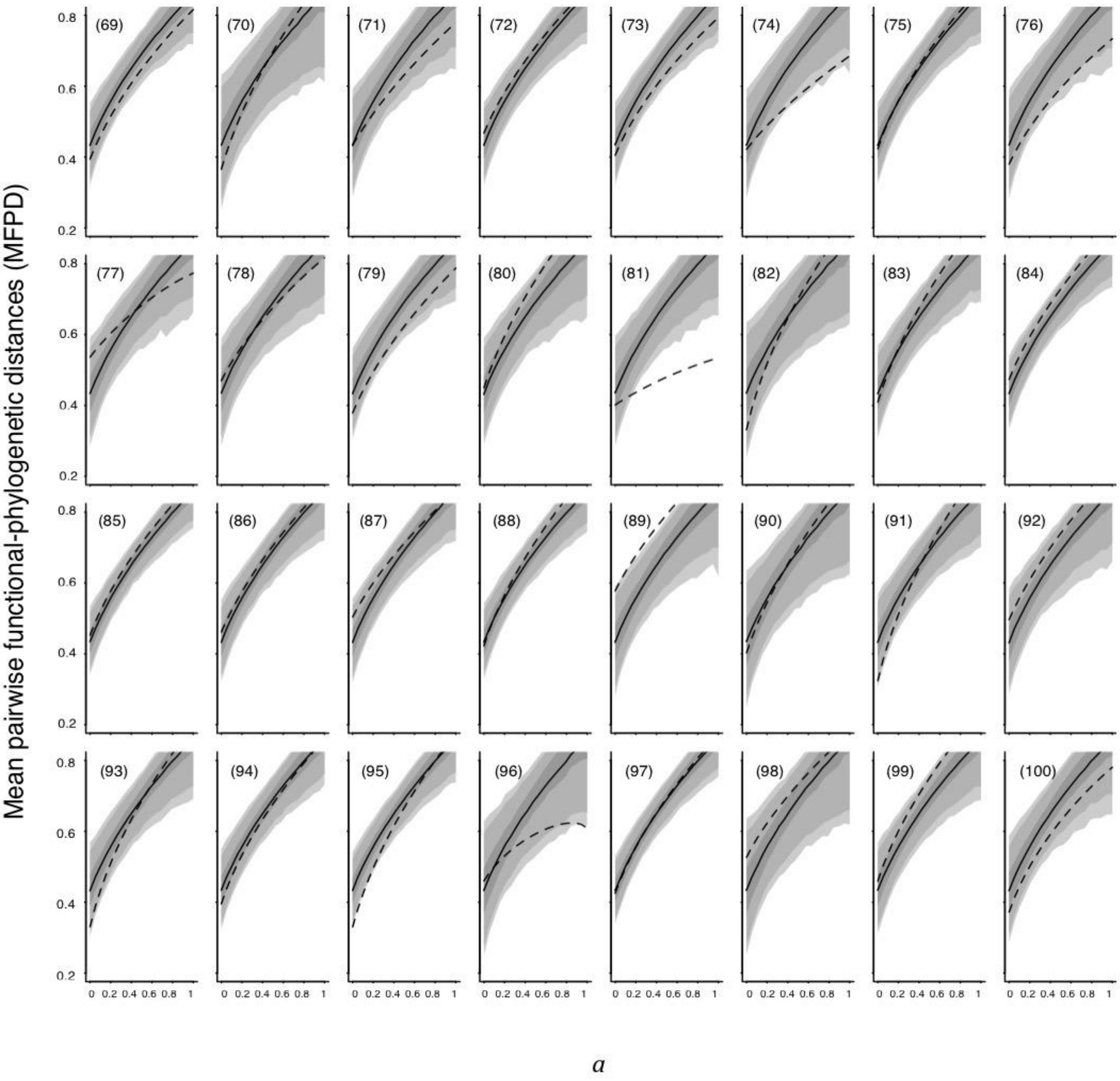
Mean pairwise functional-phylogenetic distances (MFPD)
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IV - Capítulo 3

Artigo submetido para a revista *Plant Ecology*

Leaf chemistry of woody species in the Brazilian cerrado and seasonal forest: responses to soil and taxonomy and effects on decomposition rates

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Abstract - The Brazilian cerrado occurs interspersed with the semi-deciduous seasonal forest, and soil fertility is considered the main determinant of the abrupt transitions between both vegetation types. We aimed to study patterns across chemical traits of green leaves in 121 cerrado and seasonal forest woody species from south-eastern Brazil, their response to soil nutrient status, and their effects on decomposition rates. We compared leaf traits of both cerrado and forest species and constructed multilevel models to account for partitioning of variance in each trait. We calculated the community-weighted mean of each trait to assess their response to soil nutrient status and their effects on decomposition rates. Most of the traits were significantly correlated among themselves, with cerrado species having lower nutrient concentrations than the seasonal forest. Taxonomy accounted for 52% of the total variance in leaf traits, whereas vegetation type accounted for 19%. All leaf traits but manganese and aluminium were significantly related to soil properties. The best model to predict the decomposition rates included leaf nitrogen, phosphorus, and zinc. Even with a large effect of taxonomy on leaf nutrient-related traits, soil exerted an important role on the traits. Strategies of both cerrado and seasonal forest woody species were carried out through multi-element soil control. The effect of such different strategies on functioning was, however, less prominent.

Key words: biogeochemical niche, decomposition, nutrient availability, savanna, tea bag index, tropical forest.

Introduction

The occurrence of savannas and forests adjacent to each other is a common phenomenon in tropical regions around the world (Warman et al. 2013). Apart from the climate (Archibold 1995), several factors have been proposed to explain these abrupt transitions, such as fire regimes, hidrology, herbivory, and soil fertility (Murphy and Bownman et al. 2012). In Brazil, the Central Plateau is covered by the cerrado vegetation, whose physiognomies go from grassland, through savannas, to tropical forest, in a gradient of fertility (Coutinho 1990). Very often, the cerrado vegetation occurs interspersed with the semi-deciduous seasonal forest (Coutinho 1990). The cerrado persists even when it could be replaced by the seasonal forest, considering only the climate. Even if fire and water stress contribute to the cerrado occurrence and its physiognomic gradient, soil fertility is considered the main determinant of such abrupt transitions (Goodland and Pollard 1973, Coutinho 1990). Whereas the cerrado is usually found on nutrient-poor, aluminium-rich, and sandy soils, the seasonal forest usually occurs on nutrient-rich, aluminium-poor, clayey soils, mainly derived from sandstones or volcanic rocks (Ruggiero et al. 2002, Durigan and Ratter 2006).

