

**UNIVERSIDADE FEDERAL DE SÃO CARLOS**  
**CENTRO DE CIÊNCIAS BIOLÓGICAS E SAÚDE**  
**DEPARTAMENTO DE BOTÂNICA**

**PRISCILLA DE PAULA LOIOLA**

**DISTRIBUIÇÃO ESPACIAL DE ESPÉCIES ARBÓREAS DE**  
**CERRADO: FILOGENIA E TRAÇOS DE DEFESA CONTRA**  
**HERBIVORIA**

**SÃO CARLOS**

**2010**

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CERRADO: FILOGENIA E TRAÇOS DE DEFESA CONTRA  
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Dissertação apresentada ao Programa de Pós  
Graduação de Ecologia e Recursos Naturais  
para obtenção do título de mestre em Ecologia  
e Recursos Naturais  
*Orientação: Prof. Dr. Marco Antônio Batalha*

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**Priscilla de Paula Loiola**


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contra herbivoria**

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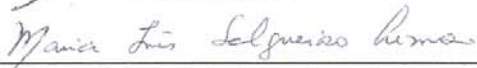
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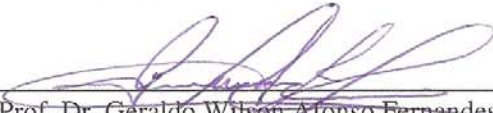
Presidente

  
\_\_\_\_\_  
Prof. Dr. Marco Antônio P. L. Batalha  
(Orientador)

1º Examinador

  
\_\_\_\_\_  
Profa. Dra. Maria Inês Salgueiro Lima  
PPGERN/UFSCar

2º Examinador

  
\_\_\_\_\_  
Prof. Dr. Geraldo Wilson Afonso Fernandes  
UFMG/Belo Horizonte-MG

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pelo seu amor, paciência, apoio e esperança  
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## RESUMO

A herbivoria deve promover um padrão de distribuição de traços de defesa em espécies de plantas coocorrentes, já que plantas similares são mais vulneráveis a herbívoros especialistas. O conservantismo dos traços é geralmente observado em linhagens de espécies de plantas, e assim, as relações filogenéticas entre as espécies também devem estar relacionadas à distribuição espacial. Dessa forma, nós esperamos que os traços de defesa em espécies coocorrentes sejam mais diferentes do que o esperado. Esperamos ainda que os traços contra a herbivoria estejam conservados, e que as distâncias filogenéticas de espécies coocorrentes sejam maiores do que o esperado pelo acaso. Em um fragmento de cerrado do estado de São Paulo, nós analisamos 100 parcelas, com 25 m<sup>2</sup> cada, e amostramos todos os indivíduos arbóreos. Para cada espécie, nós medimos alguns traços de defesa contra herbivoria, e respondemos se o grau de coocorrência das espécies está relacionado com as diferenças funcionais e com as distâncias filogenéticas. Nós também testamos se os traços de defesa são filogeneticamente conservados. Nós não encontramos correlação entre a coocorrência das espécies com os traços de defesa, nem com as distâncias filogenéticas. No entanto, nós encontramos sinal filogenético para quatro dos nove traços estudados. A ausência de correlações pode ser devido a (1) herbivoria não ser um processo forte na vegetação de cerrado como esperado ou (2) a presença de filtros ambientais, como a falta de água e solos pobres, que devem promover agrupamento filogenético, agindo em conjunto com a dispersão filogenética gerada pela herbivoria.

