UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E SAÚDE

DEPARTAMENTO DE BOTÂNICA

JULIANA RIBEIRÃO DE FREITAS

DIVERSIDADE FUNCIONAL E FUNCIONAMENTO DA COMUNIDADE:

TESTE EM UMA ÁREA DE CERRADO

SÃO CARLOS

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Dissertação de Mestrado apresentada Universidade Federal de São Carlos como parte dos requisitos para obtenção do título de Mestre em Ecologia e Recursos Naturais
Orientação: Prof. Dr. Marco Antônio Batalha.
Coorientador: Prof. Dr. Marcus Vinícius Cianciaruso

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SÃO CARLOS
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Juliana Ribeirão de Freitas

Diversidade funcional e funcionamento da comunidade: teste em uma área de cerrado

Dissertação apresentada à Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Mestre em Ecologia e Recursos Naturais.

Aprovada em 03 de março de 2011

BANCA EXAMINADORA

Presidente _____

Prof. Dr. Marco Antônio P. L. Batalha
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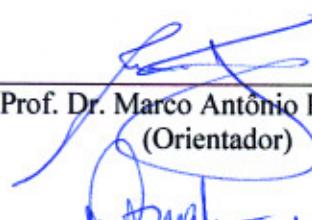
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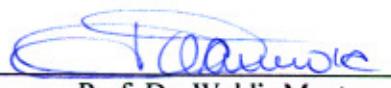
Dedico este trabalho aos meus pais, Fernando e Cristina,

pelo carinho, amor e dedicação incondicionais.

AGRADECIMENTOS

RESUMO

O funcionamento das comunidades deve ser afetado pela diversidade funcional, uma vez que mede a extensão da complementaridade no uso de recursos. Testamos se havia relação entre diversidade funcional das espécies arbóreas e o funcionamento da comunidade em escala fina, usando a FD como medida de diversidade funcional e a taxa de decomposição da serapilheira como indicadora do funcionamento. Medimos oito traços funcionais de plantas arbóreas em uma comunidade de cerrado no sudeste do Brasil. Testamos a correlação entre a FD e as taxas de decomposição, entre as taxas de decomposição e cada traço separadamente e entre FD e as taxas de decomposição considerando diferenças nas variáveis edáficas. Não houve relação significativa entre FD e decomposição, mesmo quando consideramos cada traço separadamente. As taxas de decomposição se mostraram relacionadas com as concentrações de alumínio e fósforo e não com a FD. A diversidade funcional não foi uma boa previsora do funcionamento da comunidade. A maioria dos estudos sobre a relação entre diversidade e funcionamento em escalas finas foi desenvolvida por meio da manipulação experimental da diversidade e em regiões temperadas. Nossas descobertas indicaram que a relação entre biodiversidade e funcionamento das comunidades não é tão simples como se assume e contribuem para aprimorar a abordagem atual.

Palavras-chave: Cerrado sensu stricto. Ciclagem de nutrientes. Decomposição de serapilheira. Savana.

ABSTRACT

Community functioning may be affected by functional diversity, since it measures the extent of complementarity in resource use. We tested whether there was a relationship between functional diversity of woody species and community functioning at fine-scale, using FD as a measure of functional diversity and litter decomposition rate as a surrogate for community functioning. We measured eight functional traits from a woodland cerrado community in southeastern Brazil. We tested the correlation between FD and decomposition rate, between decomposition rate and each trait separately, and between FD and decomposition rate taking into account differences in soil features. There was a non-significant relationship between FD and decomposition rate, even when we considered each trait separately. Decomposition rate was related to aluminium and phosphorus concentration in soil, but not to FD, pointing out that functional diversity was not a good predictor of community functioning. Most studies on the relationships between biodiversity and community functioning at fine scales were carried out by experimental manipulation of diversity and in temperate regions. We carried out this fine scale study as a mensurative experiment and in a tropical savanna. Our findings indicated that the relationship between biodiversity and community functioning is not so straightforward as usually assumed.

Keywords Litter decomposition. Nutrient cycling. Savanna. Woodland cerrado.