Soil is the biggest reservoir and provider of several chemical elements that sustain plant communities (Epstein and Bloom 2005). Soil nutrient availability determines plant growth rate, carbon allocation strategies, leaf nutritional content, and other key traits related to plant development (Wardle et al. 2004). Plants, in turn, regulate the vertical nutrient availability in soil through element cycling via litterfall or direct leaching from leaves and uplifting demand (Wardle el al. 2004). According to the "nutrient uplifting theory" (Jobbágy and Jackson 2001), the nutrients plants depend on the most are found in the upper soil layers in a continuous plant-soil feedback.

Besides being important for biogeochemical cycling, plant chemical traits drive physiological processes and actively regulate community functioning, affecting species interaction with competitors, consumers, and decomposers (Reich 2005, Han et al. 2011, Zhang, et al. 2012). Although great importance has been given to soil nitrogen and phosphorus (Reich 2005, Han et al. 2005), other elements are also critical for plant physiology. For instance, leaf potassium, calcium, and magnesium have been pointed out as important determinants of one axis of plant specialisation, correlated to rapid growth (Grime 1977, Wright et al. 2005). Lower concentrations of these elements in foliar tissue, in turn, tend to be associated to an opposite specialisation, towards nutrient retention under unproductive conditions, with low palatability, high toughness, and long-lived leaves (Craine 2009).

Similar to macronutrients, micronutrients, such as manganese, zinc, iron, cooper, and boron, are essential for plant functioning (Hänsch and Mendel 2009). They are mainly involved in protein synthesis, photosynthesis, cell structure, and enzymatic activity, affecting metabolism regulation, cell protection, growth, and reproduction (Hänsch and Mendel 2009, Zhang et al. 2012). Micronutrients may also affect community functioning, limiting litterfall, decomposition, and productivity (Kaspari et al. 2008, Powers and Salute 2011). For instance, manganese acts on enzymatic activation and phosphorus uptake; zinc plays an important role in protein and enzyme syntheses; iron is important for protein synthesis and for respiration; cooper acts on both photosynthesis and respiration, regulating carbon and nitrogen metabolism; and boron is important for protein synthesis, sugar transport, and nitrogen fixation (Hänsch and Mendel 2009, Lambers et al. 2014). Not only do micronutrients regulate plant metabolism and functioning (Hänsch and Mendel 2009), but they also influence litter decomposition rates by regulating the decomposer metabolism (Powers and Salute 2011).

The need to consider the effect and response of multiple elements in plant communities has been gaining recognition in terrestrial plant ecology (Asner and Martin 2011, Townsend et al. 2011, Han et al. 2011, He et al. 2015, Zhao et al. 2016). However, up to now, few studies in the cerrado and the semi-deciduous seasonal forest have considered leaf chemical elements other than nitrogen or phosphorus (Vourlitis et al. 2014, Viani et al. 2014). In fact, micronutrients have hardly been taken into account in these two vegetation types (Viani et al. 2014). Due to its high richness, high degree of endemism, and conservation status, the cerrado is among the world's hotspot for biodiversity conservation (Myers et al. 2000). The few remaining cerrado areas, most of them surrounded by an agricultural matrix, are susceptible to eutrophication (Hunke et al. 2015). Consequently, their floristic composition can be altered, and shifts in cerrado-forest transition can occur with changes in nutrient availability (Miatto et al. 2016). Understanding how plastic in their chemical traits and how tightly related with community functioning cerrado and forest species are may help us to predict whether the cerrado will be replaced by the seasonal forest in a future scenario of eutrophication.

We aimed to study patterns in chemical traits of green leaves in both cerrado and seasonal forest woody species, in their response to soil nutrient status, and in their effects on decomposition rates. More specifically, we aimed (1) to compare leaf chemical traits in cerrado and forest species; (2) to partition the variation in leaf properties into taxonomic, environmental, and residual components; (3) to test to which extent soil features influence leaf properties in the cerrado and in the seasonal forest; (4) to test the effects of community-level leaf chemical traits on litter decomposition rates. We expected that (1) cerrado species would have lower nutrient content and higher aluminium content as a consequence of their impoverished soils (Ruggiero et al. 2002); (2a) nutrients that are required in highest concentrations, nitrogen and phosphorus, would be less sensitive to vegetation type and soil nutrient-status, following the "stability of limiting nutrient" theory (Han et al. 2011); (2b) both vegetation type and taxonomy would influence other leaf traits (Fyllas et al. 2009, Zhang et al. 2012); (3) leaf traits would respond to soil nutrient status in both vegetation types (Vitousek and Farrington 1997, Fyllas et al. 2009); and (4) leaf nutrients would predict decomposition rates (Bakker et al. 2011).

Methods

We carried out this study in the Vaçununga State Park, Santa Rita do Passa Quatro municipality, São Paulo state, south-eastern Brazil (21°41’00’’–21°41’21’’S and 47°34’37’’–47°39’39’’W). The park is at 590-740 m above sea level. Regional climate is classified as Cwa, with wet summers and dry winters (Köppen 1931). Annual rainfall lies around 1,500 mm, concentrated from November to April, and mean annual temperature is 21.5°C. The park embraces 2,071 ha, of which 1,192 ha are covered by cerrado and 578 ha are covered by seasonal forest (Ruggiero et al. 2002). Soils are mainly Neosols and Latosols, according to the Brazilian classification system (Embrapa 2012), or Entisols and Oxisols, according to the USDA classification system (Soil Survey Staff 2014).