**Palavras-chave:** Cerrado. Distribuição espacial. Filogenia. Herbivoria. Traços de defesa



## ABSTRACT

Herbivory is expected to promote an overdispersed distribution of traits in co-occurring plant species, since similar plants are more vulnerable to specialised herbivores. As long as conservatism of traits is usually observed in lineages of plant species, phylogenetic relatedness may also be related to spatial distribution. Thus, we expected that defense traits against herbivory were conserved and that phylogenetic distances of co-occurring species were higher than expected by chance. In a cerrado site in southeastern Brazil, we analysed 100 quadrats, with 25 m<sup>2</sup> each, and sampled all woody individuals. For each species, we measured defense traits against herbivory and answered whether the degree of co-occurrence of species was correlated with both functional differences and phylogenetic distances. We also tested whether the defense traits were phylogenetically conserved. On the one hand, we did not find significant correlation between species co-occurrence and neither defense traits nor phylogenetic distances. On the other hand, we found phylogenetic signal for four out of nine defense traits. The absence of correlations may be due to (1) herbivory not being as strong as we expected in cerrado vegetation or (2) the presence of environmental filters, such as drought and nutrient-poor soil, promoting phylogenetic clustering, counteracting phylogenetic overdispersion by herbivory.

**Key-words:** Cerrado. Defense traits. Herbivory. Phylogeny. Spatial distribution.

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## 1. INTRODUCTION

The coevolution of herbivores and plants has been proposed as a major factor promoting the diversity of defense traits against herbivory in plants (Becerra 1997, 2007). Related insects often feed on plants that share common traits to which they are adapted (Berembaum 1983; Becerra 1997). Consequently, plant-herbivore interactions may contribute to the interactions among plants (Carson & Root 2000; Fine *et al.* 2006), changing their abundance and spatial distribution (Olf & Ritchie 1998; Maron & Crone 2006). Studies on plant-herbivore coevolution and its impact on plant defenses have focused primarily on interactions that involve a small number of species or populations (Agrawal & Fishbein 2006; Becerra 2007). Here we focused on the question of whether coevolution creates spatial patterns that structure plant community at fine scale.

Herbivory could limit the coexistence of plants that share common defense traits, since selection would favor trait divergence in co-occurring similar plants (Becerra 2007; Kursar *et al.* 2009). The effect of the herbivory on diversification should be stronger for narrowly coevolved systems involving few interacting species, which tend to develop specific adaptations to the features of their counterparts (Van Zandt & Agrawal 2004; Becerra 2007). Consequently, a plant similar to its neighbour should be more vulnerable to a specialised herbivore able to handle many of its defense traits (Becerra 2007; Kursar *et al.* 2009). Community spatial structuring is more likely to be observed at fine spatial scales, within a uniform habitat, than at large spatial scales, which encompass different habitats (Cavender-Bares *et al.* 2004, 2006). High specialisation in defense strategies and high differences in the trait values of co-occurring species (that is, trait overdispersion) occur at smaller scales, probably due to stronger selective pressure for trait divergence in the locally present plant species (Becerra 2007). Thus, as coevolutionary specialisation increases, and spatial scale decreases, co-occurring species tend to be more dissimilar (Becerra 2007). Therefore, we expected to find overdispersion of defense traits against herbivory at fine spatial scale.

Strategies against herbivory might include nutritional quality, such as proteins and anti-proteins; physical characteristics, such as spines, trichomes, and leaf toughness; toxicity, such as alkaloids; phenology; regrowth capacity; and indirect defenses, like volatiles and branching architecture (Agrawal & Fishbein 2006). Synergistic interactions among multiple traits may potentially provide a greater level of defense than would be possible if the traits were present independently (Berenbaum *et al.* 1991; Stapley 1998). Therefore, traits acting together may

provide a more efficient defense strategy to the individual, and the herbivore pressure may act in the syndrome of traits to divergence in space.

Recently, we are becoming increasingly aware that the evolutionary processes, particularly the way that traits evolve within lineages, influence community assembling (Webb *et al.* 2002; Chazdon *et al.* 2003; Cavander-Bares *et al.* 2004). Evolution of plant defenses against herbivory may be central to understand tropical biodiversity (Kursar *et al.* 2009). In general, there is a great conservatism of functional traits in plant lineages (Ackerly 2003; Reich *et al.* 2003), including chemical and morphological characteristics that constrain the use by herbivores (Ward & Spalding 1993; Futuyma & Mitter 1996). As a consequence, closely related plants generally present closely related herbivores and pathogens (Becerra 2007; Gilbert & Webb 2007). As herbivores present a selective pressure for trait divergence on co-occurring plants (Becerra 2007; Kursar *et al.* 2009), we expected to find co-occurring species that are also phylogenetically distant.