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SUMÁRIO

1. INTRODUÇÃO GERAL

A percepção da diversidade dos organismos vivos e de onde eles vivem é parte do conhecimento que a espécie humana vem acumulando e transmitindo ao longo de gerações. Até recentemente na história da biologia, o desenvolvimento do conhecimento sobre a diversidade estava relacionado à sua utilidade (por exemplo, em alimentos, medicamentos e fibras), à exibição em zoológicos ou jardins botânicos e à catalogação em museus (Townsend et al. 2006). Sem a compreensão de como os organismos se desenvolvem, se relacionam entre si e com o meio onde vivem e evoluem, tais catalogações se parecem mais com uma coleção de selos do que com uma catalogação científica. As primeiras explicações sobre padrões de distribuição da diversidade no planeta foram baseadas na história geográfica e evolutiva (Townsend et al. 2006). Charles Darwin e Alfred Wallace, os dois grandes exploradores e naturalistas do século XIX, foram os primeiros a perceber uma alta diversidade de espécies nos trópicos, até então desconhecida dos europeus. Essa alta diversidade foi atribuída à persistência ininterrupta do clima nesses locais. À medida que se caminha em direção aos polos, a diversidade vai diminuindo, porque mudanças climáticas severas associadas à glaciação teriam causado fases de extinções. Em outras palavras, os trópicos teriam tido mais tempo para acumular diferentes espécies (Ricklefs e Schluter 1993).

No último século, os ecólogos têm abordado padrões de diversidade de espécies como um problema científico e embarcaram intensamente na pesquisa em ecologia de comunidades. Durante os anos 1920, Lotka e Volterra desenvolveram descrições matemáticas das interações entre as espécies (Townsend et al. 2006). Esses estudos culminaram no princípio da exclusão competitiva. Durante a década de 1960, MacArthur e Levins (1967) formalizaram o conceito de similaridade limitante, isto é, o nível máximo dentro do qual as espécies poderiam cobrir parcialmente o espaço do nicho ecológico e continuar coexistindo localmente. Seguindo esse caminho, Tilman (1982) desenvolveu modelos de interação entre as espécies consumidoras nos quais a relação entre a produtividade do hábitat e o número de espécies que podem coexistir deveria ser negativa e não positiva.

Apesar de a diversidade ser objeto de estudos em ecologia e de este termo estar presente tanto na literatura científica quanto na literatura leiga, não há ainda uma definição consistente para seu significado (Ricotta 2005). De forma mais simples, o termo é usado para expressar o número de espécies, que pode ser expresso em função da área em que ocorrem - isto é, densidade de espécies - ou do número de indivíduos amostrados - ou seja, riqueza de espécies (Ricklefs 2003). O número total de espécies incluídas em uma amostra varia com o seu tamanho, porque à medida que mais indivíduos são amostrados, a probabilidade de se encontrar espécies raras aumenta. Uma solução para esse problema foi a criação de índices de diversidade nos quais a contribuição de cada espécie é ponderada por sua abundância relativa. Dentre os índices de diversidade mais comuns, estão os índices de Shannon e o de Simpson (Magurran 2004). Nesse contexto, a diversidade é analisada como o reflexo da composição da comunidade regulada por fatores bióticos e abióticos e pela coexistência e dominância de espécies. O principal objetivo científico é, portanto, entender a regulação e manutenção da diversidade (Ricklefs 2003).

A enumeração das espécies, que se constitui como base dessas medidas de diversidade de espécies não leva em conta a variação dos papéis ecológicos de cada uma delas. Portanto, assumem implicitamente que todas as espécies são igualmente importantes na manutenção dos processos da comunidade (Magurran 2004) Além disso, essas medidas não levam em conta as variações fenotípicas individuais, ou seja assumem que dentro de uma dada espécie, os indivíduos são equivalentes (Magurran 2004). Assim, as medidas tradicionais de diversidade não têm respondido às questões ecológicas mais recentes e não temos conseguido fazer boas predições com elas (Cianciaruso et al. 2009).