We established 100 25 m^2 plots across all the areas that were accessible to researchers. We placed the plots using a random stratified sampling (Krebs 1998; Sutherland 2006), taking into account the proportion covered by each vegetation type. Thus, we placed 68 plots in the cerrado and 32 plots in the seasonal forest. In each plot, we sampled all the individuals belonging to the woody component, defined as those woody individuals with stem diameter at the soil level equal to or higher than 3 cm (SMA 1997). We identified the individuals to species level, comparing the collected material to vouchers lodged at the Botanical Institute of São Paulo herbarium or using identification keys based on vegetative characters (Batalha et al. 1998; Batalha and Mantovani 1999). We randomly selected 5-10 individuals of each species to be sampled. For species with less than five individuals, we made an additional effort, looking for other individuals close to the plots and trying to reach five individuals per species. From the 121 species we sampled for nutrient analyses, 60 occurred exclusively in the cerrado, 55 occurred exclusively in the seasonal forest, and six occurred in both vegetation types.

In the wet season, from October 2013 to April 2014, we collected five green leaves from the selected individuals. We placed the leaves in plastic bags, put them in a thermal box, and took them to the laboratory. We sent dried samples of 2 g each to the Luiz de Queiroz College of Agriculture, at the University of São Paulo, where micro- and macronutrient, as well as aluminium, concentrations were determined. In each plot, we collected soil samples to 5 cm deep and sent them to the Luiz de Queiroz College of Agriculture, for determination of pH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminium, sum of bases, base saturation, aluminium saturation, cation exchange capacity, and sand, silt, and clay content (see Miatto et al. 2016 for more details).

To obtain the decomposition rate in each plot, we calculated the Tea Bag index by using green and rooibos tea bags (Keuskamp et al. 2013). In January 2014, we buried two bags of green tea and two bags of rooibos tea per plot. After three months, we dug up the tea bags, removed adhered soil particles, and dried them in a stove for 48h at 70°C. Then, we removed the label and left the string, weighed the bag, and subtracted the mass of an empty bag without the label to determine the mass after incubation. After having the initial and final mass of each bag, we calculated the decomposition rate (k), using a modified version of the classical decomposition equation of Wieder and Lang (1982): $W(t) = ae^{-kt} + (1 - a)$, in which W(t) was the mass of the substrate after incubation time t, a was the labile, and $1 - a$ was the recalcitrant fraction of the litter. This modified equation assumes that "during a short field incubations, mass loss of the recalcitrant fraction is negligible" (Keuskamp et al. 2013).

After measuring specific leaf area and obtaining the chemical results for all samples, we calculated average values of each leaf trait per species and log-transformed the data to reach normality. First, we applied Pearson correlation tests to test whether leaf traits were correlated to each other. Then, we tested for differences in leaf traits between cerrado and forest species with a t-test. To account for partitioning of variance in each leaf trait, we applied a multilevel model as proposed by Fyllas et al. (2009):

$$T = \mu + v + f/g/s + \varepsilon,$$

in which μ was the mean value for trait T, v was the vegetation type effect, $f/g/s$ represented the taxonomic hierarchy effect in the data, since each individual belonged to a species s that belonged to a genus g that belonged to a family f, and ε was the residual effect, which represented both within species variability and measurement error. For each trait, we had a multilevel model. To test the significance of each component for each model, we constructed new models without a given component (family, genus, species, or vegetation type) and compared these models with the complete one by using an analysis of variance and a likelihood ratio test.

To obtain the community-weighted mean for each trait, we calculated mean trait values of each species present in the community weighted by its relative abundance (Garnier et al. 2004). In addition, to summarise the dimensions of the leaf trait matrix, we conducted a principal component analysis with the leaf trait data, standardising the traits by their ranges. Then, we used species scores of the first axis to calculated a community-weighted "general leaf trait". To account for the influence of soil fertility on leaf components, we conducted a principal component analysis with soil data, excluding variables that were strongly correlated to others (Pearson's r > |0.70|). We then used the first two principal components as a measure of soil fertility (Miatto et al. 2016). We did analyses of covariance, using the community-weighted mean of each trait as response variable and the first two principal components of soil data and vegetation type as explanatory variables. Similarly, we also did a covariance analysis using the community-weighted general leaf trait as response variable and the first two principal components of soil data and vegetation type as explanatory variables.

To test whether cerrado and seasonal forest leaf nutrient content would affect decomposition rates, we did an analysis of covariance, using the tea bag decomposition rate as response variable and the community-weighted mean of each leaf trait and the community-weighted general leaf trait, along with vegetation type, as explanatory variables. We selected the best model, using the Akaike Information Criterion. We carried out the analyses in the R environment (R Core Team 2015), using the lme4 (Bates et al. 2014), vegan (Oksanen et al. 2014), FD (Laliberté and Legendre 2010), and Hmisc (Harrell Jr et al. 2015) packages.

Results

Most of the leaf traits were weakly but significantly correlated among themselves (Table 1). The only strong correlation was between magnesium and calcium (R = 0.76). Aluminium was weakly but significantly correlated only with zinc (R = 0.18) and iron (R = -0.19). Manganese was not correlated with any other trait (Table 1). Most of the trait values – nitrogen, phosphorus, potassium, calcium, magnesium, boron, copper, zinc, and iron – were lower in the cerrado than in the seasonal forest (Table 2). Manganese, sulphur, and aluminium concentrations did not differ between the two vegetation types (Table 2).

According to the multilevel model fitted for each leaf trait, vegetation type accounted for an average of only 19% of the total variance in leaf traits, whereas the taxonomic component – from family to species – accounted for an average of 52%. The residual effect, which represents the proportion of variance attributed to intraspecific variability or any other systematic font of error, accounted for an average of 28% of the total variance. Vegetation type accounted for a significant proportion of the variance for nitrogen, potassium, calcium, magnesium, boron, zinc, and iron (Figure 1). Family accounted for a significant proportion of the variance for phosphorus, potassium, and calcium; genus, for nitrogen; and species, for copper (Figure 1). Sulphur, aluminium, and manganese had no significant component of variance (Figure 1).