The cerrado is characterised by marked rainfall seasonality and experiences a pronounced dry season (Gottsberger & Silberbauer-Gottsberger 2006). The nutrient poor, well drained, acid soils are additional environmental constraints for plant growth in this vegetation types (Gottsberger & Silberbauer-Gottsberger 2006). In communities where resources are not abundant, such as the cerrado (Gottsberger & Silberbauer-Gottsberger 2006), plants tend to concentrate their investments in defenses against herbivory (Coley & Barone 1996; Fine *et al.* 2006), since they cannot replace damaged tissues as fast as in communities with abundant resources (Janzen 1974; Coley *et al.* 1985). So, herbivory is expected to be strong in cerrado plant communities, selecting species with a great investment in defense traits and determining their spatial distribution.

Additionally, the cerrado vegetation seems to present a high specificity between herbivores and host plants (Marquis *et al.* 2002; Dyer *et al.* 2007). For example, Diniz and Morais (1997) found that faunal similarities among host plant genera, and even within genus, were low in cerrado vegetation. In communities with such a specialisation between herbivores and host plants, the effects of herbivory on the diversity of defense traits tend to be high, and the co-occurring species are expected to present different defense traits (Coley & Barone 1996; Becerra 2007). This divergence is expected to occur at fine spatial scales, since insect herbivores play an important divergence pressure, especially in distances smaller than 10 meters (Coley & Barone 1996; Becerra 2007). Thus, we expected to find an overdispersion among defense traits of co-occurring cerrado plant species at fine spatial scale.

In a nutshell, we addressed whether the levels of species co-occurrences were correlated

with defense traits against herbivory and with phylogenetic distances. We answered three questions: (1) are species that share similar traits against herbivory spatially more dispersed than expected by chance?; (2) are defense traits conserved on the phylogeny of the sampled plant species?; and (3) are closely related species spatially more dispersed than expected by chance?

## **2. METHODS**

### **2.1 Study site**

We surveyed a woodland cerrado site (21°58'05.3"S, 47°52'10.1"W), in São Carlos, São Paulo State, southeastern Brazil. The soil is a dystrophic Oxisoil, and the mean altitude is 850 m (Santos *et al.* 1999). Regional climate is mesothermic, subtropical, with rainy summer and not severely dry winter (Cwa; Köppen 1931). According to data collected on the meteorological station of São Carlos, from 1969 to 1998, the annual mean temperature is 21.3°C and the monthly precipitation is 131.3 mm.

### **2.2 Defense trait data**

In the rainy season of 2008, we placed a grid with contiguous 100 quadrats (each one with 25 m<sup>2</sup>), in which we sampled all woody individuals with stem diameter at soil level equal to or larger than 3 cm (SMA 1997). We identified the sampled species with an identification key (Batalha & Mantovani 1999) and comparing the collected material to vouchers lodged at Federal University of São Carlos and Brazilian Institute of Geography and Statistics herbaria. For species with more than ten individuals inside the quadrats, we randomly picked ten individuals for trait measurement (Cornelissen *et al.* 2003). For the species with less than ten individuals inside the quadrats, we made an extra effort, looking for other individuals nearby the quadrats and trying to reach 10 individuals per species.