No últimos anos, essa abordagem tem sido substituída por uma nova, na qual a diversidade direciona os processos que ocorrem nas comunidades. Nesse contexto, o principal objetivo é entender o papel que cada espécie desempenha dentro de uma dada comunidade e assim prever as consequências de alterções na composição desta comunidade (Hooper et al 2005; Hillebrand 2009). Podemos definir diversidade funcional como 'o valor e a variação das espécies e de suas características que influenciam o funcionamento das comunidades' (Tilman 1997). A função de uma espécie dentro da comunidade está relacionada a seus traços funcionais, que são

características relacionadas ao seu nicho ecológico, isto é, que alteram seu desenvolvimento, reprodução e capacidade de competição (Hooper 2005). Cada comunidade ecológica pode ser pensada como um espaço de nicho total dentro do qual todos os nichos de seus membros devem se ajustar. Dentro desse espaço de nicho, acrescentar ou remover espécies tem certas consequências, porque o nicho das espécies pode aumentar ou diminuir. A identidade e as características das espécies incluídas ou retiradas são fundamentais para prever tais consequências.

Os traços funcionais podem ser complementares no que diz respeito ao uso dos recursos e, devido à diminuição da competição, devem intensificar processos envolvidos em seu funcionamento, como as taxas médias de produtividade, a ciclagem de nutrientes, sequestro de carbono, invasibilidade, heterogeneidade de hábitats e estabilidade (Diaz e Cabido 2001). Por isso, apresentam uma relação potencial com o funcionamento da comunidade. Atualmente, a perda de diversidade de espécies e suas consequências é uma preocupação global, que ultrapassa a comunidade científica e tem se se tornado tema de debate político e institucional. É papel dos cientistas prever as consequências da perda da diversidade para o modo do funcionamento das comunidades e para a disponibilidade dos serviços ambientais que elas proporcionam (Quijas 2010). Medidas de diversidade funcional devem ser mais adequadas para responder perguntas cientificas e fazer tais predições (Cianciaruso et al. 2009).

Neste trabalho, testamos se há relação entre a diversidade funcional e o funcionamento de uma comunidade de cerrado. A identificação de quais e quantas espécies atua de maneira complementar nas comunidades complexas estão apenas começando. Portanto, estudos como este têm implicações significativas na construção do conhecimento sobre como a diversidade e o funcionamento das comunidades se relacionam e contribuem para o desenvolvimento de métodos mais eficientes para prever as consequências das alterações da diversidade no funcionamento das comunidades.

2. INTRODUCTION

Biological diversity may affect community functioning by the role of each species in a given community (Díaz and Cabido 2001). At first, studies on the relationship between diversity and community functioning used species richness as a measure of diversity (Naeem et al. 1994). However, such measure implicitly assumes that all species are equally different and, consequently, the addition of any species to a community should increase the functioning by one unit (Petchey et al. 2004). Recently, the consensus that species contribution to the processes is different has been growing (Hooper et al. 2005). Species richness has been viewed as a measure that incorporates little or no information about individual species and, thus, explains and predicts poorly (Hooper et al. 2002; Hooper et al. 2005; Petchey et al. 2004; Petchey and Gaston 2006). Community functioning must be determined by the value and range of species functional traits, that is, characteristics that affect the organism fitness through direct or indirect effects on growth, reproduction, and survival (Díaz and Cabido 2001; Hooper et al. 2005; Petchey and Gaston 2002). The functional approach is closely related to the niche models, in which separation in niche space allows coexistence through lack of competition for similar resources and, thus, leads to greater complementarity (MacArthur 1972). Since an increase in functional diversity should be related to an increase in the intensity of the processes in community functioning, functional diversity is expected to be a good predictor of functioning (Petchey and Gaston 2002).

Community functioning is defined as the flow of matter and energy through the arrangement of biotic and abiotic components of the communities (Díaz and Cabido 2001). Since decomposition is a process closely related to nutrient cycling (Swift 1979), it can be used as a surrogate for community functioning. Litter decomposition may be affected by plant diversity through two mechanisms: directly, through changes in litter species composition, and indirectly, by altering the decomposition microenvironment (Madritch and Cardinale 2007; Vivanco and Austin 2008). Litters of different architecture may complement one another by providing more favourable physical living space, because the resulting pockets may encourage microbial growth

and macroinvertebrate fauna invasion (Hansen 2000). Plant species can also determine the litter macroinvertebrate community and decomposition process below their canopies (Negrete-Yankelevich et al. 2008). Moreover, different species of plants may create specific conditions that increase the breakdown of their own litter, establishing affinity effects between species and their microenvironment (Vivanco and Austin 2008). In this sense, plant species produce conditions in their environment that affect the processes of decomposition.