The first axis of the principal component analysis carried out with leaf traits explained 34.4% of the variation and was related to all traits, except aluminium (Figure 2). The second axis of the principal component analysis explained 13.6% of the variation in leaf traits and was mostly correlated to aluminium concentration (Figure 2).

Soil ordination was divided in two axis of fertility. The first one, explaining 48% of the variation, was related to clay content, pH, cation exchange capacity, organic matter, and sum of bases, being considered a general index of soil fertility (Miatto et al. 2016). The second one, explaining 18% of the variation, was positively related to total nitrogen and aluminium and negatively related to available phosphorus (Miatto et al. 2016). All leaf traits but manganese and aluminium were significantly related to the first axis of the principal component analysis carried out with soil data and to vegetation type (Table 3). Conversely, only copper was significantly related to the second axis of the principal component analysis carried out with soil data (Table 3).

When we considered all leaf traits and vegetation type together, we could not predict decomposition rate ($R^2_{adj} = 0.06, P = 0.14$). The best model was that with nitrogen, phosphorus, and zinc as explanatory variables ($R^2_{adj} = 0.11, P = 0.003$). Decomposition rates ranged from 0.004 to 0.043 g g^{-1} d^{-1} in the cerrado and from 0.003 to 0.045 g g^{-1} d^{-1} in the seasonal forest. Decomposition rates varied more as a function of the green leaf nutrient concentrations in the cerrado than in the seasonal forest (Figure 3).

Discussion

Except for aluminium and manganese, leaf chemical traits were positively related to each other. Plants have basically the same requirements for nutrients devoted to growth and survival (Westoby et al. 2002). Besides, the assimilation and use of multiple elements are not independent (Zhao et al. 2016). Not only are leaf nutrients usually correlated among themselves, but they also tend to be correlated to other traits, such as leaf longevity, leaf palatability, and photosynthetic rate (Grime 1977). All these traits together form one main axis of plant variation, describing the capacity of a species to benefit from advantageous growth opportunities, so that plants in more productive conditions have higher leaf nutrient concentrations associated with rapid growth (Grime 1977).

As we expected, cerrado and seasonal forest species differed in almost all traits, with cerrado species having lower nitrogen, phosphorus, potassium, calcium, magnesium, boron, copper, and iron concentrations. Nitrogen and phosphorus concentrations in green and senesced leaves are tightly correlated to specific leaf area and other structural traits, with cerrado species being at one extreme of the leaf economic spectrum, showing a conservative strategy, and forest species being at the other extreme, showing an acquisitive strategy (Miatto et al. 2016). Although nutrients other than nitrogen and phosphorus do not describe properly the leaf economic spectrum (Wright et al. 2005), our results indicated that the distinct strategies of cerrado and forest species have an effect over leaf nutrients concentrations in general due to the construction costs and trade-offs involved in each strategy: whereas, in the cerrado, slow growth and conservative strategy prevail, with low specific leaf area and nutrient concentrations, in the seasonal forest, fast growth and acquisitive strategy prevail, with high specific leaf area and nutrient concentrations.

Several studies on leaf elemental composition have been finding similar patterns for plant micro- and macronutrients distribution into groups or axis. For instance, Garten (1976, 1978), who first explored this issue, identified three different axes of leaf elemental composition: (1) the "nucleic acid-protein" axis, including nitrogen, phosphorus, copper, sulphur, and iron; (2) the "structural and photosynthetic" axis, including nitrogen, potassium, calcium, magnesium, manganese, and zinc; and (3) the "enzymatic" axis, including potassium, magnesium, and manganese. Zhang et al. (2012), in turn, found two main axes, divided into a "photosynthesis and protein synthesis set" and a "cell structure and enzyme activity set". In our case, whereas all other traits were related to the first axis, aluminium and manganese were related to the second axis. For 670 terrestrial plant species, aluminium and manganese also explained additional variation of leaf elemental composition at both species and family levels (Watanabe et al. 2007).

Although cerrado and forest species were separated along the first principal component of leaf traits, there was not a distinction between both vegetation types in the second axis. Manganese was not useful in separating cerrado from forest species, probably due to its important enzymatic role and its role in phosphorus uptake (Lambers et al. 2015), given that both cerrado and forest soils are equally deficient in phosphorus (Miatto et al. 2016). Aluminium was also not useful in distinguishing cerrado and forest species. Even though cerrado soils have higher aluminium concentrations, the capacity of accumulating aluminium is restricted to some families, being less expressive in the southern portion of the Cerrado domain than in other portions (Haridasan 1982, Souza et al. 2015). In addition, both the cerrado and the seasonal forest communities we studied presented some aluminium accumulators, especially among the members of *Melastomataceae* family.

Taxonomy exerted a strong role in leaf elemental composition, and different traits were influenced by different taxonomic levels, as found for other floras (Watanabe et al. 2007, Han et al. 2011, Metali et al. 2015). Moreover, when a taxonomic level influenced a given trait, other taxonomic levels did not. However, leaf nitrogen and phosphorus were notably much less influenced by vegetation type than by taxonomy when compared to the other elements, which is supported by the "stability of limiting elements" (Han et al. 2011), a theory that states that, for nutrients needed in higher concentrations in leaves and often limiting, plants should have lower sensitivity along environmental gradients. Low nitrogen and phosphorus concentrations in plant tissue should be constrained by stoichiometry requirements, as it would cause suboptimal growth. Similarly, high concentrations would also be unlikely, because an increased availability in nitrogen and phosphorus would lead to higher growth rates, with a consequent dilution of these nutrients in plant tissues (Han et al. 2011).