We collected expanded leaves, without symptoms of herbivore and pathogen attack, and measured the following defense traits: specific leaf area, water content, trichomes, latex content, toughness, chemical defenses, and nutritional quality (Agrawal & Fishbein 2006). Specific leaf area is positively related to mass-based maximum photosynthetic rate, or its potential relative growth (Cornelissen *et al.* 2003). Lower values of specific leaf area tend to correspond with relatively high investments in leaf defenses, particularly structural ones (Cornelissen *et al.* 2003), indicating fast growth and low palatability (Agrawal & Fishbein 2006). Low values of specific leaf area are correlated to low herbivory rate (Neves *et al.* 2010). Water content is also related to palatability, and a leaf with low water content might resist herbivory (Agrawal & Fishbein 2006). We collected two leaves per individual to assess specific leaf area and water content. We reserved the leaves in a fresh recipient and weighted them still fresh. We digitalised the leaves to determine leaf area with ImageJ 1.33 software (Rasband 2004). After that, we oven-dried each leaf sample at 80°C for 72 h, and then weighted the dry mass to obtain the specific leaf area (Cornelissen *et al.* 2003).

We sampled another leaf of the individuals and collected latex, an important physical defense against herbivory (Agrawal & Fishbein 2006; Agrawal & Konno 2009). We measured latex from 10 replicates from each species by cutting the tip of an intact leaf in the field and collecting the exuding latex onto a 1 cm disc filter paper. When latex stopped flowing and was absorbed on the filter paper, we covered it with another dry filter paper. We oven-dried the discs at 75°C for 24 h, and weighted them (Agrawal & Fishbein 2006). We measured leaf toughness with a force gauge penetrometer (dinamometer DFE 010, Chatillon). We used the conical tip to penetrate the surface in each side of the mid-rib. For statistical analyses, we used the mean of these two measures. Leaf toughness is related to nutritional and defense components (Agrawal & Fishbein 2006) and is considered the main defense trait against herbivore activity (Coley & Barone 1996). Trichomes are also important physical defenses against herbivory. We used five replicates for each species and counted trichomes on upper and lower sides of 28 mm<sup>2</sup> leaf discs with a dissecting microscope (Agrawal & Fishbein 2006).

We determined presence of chemical compounds on leaves following procedures described by Falkenberg *et al.* (2003). We determined presence of alkaloids, terpenoids, and tannins – chemicals frequently found in Brazilian plants that could work as defense against herbivores (Lima 2000). We used a series of three essays, Mayer, Dragendorff, and Wagner reactions to determine presence of alkaloids, considering positive the samples that reacted to at least two essays (Falkenberg *et al.* 2003). We used Liebermann-Burchard and Salkowisk reactions to



test the presence of terpenoids and a ferric chloride reaction to determine presence of tannins (Falkenberg *et al.* 2003). Nutritional quality may also influence the attack to vegetal tissue, since higher C:N ratios might decrease the nitrogen acquisition by the herbivore (Agrawal & Fishbein 2006), which may lead to decreased herbivore attack due to the difficulty to assess the nitrogen (Coley & Barone 1996; Agrawal & Fishbein 2006). Total leaf carbon (C) and nitrogen (N) concentrations were measured from five replicates from each species to assess the C:N ratio. This measure is considered as an indicator of plant nutritional quality (Agrawal & Fishbein 2006). The C and N concentrations samples were determined by the Laboratory of Stable Isotopes of the University of São Paulo. Our defense traits are related to chewing insects, since, in tropical plant communities, folivorous insects are the most important consumers, and chewing insects contribute with 75% or more of the annual leaf consumption (Coley & Barone 1996).

We used the mean of each trait to calculate the pairwise Euclidean distances of species, standardising the data to zero mean and unit variance, with the Vegan package (Oksanen *et al.* 2009) in R environment (R Development Core Team 2009). We calculated the pairwise co-occurrence ( $C$ ) based on proportional similarity (Schoener 1970) as:

$$C_{ih} = 1 - 0.5 \sum |p_{ij} - p_{hj}|,$$

where  $C_{ih}$  is the co-occurrence of species  $i$  and  $h$ ,  $p_{ij}$  is the proportion of occurrences of the  $i$ th or  $h$ th species in the  $j$ th quadrat. With this index, we obtained the co-occurrence degree of species in the space: the closer to 1 the  $C$  value, the more co-occurring the pair (Schoener 1970). As the 100 quadrats were close to each other, we used 50 randomly picked quadrats to calculate the co-occurrence index. So, we decreased the possible bias due to the proximity of the individuals within two quadrats. We obtained the co-occurrence matrix, using the Picante package (Kembel *et al.* 2009) in R environment (R Development Core Team 2009). Then, we compared the correlation coefficient between  $C$  values and the Euclidean distances of all species pairs to a null model generated from 1,000 randomisations of the trait matrix (Mantel test; Manly 2000), also using the Vegan package (Oksanen *et al.* 2009).

### 2.3 Phylogenetic data

We examined the spatial phylogenetic structure of co-occurring woody species in cerrado by comparing the degree of co-occurrence of species pairs in the quadrats to the phylogenetic

distance between them. We initially constructed a phylogenetic tree using Phylomatic software, a phylogenetic database and a toolkit to assembly phylogenetic trees (Webb & Donoghue 2005). The generated tree was based on references of molecular phylogenies (APG III 2009). We assigned branch lengths to the phylogenetic tree using the Branch Length Adjustment averaging algorithm of the Phylocom 4.1 software (Webb *et al.* 2009). The branch length was based on minimum ages of nodes determined for genera, families, and higher clades according to Davies *et al.* (2004), by spacing undated nodes evenly between nodes in the trees. Finally, we compared the correlation coefficient between *C* values and phylogenetic distances of all species pairs to a null model, in which the phylogenetic relationships among species were randomised (Mantel test; Manly 2000).

We investigated whether the functional traits were phylogenetically conserved or convergent in the phylogeny of local tree assemblage, using the analysis of traits module implemented in Phylocom software (Webb *et al.* 2009). In this method, we analysed the variance of the phylogenetically independent contrasts (PICs) to test which traits presented phylogenetic signal. Phylogenetic signal may be defined as the tendency of closely related species to resemble each other (Webb *et al.* 2009). If the evolution of some trait is conserved in the phylogeny, the divergences will be small and related species will be similar to each other (Webb *et al.* 2009). To test the significance of the phylogenetic signal, we compared the observed variance of the PICs with pseudo-variances generated by randomisation of the trait values in the phylogenetic tree (Blomberg *et al.* 2003). We also used the Picante package (Kembel *et al.* 2009) in R environment (R Development Core Team 2009).

### 3. RESULTS

We sampled 2,062 individuals, comprising 61 species and 29 families (Fig. 1, Supporting information). We obtained trait defense data to specific leaf area, water content, trichomes, latex, toughness, alkaloids, terpenoids, tannins, and nutritional quality (Supporting information). We did not find significant correlation between the co-occurrence of species and neither defense traits against herbivory ( $P > 0.05$ , Table 1) nor phylogenetic distances ( $R = 0.10$ ;  $P = 0.09$ ). However, we found significant phylogenetic signal for specific leaf area, water content, latex, and nutritional quality (Table 2).

#### 4. DISCUSSION

We investigated the influence of defense traits against herbivory and phylogeny on patterns of co-occurrence of tree species in cerrado. We expected to find co-occurring defense traits more different than expected by chance, due to the decrease of conspecific individuals caused by herbivory at fine spatial scale (Coley & Barone 1996; Becerra 2007). However, our results indicated that trait similarity did not limit species co-occurrence at fine spatial scales of woody cerrado plant species. Evidence of correlation between the defense traits and species co-occurrence would indicate a determinant role of herbivory in the cerrado. So, the herbivory in cerrado may not be strong enough to determine the spatial distribution of the woody species at fine spatial scale. In addition, environmental filters and herbivory may act in opposite directions, generating random co-occurrences relative to functional differences and phylogenetic distances. Thus, the herbivory may not decrease the functional similarity and the phylogenetic relatedness of the co-occurring plant species in cerrado.