Up to now, most studies that addressed the effect of diversity upon decomposition used traditional measures, such as species richness (for example, Negrete-Yankelevich et al. 2008; Vivanco and Austin 2008). In these cases, diversity effects could only arise if species differed in relevant functional characteristics to the studied process. If so, species richness and other diversity measures could be useful proxies of functional diversity in a community (Gessner 2010). However, direct functional characterisation of communities, such as functional trait distributions including dissimilarity patterns, is likely to be more compelling predictors of the effect of diversity upon litter decomposition. Indeed, recent studies that analysed species richness, number of functional groups, and functional composition suggested that the functional approach tends to be more predictive (Petchey et al. 2004; Ricotta 2005; Scherer-Lorenzen 2008).

Many studies that used the functional approach used the number of functional groups in a community as diversity measure (for example, Denyer et al. 2010; McLaren and Turkington 2010; Scherber et al. 2010). Of the problems associated with assigning species to groups, perhaps the least tractable is the arbitrary scale at which differences among species qualify as functionally significant (Petchey and Gaston 2002). Here, we used a broadly accepted, continuous measure of functional diversity, FD (Petchey and Gaston 2002). To calculate FD, one may use the functional trait values and construct a dendrogram based on the differences among species (Petchey and Gaston 2002; 2006). The sum of the branches necessary to connect all species in the community is FD (Petchey and Gaston 2002). The more different the functional trait values, the higher the sum of the branches and, thus, the higher the FD (Petchey and Gaston 2002; 2006). As long as litter decomposition can be used as a surrogate for community functioning, we expected that sites with higher FD values should present higher litter

decomposition rates.

In larger-scale patterns, functioning and diversity are both covarying with environmental factors that change from place to place (Loreau 1998; Loreau and Hector 2001), because in such scale physical processes may dominate or dissipate biological effects (Wiens 1989). We developed our study in local scale (sensu Leibold et al. 2004), in which the influence of diversity on community functioning will depend rather on the traits of the species present and their ecological interactions than on direct physical determination (Wiens 1989). Although many authors suggested a relationship between functional diversity and community functioning (Díaz and Cabido 2001; Hooper et al. 2005; Tilman 1997), there are few studies focused on testing it (Scherer-Lorenzen 2008), especially in tropical regions. The Brazilian cerrado is the largest Neotropical savanna region and present seasonal climate with dry winter and wet summer. The occurrence of the cerrado and its physiognomic variation are considered by some authors to be a fertility gradient (Goodland and Pollard 1973). Both decomposition process and floristic composition may be affected by abiotic variables and, in particular, soil features play an important role (Swift 1979). On the one hand, since we carried out this study at fine scale, climate and fire frequency were homogeneous; on the other hand, since changes in soil features may be found at distances as small as 1 m (Souza and Martins 2004), soil is an important candidate to exert effects upon vegetation and decomposition process in such scale.

Moreover, there is a lack of information on the relative importance of different traits for different community functions (Petchey and Gaston 2002). Perhaps some traits could show greater differences among species and others, less. In this way, including traits that present small differences could dilute differences among species and reduce the value of FD, masking a possible relationship between FD and decomposition. To avoid this problem, we also tested whether each trait separately was related to decomposition rate. In sum, we tested the relationship between functional diversity and community functioning, in a southern cerrado site, by sampling woody species at fine scale and using litter decomposition rate as a surrogate for community functioning. We addressed the following questions: (1) is FD related to the litter decomposition rate?; (2) analysing functional traits separately, are they related to decomposition rate?; and (3) is

FD related to decomposition rate taking soil features into account?