Almost all leaf nutrients were related to the first axis of the soil ordination. Soil drives plant functional traits through multiple nutrient control on leaf traits and strengthens the importance of both cerrado and seasonal forest floras in redistributing nutrients from the soil (Jobbágy and Jackson 2004, Paiva et al. 2015). Viani et al. (2014), however, did not find many differences in leaf nutrient concentrations and responsiveness to soil nutrient status between cerradão, the tall and closed woodland physiognomy of cerrado (Coutinho 1978), and seasonal forest. Whereas they suggest that cerradão and seasonal forest have balanced nutrient acquisition and growth strategies despite the less fertile soils in the former, we suggest the contrary when considering cerrado sensu stricto, a savanna physiognomy of the cerrado (Coutinho 1978): that there are considerable differences in nutrient use and growth strategies. These contrasting patterns found for soil-plant relationships in spatially close cerrado-forest transitions also put on evidence the need for broad-range studies.

The importance of macro- and micronutrients for litter decomposition has been experimentally demonstrated (Kaspari et al. 2008, Power and Salute 2011). Besides the effect of direct fertilisation, it is also recognised that fresh leaf nutrients can be crucial for litter decomposition rates (Bakker et al. 2011). Sometimes, the effect of a single element can be even a stronger predictor of decomposition rates than the effect of multiple elements (Bakker et al. 2011). We found a significant but weak effect of nitrogen, phosphorus, and zinc contents in fresh leaves on decomposition rates. Fresh leaf nitrogen and phosphorus have been recognised as important predictors of decomposition rates in tropical terrestrial environments (Cornwell et al. 2008, Power and Salute 2011, Bakker et al. 2011), but the effect of zinc has hardly been reported. Higher nitrogen and phosphorus concentrations stimulate decomposers activity, because they are also essential and limiting elements for decomposers metabolism (Bakker et al. 2011). Since leaves with higher nutrient content are associated with higher specific leaf area and softness, they are more easily decomposed (Wieder et al. 2009, Bakker et al. 2011). Nitrogen tend be more important in earlier stages of decomposition and phosphorus in later ones (Santiago 2007, Bakker et al. 2011). Zinc, in turn, stimulates litter mass loss and carbon dioxide mineralisation experimentally (Powers and Salute 2011) and acts as co-factor in microbial decomposition enzymes (Wackett et al. 1989).

The relationships between leaf nutrients and decomposition rates were opposite from the expected, and the decomposition rates varied more as a function the leaf nutrient concentration in the cerrado than in the seasonal forest. One possible explanation for this fact is that the cerrado microorganisms and mesofauna, used to low-nutrient and tough leaves, were more plastic and more active in decomposing the teas than the forest ones. Alternatively, the more heterogeneous canopy cover across the cerrado plots might have created a more diversified environment for litter decomposition in terms of light and temperature, favouring the high range of decomposition rates in comparison to the more homogeneous canopy cover across the forest plots. The effect of fresh leaf nutrients in creating microhabitatis may not always be linear to the decomposer diversity and to decomposition rates due to the complexity and niche complementarity among decomposers (Hattenschwiller et al. 2011).

Although taxonomy accounted for a large part of the variation in leaf nutrient-related traits, our results showed that soil exerts an important role on the traits and strategies of both cerrado and seasonal forest woody species and that this is carried out through multi-elemental soil control. Nevertheless, the effect of such different strategies on functioning is less prominent, at least when accounting only for decomposition rates. Our results reinforced that soil nutrient status and plant-soil feedbacks are crucial for the maintenance of the alternate stable states of cerrado and seasonal forest. Consequently, the cerrado vegetation may be impacted or even replaced by the seasonal forest, since it is susceptible to eutrophication (Hunke et al. 2015).

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Table 1. Pearson's correlations among specific leaf area (*SLA*) and leaf nutrients in cerrado and seasonal forest woody species. Significant values ($P < 0.05$) are in bold.

Trait	**SLA**	**N**	**P**	**K**	**Ca**	**Mg**	**S**	**B**	**Cu**	**Mn**	**Zn**	**Fe**
N	**0.54**											
P	**0.41**	**0.62**										
K	**0.59**	**0.57**	**0.63**									
Ca	**0.43**	**0.25**	**0.35**	**0.59**								
Mg	**0.52**	**0.38**	**0.49**	**0.67**	**0.76**							
S	**0.32**	**0.46**	**0.45**	**0.44**	**0.22**	**0.26**						
B	**0.31**	**0.23**	**0.33**	**0.35**	**0.45**	**0.37**	**0.29**					
Cu	**0.35**	**0.32**	**0.55**	**0.37**	**0.19**	**0.32**	**0.44**	**0.34**				
Mn	0.07	0.06	0.06	-0.02	0	0.03	0.06	0	0.01			
Zn	**0.45**	**0.45**	**0.52**	**0.57**	**0.42**	**0.46**	**0.38**	**0.42**	**0.51**	0.12		
Fe	-0.02	0.04	**0.19**	0.03	**0.33**	**0.19**	0.16	**0.3**	**0.25**	0.1	0.15	
Al	0.02	0.04	0.09	0.12	-0.01	0.07	-0.09	-0.02	0.09	0.04	**0.18**	**-0.19**

Table 2. Mean, standard deviation (SD), and ranges of each leaf trait for cerrado and seasonal forest woody species. Significant differences between the two vegetation types (*P* < 0.05) are in bold.

Trait	**Cerrado**		**Forest**	
	Mean +- SD	**Range**	**Mean +- SD**	**Range**
N (g.kg^{-1})	**21.52 +- 7.63**	**10.78- 43.62**	**26.29 +- 5.84**	**11.93- 57.89**
P (g.kg^{-1})	**1.00 +- 0.38**	**0.45-2.19**	**1.25 +- 0.44**	**0.44 - 2.53**
K (g.kg^{-1})	**5.24 +- 3.27**	**1.53-16.32**	**10.83 +- 6.29**	**3.06 - 34.42**
Ca (g.kg^{-1})	**3.56 +- 1.48**	**0.92-8.47**	**8.78 +-3.99**	**1.94-22.37**
Mg (g.kg^{-1})	**1.43+-0.51**	**0.60-2.8**	**2.72 +- 1.8**	**1.20-5.40**
S (g.kg^{-1})	1.29 +- 0.48	0.41-2.33	1.64+-1.50	0.59-9.90
B (g.kg^{-1})	**36.05+-19.88**	**10.01-157.82**	**49.79+-19.70**	**6.64-88.49**
Cu (g.kg^{-1})	**8.40+-5.31**	**2.50-40.50**	**11.99 +-9.89**	**1.50-53.95**
Mn (g.kg^{-1})	174.80+-63.42	5.50-313.00	175.32+-78.97	8.00-331.00
Zn (g.kg^{-1})	**16.45 +- 5.85**	**6.90-32.66**	**23.94 +-10.46**	**5.50-50.75**
Fe (g.kg^{-1})	**123.68+-65.90**	**47.25-359.50**	**186.5+-102.87**	**20.00-491.00**
Al (g.kg^{-1})	102.43 +-42.95	7.00-181.67	101.96 +- 48.27	19.00-203.00