The strength of the herbivory in plants is associated mainly to nutritional quality of the soil that may result in leaves with low value for herbivores (Fine *et al.* 2006). More nutrients available in the soils are related to species less defended against herbivory (Neves *et al.* 2010). In cerrado, the soils present low nutritional quality, especially low availability of nitrogen and phosphorus, and might present low herbivory rate in relation to other vegetation types (Gottsberger & Silberbauer-Gottsberger 2006; Neves *et al.* 2010). For example, leaves of forest trees, where soils were richer in nutrients and organic matter, suffered consumption rates three times higher than those recorded for cerrado leaves (Neves *et al.* 2010). Although leafcutter ants remove about 13-17 percent of the annual leaf production in savannas (Costa *et al.* 2008), quantification of the impact of herbivores in savannas are very rare (Marquis *et al.* 2002; Costa *et al.* 2008). Therefore, herbivory may not be strong enough to determine the spatial distribution of the woody species.

The several environmental filters in cerrado, such as drought, fire, and nutrient-poor soils (Gottsberger & Silberbauer-Gottsberger 2006), also affect the co-occurrence of plant species at fine spatial scale (Silva & Batalha 2009; Silva & Batalha 2010). Environmental filters tend to select co-occurring species with similar niches, that is, species with similar functional traits, because only those species with similar tolerances to the environmental constraints may survive (Chase 2003). In this case, one would find two opposing forces: herbivory leading to

trait overdispersion and environmental filters leading to trait clustering. As selection, by definition, is the relationship between a trait and fitness (Strauss & Irvin 2004), there would be a trade-off between overcoming herbivory and overcoming water and nutrient stress. For instance, in African savannas, bottom-up soil nutritional factors and top-down herbivory have both been suggested to control distribution patterns (Stock *et al.* 2010). In our study, most of functional traits may also be selected by environmental filters, such as specific leaf area, water content, toughness, and nutritional quality (Cornelissen *et al.* 2003; Pais & Varanda 2003; Neves *et al.* 2010). Thus, environmental filters and herbivory may act in opposite directions, with similar strength (Cavender-Bares *et al.* 2006), creating random co-occurrences relative to functional differences and phylogenetic distances.

The phylogenetic pattern of co-occurring species depends on the evolutionary history of species traits, the interaction between herbivores and plants, and the environmental filters (Webb *et al.* 2002; Becerra 2007). However, we found neither clustered nor overdispersed phylogenetic pattern at fine spatial scale. In some genera of tropical forests, phylogeny and defense traits may not be correlated due to the rapid evolution of antiherbivore defenses in one genus of tropical forest (Kursar *et al.* 2009). However, in our community-level approach, this absence of correlation may be partly attributed to the random distribution of most defense traits in the phylogeny of cerrado plants. Wherever defense traits are not conserved in the phylogeny, neither herbivory nor environmental filters may determine the phylogenetic pattern of the spatial distribution of plants (Becerra 2007; Silva & Batalha 2009). Although trait conservatism is very common in lineages of plants (Prinzing *et al.* 2001; Ackerly 2003; Reich *et al.* 2003), we may expect a random distribution of traits in rich communities, such as the Brazilian cerrado (Castro *et al.* 1999). In these rich communities, trait evolution tends to be a complex mixture of conservatism and convergence (Webb *et al.* 2002). As a consequence, overall trait conservatism in the phylogeny of cerrado woody species may be hard to detect (Silva & Batalha 2009).

Nevertheless, the phylogenetic signals observed in some defense traits reinforced the idea that environmental filters and herbivory may act in opposite direction, generating random species co-occurrences. As a matter of fact, most of the conserved traits we found (specific leaf area, leaf water content, and nutritional quality) are traits also related to the environmental filters (Cornelissen *et al.* 2003). For instance, nutrient-poor soils are positively correlated to low specific leaf area (Ordonéz *et al.* 2009). Comparisons between the same genus of cerrado and forest species showed that specific leaf area is lower in the cerrado, where availability of water and nutrients in the soil are low (Hoffmann & Franco 2008).