3. METHODS

We carried out this study in a woodland cerrado site located at Federal University of São Carlos, southeastern Brazil (approximately, 21°58'05"S, 47°52'10"W, 872 m asl). Regional climate is seasonal, with dry winter and wet summer, defined as Cwa (Köppen 1931). We established a 50 m x 50 m grid, in which we placed 100 contiguous 25 m^2 plots. We sampled all individuals belonging to the woody component, defined as those with stem diameter at soil level equal to or higher than 3 cm (SMA 1997), which we identified to species level. For each individual, we measured eight functional traits related to community functioning: leaf size, specific leaf area, leaf dry matter content, stem specific density, height, basal area, resprouting capacity, and bark thickness (Cornelissen et al. 2003; see Table 1).

For leaf size, leaf specific area, and leaf dry matter content, we collected five undamaged, fully expanded leaves from each individual during the morning, until 10:00 (Cornelissen et al. 2003). We kept the leaves in plastic bags and stored them in a cooler to avoid water loss or deterioration. In the laboratory, we measured fresh mass, scanned the leaves, and calculated leaf size with ImageJ 1.33 (Rasband 2004). Then, we oven-dried the leaves at 80°C for 72 hr and measured dry mass. We divided leaf size by dry mass to find specific leaf area. We also divided dry mass by fresh mass to find dry matter content. Stem specific density is the dry mass of a section of the main stem divided by its volume (Cornelissen et al. 2003). We cut 10 cm long sections of the stems, removed the bark, and placed the sections in plastic bags. In the laboratory, we estimated volume, by immersing them in water for 5 s in volumetric flask and measuring the increase in volume (Cornelissen et al. 2003). Next, we oven-dried them at 80°C for 72 hr and weighted them. Using a telescopic ruler, we measured height, the shortest distance between the upper boundary of the main photosynthetic tissues and soil level (Cornelissen et al. 2003). We calculated basal area by measuring stem perimeter at soil level. We measured resprouting capacity by counting branches at the base of the trunk. We removed a portion of the stem at 30

cm high with a knife and measured bark thickness with a digital caliper.

We collected leaves recently shed, oven-dried them at 80°C for 24 hr, and put 5 g in each of 2,000 litterbags. In each plot, we placed four sets of five litterbags, that is, 20 litterbags per plot. We collected four bags from each set in each plot after 1, 2, 3, 6, and 12 months. In the laboratory, we gently brushed the material to remove soil particles and other debris, oven-dried the bags at 80°C for 24 hr, and weighted them. Comparing the initial and the final masses, we found the amount of litter that was decomposed. For each plot and each month, thus, we found the average remaining amount of matter. The exponential model is the best descriptor of mass loss during decomposition (Wieder and Lang 1982). Therefore, we adjusted the values to an exponential equation ($y = ae^{-kt}$), in which y is the portion of the remaining mass at time t (in months), a is the initial mass, and k is the rate of decomposition. We used soil data collected in the same plots (Dantas and Batalha 2011) to take the effects of soil upon functional diversity into account, selecting pH, organic matter, available phosphorus, total nitrogen, sum of bases, base saturation, aluminium saturation, and sand, silt, and clay proportions.

We calculated FD for each plot, following the method described by Petchey and Gaston (2002, 2006): (1) we obtained a trait matrix with species in rows, functional traits in columns, and average trait values in entries; (2) after standardising the trait matrix to zero mean and unit variance, we transformed it into a distance matrix, using Euclidean distance; (3) we used the distance matrix to produce a dendrogram with unweighted pair-group clustering method using arithmetic averages; and (4) we calculated the total branch length of the dendrogram necessary to connect all species in a given plot. To answer the first question, we did a linear regression analysis, using FD as explanatory variable and decomposition rate as response variable. To answer the second question, we used the average value of each trait and produced new dendrograms, with which we calculated new FD values. For each trait, we did a linear regression analysis, using the decomposition rate as the response variable. To answer the third question, we did multiple linear regression analyses, using both FD and soil features as explanatory variables. We selected the best stepwise model, using the Akaike Information Criterion, which considers the complexity of an estimated model and how efficient is this model in fitting the data (McNeil

et al. 1996). We carried out all analyses in R (R Development Core Team 2008).