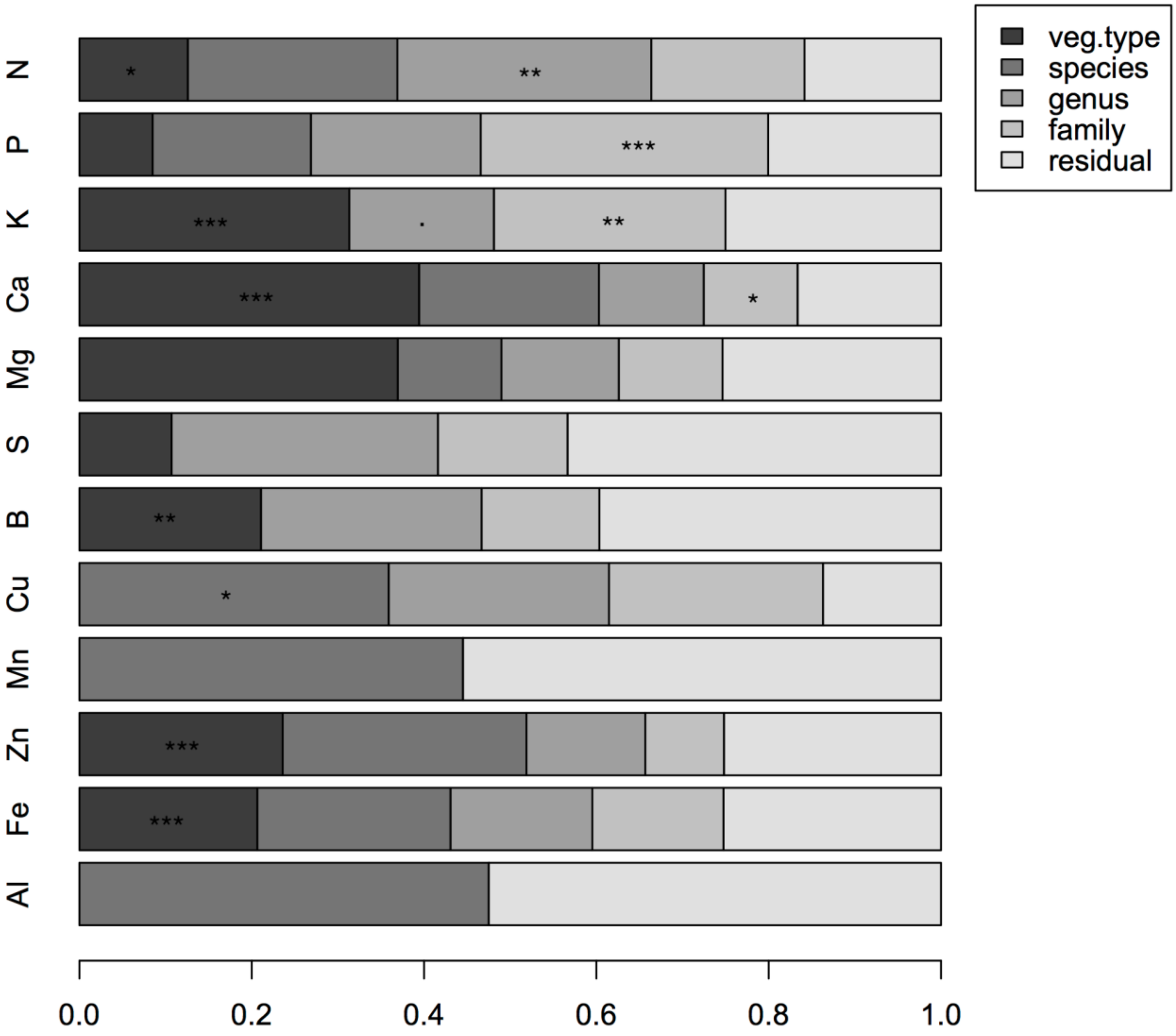
Table 3. P-values of the analyses of covariance between leaf trait community-weighted means as response variables and the first two principal components carried out with soil data and vegetation type as explanatory variables. Significant values (*P* < 0.05) are in bold. SLA = specific leaf area.; Leaf PC1 = first principal component carried out with leaf trait data.

Trait	**Soil PC1**	**Soil PC2**	**Vegetation type**	**R_{adj}^2**
N ($g.kg^{-1}$)	**<0.001**	0.945	**<0.001**	**0.572**
P ($g.kg^{-1}$)	**<0.001**	0.361	**<0.001**	**0.724**
K ($g.kg^{-1}$)	**<0.001**	0.524	**<0.001**	**0.740**
Ca ($g.kg^{-1}$)	**<0.001**	0.082	**<0.001**	**0.859**
Mg ($g.kg^{-1}$)	**<0.001**	0.475	**<0.001**	**0.850**
S ($g.kg^{-1}$)	**0.052**	0.949	**<0.001**	**0.139**
B ($g.kg^{-1}$)	**<0.001**	0.43	**<0.001**	**0.711**
Cu ($g.kg^{-1}$)	**<0.001**	**0.003**	**<0.001**	**0.539**
Mn ($g.kg^{-1}$)	0.909	0.228	**0.015**	0.045
Zn ($g.kg^{-1}$)	**<0.001**	0.517	**<0.001**	**0.720**
Fe ($g.kg^{-1}$)	**<0.001**	0.741	**<0.001**	**0.554**
Al ($g.kg^{-1}$)	0.8448	0.659	0.4306	**0.834**
Leaf-PC1	**<0.001**	0.092	**<0.001**	**0.901**

Figure 1. Partitioning of the total variance for each leaf trait into taxonomic (family/genus/species), environmental (vegetation type) and error (residual) components. All nutrient concentrations are given in g.kg^{-1}.Significance of each variance component was tested with a likelihood ratio test. Significance codes: *** $P<0.001$, ** $P<0.01$, *$P<0.05$, . $P<0.06$.