Cerrado physiognomies with intense drought and poor soils are expected to assemble species with low specific leaf area, leaf water content, and nutritional quality (Pais & Varanda 2003). Thus, conserved traits that act as defense traits against herbivory may be selected by herbivores towards an overdispersed pattern (Kursar *et al.* 2009) and, at the same time, be selected by environmental filters towards a clustered pattern (Webb *et al.* 2002), generating a random co-occurrences of species.

Our results also supported that the associations of herbivores and plants may not be as tight as predicted by literature. More diffuse associations may have more generalist adaptations, because selection pressures of defense traits conflict with multiple herbivores (Strauss & Irwin 2004). In communities where the species present such interactions, community-level overdispersion in defense traits is less likely to occur (Becerra 2007). Although there is evidence of high degree of specialisation between host plants and herbivores in cerrado (Diniz & Morais 1997; Marquis *et al.* 2002), few species of plants were studied, preventing to a certain extent the generalisation of this statement. Here we studied the whole tree community and the defense traits associated to chewing insects, the most important consumers in tropical plant communities (Coley & Barone 1996). In this community context, random spatial distribution of defense traits against herbivory may also be explained by a diffuse interaction between plants and herbivores.

Plant-herbivore coevolution and its impact on defense traits have focused on a small number of species and populations (Agrawal & Fishbein 2006; Becerra 2007; Kursar *et al.* 2009). However, our approach focused on the community, which may be structured by a combination of processes acting simultaneously and in opposite directions (Kraft *et al.* 2007), such as environmental filtering and herbivory. Consequently, a clear pattern of functional and phylogenetic overdispersion may not emerge in plant defense traits in cerrado. Moreover, it is important to include all possible species that may contribute with information about environmental filtering and species interactions. Accordingly, future studies in cerrado should also consider the herbaceous species, which represents twice the number of tree species (Castro *et al.* 1999).

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Table 1. Correlation between the co-occurrence of species in a southern cerrado site (21°58'05.3"S, 47°52'10.1"W) and the defense traits against herbivory: specific leaf area, water content, toughness, trichomes, latex, nutritional quality, alkaloids, terpenoids, and tannins. No correlation was significant.

<b>Trait</b>	<b>R</b>	<b>P</b>
Specific leaf area	0.08	0.19
Water	-0.05	0.70
Toughness	0.14	0.09
Trichomes	0.01	0.13
Latex	-0.01	0.29
C:N ratio	-0.04	0.72
Alkaloids	-0.02	0.44
Terpenoids	0.01	0.35
Taninns	0.11	0.16

Table 2. Phylogenetic signal to defense traits, measured from the variance of the phylogenetically independent contrasts in tree species of a southern cerrado site (21°58'05.3"S, 47°52'10.1"W). Test for phylogenetic signal in each trait sampled: specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ); leaf water content ( $\text{mg cm}^{-2}$ ); leaf toughness (N); trichome density ( $\text{cm}^{-2}$ ); latex content (mg); C:N (carbon: nitrogen ratio); and presence of alkaloids, terpenoids, and tannins determined following Falkerberg et al. (2003).

	Observed	Random	
	PICs	PICs	P
Specific leaf area	0.016	0.023	0.033 <sup>*</sup>
Water	0.017	0.023	0.044 <sup>*</sup>
Toughness	0.021	0.024	0.26
Trichomes	0.036	0.024	0.919
Latex	0.011	0.024	0.029 <sup>*</sup>
C:N	0.012	0.024	0.001 <sup>***</sup>
Alkaloids	0.016	0.024	0.265
Terpenoids	0.021	0.022	0.303
Tannins	0.017	0.019	0.426