4. RESULTS

We sampled 1,995 individuals, belonging to 60 species and 28 families. The commonest species were *Myrsine umbellata* (557 individuals) and *Vochysia tucanorum* (168 individuals). The rarest species were *Annona crassifolia, Banisteropsis megaphylla, Davilla rugosa, Ilex cerasifolia, Miconia rubiginosa, Palicourea rigida, Rapanea guianensis, Trapirira guianensis* (one individual each). The richest families were Fabaceae (with eight species), Myrtaceae (with seven species), Malpighiaceae and Melastomataceae (with four species each), and Annonaceae, Erythroxylaceae, and Rubiaceae (with three species each). Mean (± sd) species number in each plot was 9.54 ±2.35 and mean FD was 31.79 ±8.99. During the year, 32% of the litter was decomposed. The annual decomposition coefficient k was 0.36, and mean decomposition rate in the plots was -0.030 ± 0.005.

The relationship between FD and decomposition rate was not significant ($P = 0.80$, $R^2 < 0.001$) and, thus, FD was not a good predictor of community functioning. Considering each trait separately, we also find no significant relationship ($P > 0.05$ in all cases, Table 2). The best model to predict decomposition rate based on FD and soil features was that with aluminium and phosphorus concentration as explanatory variables. This model was significant ($P = 0.003$), but had a weak explanatory power ($R^2 = 0.1$).

5. DISCUSSION

In the cerrado, FD was not a good predictor of community functioning at fine scale. Many authors suggested that living plant traits should be a powerful tool to predict decomposition rate and, thus, community functioning (for example, Cornwell et al. 2008; Díaz and Cabido 2001; Fortunel et al. 2009; Hector et al. 2000), but this assumption has been rarely tested. Functional diversity presented a significant relationship with decomposition rate in

another vegetation type and when another index was used (Q; Scherer-Lorenzen 2008), but we did not find it when using FD. Comparisons between functional diversity measures based on artificial data found no correlation between Q and FD (Mouchet 2010), but they were correlated when functional diversity measures were based on field data (Scherer-Lorenzen et al. 2007). We chose FD as a measure of functional diversity, because it does not violates set monotonicity as Q does (Petchey and Gaston 2007).

Many studies concluded that functional traits of living leaves affect the decomposability of their own litterfall as a legacy (Cornelissen and Thompson 1997; Fortunel 2009), but these studies were carried out in temperate regions and caution should be taken when extrapolating these results to tropical communities. The cerrado dynamics did not fit this framework. Litter of high quality could be expected to enhance decomposition of other litters, whereas litter of poor quality would have negative effects (Seastadt 1984). In poor soil environments, such as the cerrado, plants tend to maximise nutrient absorption before leaf fall (Haridasan 2000), and there are strong differences between living and dead leaf traits (Delitti 1998). Nevertheless, we expected dead leaf traits to be also unrelated to functional diversity, since there is a widespread occurrence of synergistic and antagonistic patterns during decay of leaf litter (Gartner and Cardon 2004; Gessner 2010).

The choice of traits is the most important step for calculating functional diversity. We must consider all traits related to the process under study and exclude traits that are functionally uninformative (Petchey and Gaston 2006). The cerrado tends to occur on well-drained, acid, and nutrient-poor soils, with high levels of exchangeable aluminium (Goodland and Ferri 1979). Thus, we considered traits related to resource uptake and storage, such as stem specific density, basal area, and resprouting capacity, differently from another study, which considered only leaf traits (Scherer-Lorenzen 2008). The inclusion of these non-leaf traits was not masking the relation, because we did not find significant relationships between traits and decomposition rate even when we considered each trait separately. So, in the cerrado and at fine scale, both leaf and non-leaf traits were not related to community functioning.

Aluminium and phosphorus had some effect in decomposition rates. Since these

variables presented a weak explanatory power, soil composition may not influence decomposition directly, but via other biotic components that affect nutrient cycling. For example, detritivore and decomposer subsystems play an important role in decomposition process, and differences between above- and below-ground processes affect community functioning (Hooper et al. 2002; Naeen 2002; Spehn 2005). Functional dissimilarity among detritivores drives community compositional effects on leaf litter mass loss (Heemsbergen et al. 2004; Srivastava et al. 2009; Zimmer 2005). We expected functional diversity of woody plants to be determinant in detritivore activity by altering the microenvironment. However, abiotic conditions, such as soil features, might be more tightly coupled to decomposer activity than to plant diversity, contrary to our expectations.