Figure 2. Ordination diagram for the leaf-trait matrix of the woody species in the Vaçununga State Park (21°36-47’ S and 47°34-41’ W). White circles represent cerrado species, black squares represent forest species, crosses represent species common to both vegetation types occurring in cerrado, and x represents species common to both vegetation types occurring in the forest.

Figure 3. Decomposition rate (*k*) in relation to (a) nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) magnesium, (f) sulphur, (g) boron, (h) cooper, (i) manganese, (j) zinc, (k) iron, and (l) aluminium in 100 plots in the Vaçununga State Park (21°36-47’ S and 47°34-41’ W). White circles represent cerrado plots, grey squares represent forest plots. Slopes significant according to the analysis of covariance are drawn.


veg.type
species
genus
family
residual
N
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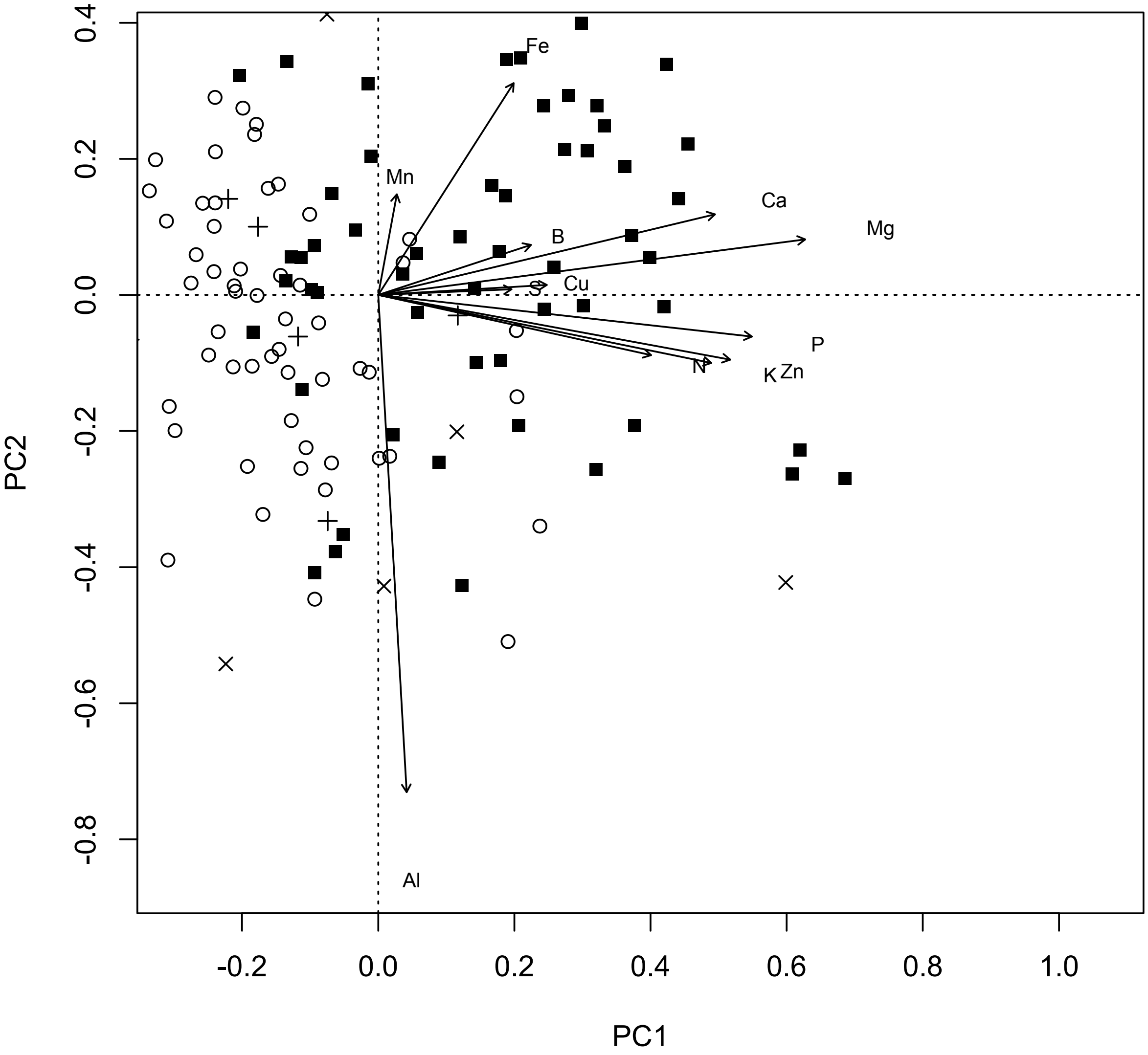
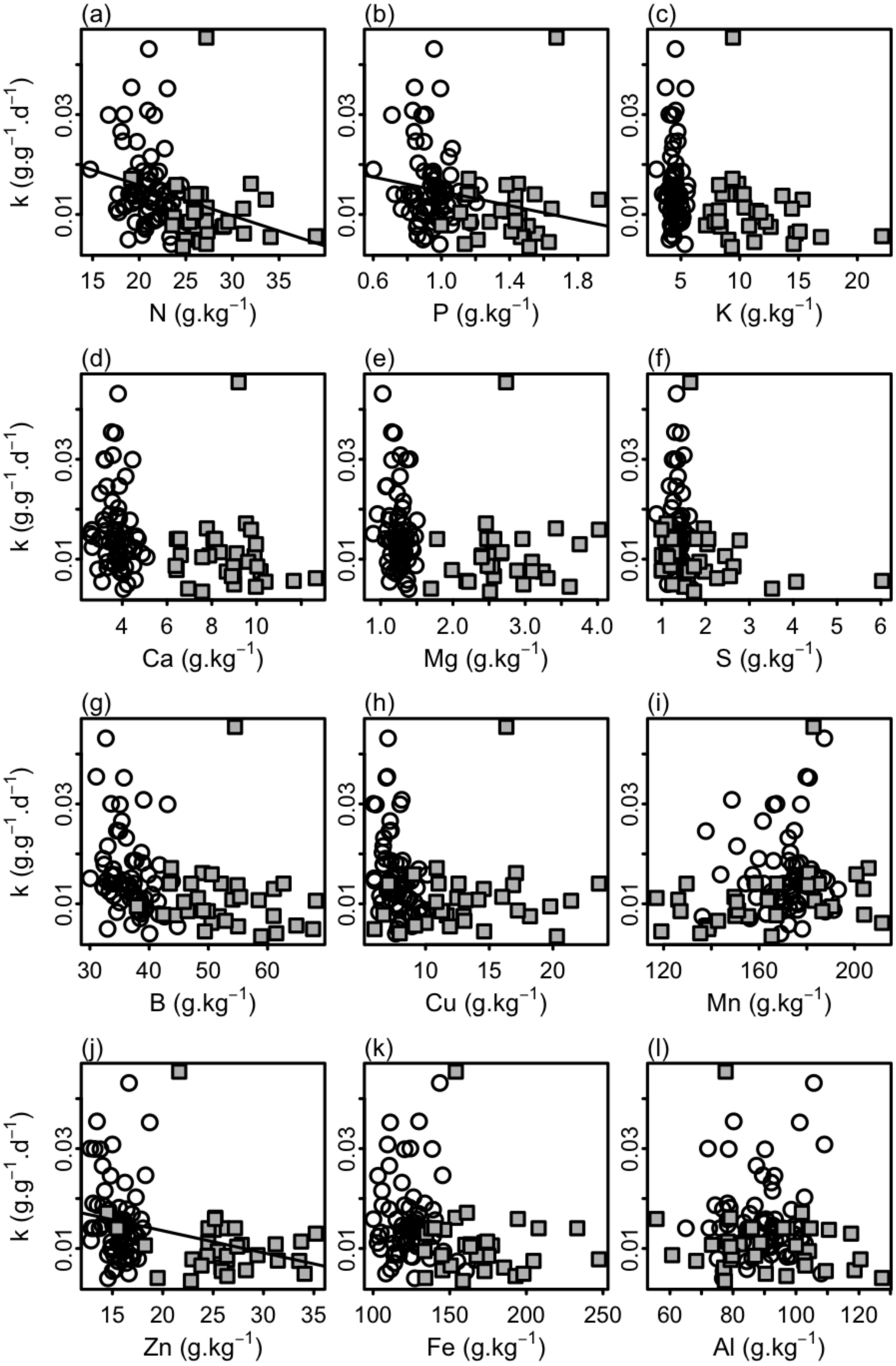