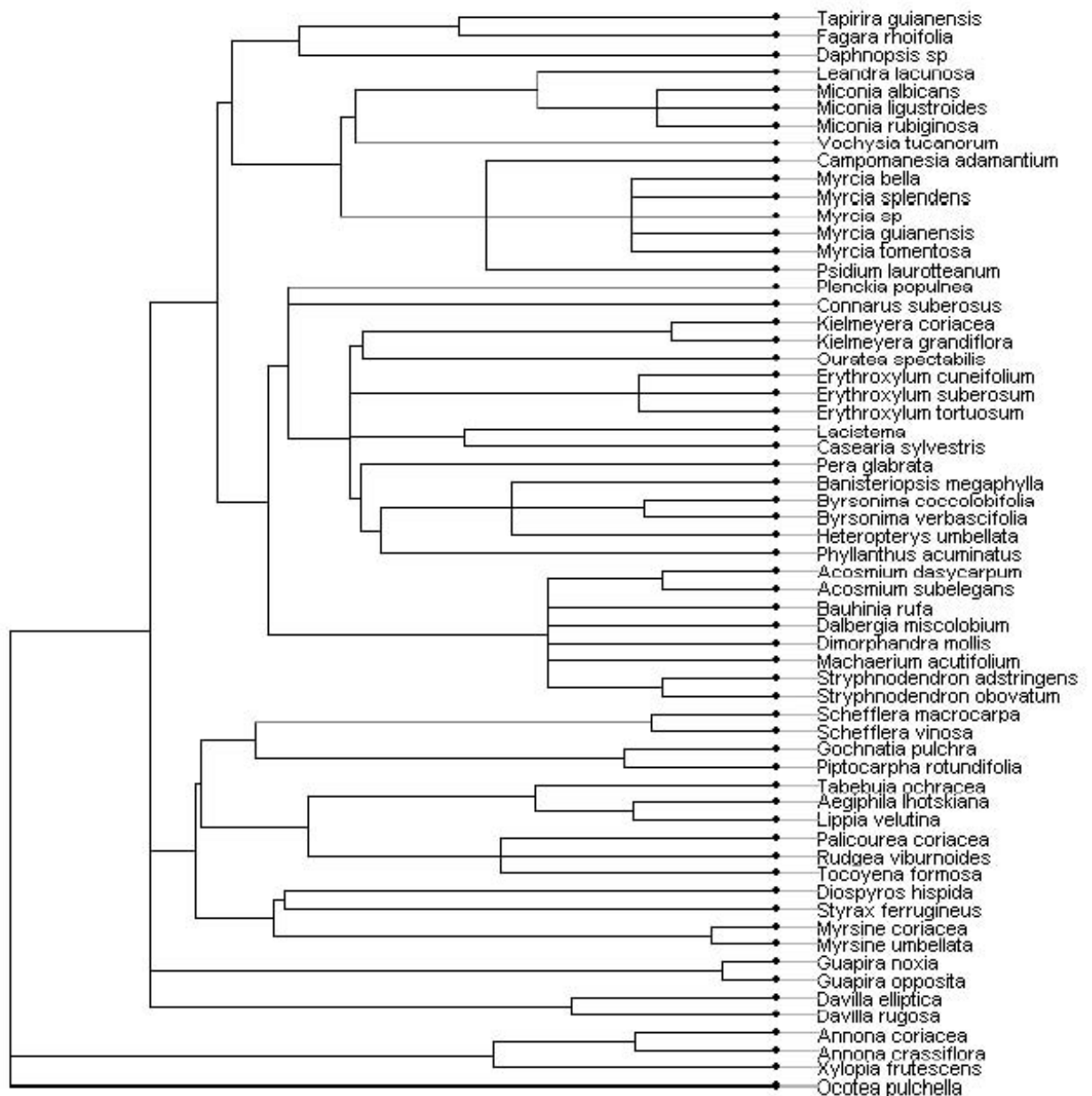


Fig. 1. Phylogenetic tree of species sampled in a southern cerrado site (21°58'05.3"S, 47°52'10.1"W). The relationship among species was based on Davies *et al.* (2004).

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