Our study was developed at fine scale, which may reveal greater detail about the biological mechanisms underlying patterns, but generalisations are more likely to emerge at larger scales (Wiens 1989). For example, at local scale, properties of the litter and the decomposers explain most of the variation in litter decomposition rate (Ferrari 1999). Otherwise, at larger scales, both climatic variables and plant functional traits control it (Cornwell 2008). Decomposition rate tend to increase from open to closed cerrado physiognomies (Cianciaruso et al. 2006; Valenti et al. 2008). If species occurring in different physiognomies present different traits, we may expect functional diversity and decomposition rate to be correlated at regional scale. So, even if functional diversity was not a predictor of community functioning in the cerrado at fine scale, it is possible that it predicts community functioning at larger scales.

Most studies on the relationships between biodiversity and community functioning have been carried out in temperate regions (Cornelissen and Thompson 1997; Fortunel 2009; Hector et al. 2000; Knops et al. 2001; Scherer-Lorenzen 2008; Scherer-Lorenzen et al. 2003; 2007; Spehn 2000). Moreover, at fine scale, only studies by experimental manipulation of diversity were developed (Hector and Loreau 2005; Knops et al. 2001; Scherer-Lorenzen 2008; Scherer-Lorenzen et al. 2003; 2007; Spehn 2000). Manipulative experiments allow controlling variation in environmental conditions (Hector and Loreau 2005), but tend to oversimplify the processes. We developed this study in a tropical savanna, at fine scale, as a mensurative

experiment (Krebs 1999). Our findings indicated that the relationship between biodiversity and community functioning is not so straightforward, as usually assumed. Plant functional diversity may reduce the success of invasive species (Dukes 2001) and promote heterogeneity in vertebrate habitats (Price 2010). Moreover, detritivore functional diversity may affect decomposition (Heemsbergen et al. 2004). However, we did not find relationship between functional diversity and community functioning. Thus, we can postulate that certain process in community functioning presents no relationship with certain biodiversity components, such as functional diversity of woody species and decomposition rate. Further studies should focus in answering to which processes biodiversity components are linked and distinguish patterns that act at local and regional scales.

6. ACKNOWLEGMENTS

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Table 1 Functional traits used to calculate functional diversity of woody species in a woodland cerrado (21°58'05"S, 47°52'10"W, São Carlos, Brazil). For more details, see Cornelissen et al. (2003).

Trait	Measurement	Functional importance
Leaf size	continuous measure, mm²	Energy and water balance, related to allometric factors, environmental nutrient stress, and disturbance
Specific leaf área	continuous measure, mm² mg^{-1}	Leaf lifespan, leaf structural defences, positively correlated with potential relative growth rate or mass-based maximum photossintetic rate
Leaf dry matter content	continuous measure, mg g^{-1}	Related to average density of leaf tissues, negatively correlated with potential relative growth rate and positively correlated with leaf lifespan
Stem specific density	continuous measure, mg mm^{-3}	Structural strength, leaf lifespan, carbon storage
Height	continuous measure, m	Competitive vigour, whole plant fecundity, time intervals plant species are given to grow between disturbances, correlated with aboveground biomass, rooting depth, lateral spread, and leaf size
Basal area	continuous measure, m²	Space ocupation, resource uptake, and total biomass
Resprouting capacity	continuous measure, count	Structural strength and resource availability
Bark thickness	continuous measure, mm	Meristem protection

Table 2 Values calculated for the relationship between decomposition rates and each trait separately for woody species in a cerrado site at São Carlos, Brazil (21°58'05"S, 47°52'10"W, 872 m asl).

Trait	P value
Leaf size	0.1604
Specific leaf area	0.8134
Leaf dry matter content	0.6593
Stem specific density	0.6341
Height	0.4505
Basal area	0.7181
Resprouting capacity	0.6728
Bark thickness	0.1635