0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
PC2
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
PC1
Fe
Mn
Ca
Mg
B
Cu
S
P
N
K
Zn
Al


(a)
(b)
(c)
k (g.g^{-1}.d^{-1})
0.01
0.03
15
20
25
30
35
N (g.kg^{-1})
0.6
1.0
1.4
1.8
P (g.kg^{-1})
5
10
15
20
K (g.kg^{-1})
(d)
(e)
(f)
k (g.g^{-1}.d^{-1})
0.01
0.03
4
6
8
10
Ca (g.kg^{-1})
1.0
2.0
3.0
4.0
Mg (g.kg^{-1})
1
2
3
4
5
6
S (g.kg^{-1})
(g)
(h)
(i)
k (g.g^{-1}.d^{-1})
0.01
0.03
30
40
50
60
B (g.kg^{-1})
10
15
20
Cu (g.kg^{-1})
120
160
200
Mn (g.kg^{-1})
(j)
(k)
(l)
k (g.g^{-1}.d^{-1})
0.01
0.03
15
20
25
30
35
Zn (g.kg^{-1})
100
150
200
250
Fe (g.kg^{-1})
60
80
100
120
Al (g.kg^{-1})

V - CONCLUSÃO GERAL

Conclusão geral

Neste trabalho, mostramos que os solos mais ácidos e pobres em nutrientes do cerrado acarretam diferenças funcionais em relação à floresta estacional. No primeiro capítulo, vimos que a fertilidade geral do solo selecionou diferentes estratégias de uso de nutriente no cerrado e na floresta estacional, mas seu efeito sobre a reabsorção proporcional de nitrogênio e fósforo não foi evidente. No segundo capítulo, ao olharmos para um conjunto maior de traços e para a distância filogenética-funcional das espécies, observamos uma ampla variação nas distâncias das espécies, apesar de o cerrado ser funcionalmente menos diverso do que a floresta. Logo, concluímos que as comunidades de cerrado não foram exclusivamente moldadas pela filtragem do solo distrófico, mas também pela competição interespecífica por recursos escassos. No terceiro capítulo, vimos que boa parte da variação nos traços foliares relacionados aos nutrientes foi explicada pela taxonomia das espécies, mas, ainda assim, o solo desempenhou um papel importante nos traços e estratégias das espécies vegetais. O efeito dos diferentes traços e estratégias sobre o funcionamento do cerrado ou da floresta estacional foi, porém, menos evidente, pelo menos ao considerarmos apenas as taxas de decomposição. Os resultados dos três capítulos suportaram a ideia de que o solo distrófico do cerrado tem um papel importante na manutenção dessas comunidades, selecionando espécies, estratégias e funções diferentes daquelas da floresta estacional, corroborando que uma possível eutrofização dos fragmentos remanescentes de cerrado acarretaria mudanças nos limites entre o cerrado e a floresta e que, em última instância, aquele poderia ser substituído por esta.