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Defesas contra herbivoria no cerrado: síndromes de defesa e
originalidades

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de mestre em Ecologia e Recursos Naturais.

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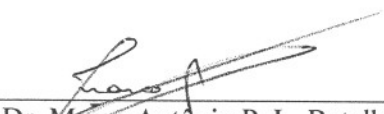
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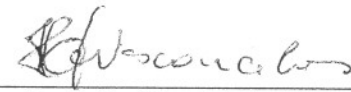
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Resumo

As plantas possuem traços contra herbivoria que podem ocorrer conjuntamente e aumentar a eficiência da defesa. Testamos se há síndromes de defesa em uma comunidade de plantas do cerrado e caso haja, se elas apresentam sinal filogenético. Medimos nove traços de defesa em uma comunidade de cerrado *sensu stricto* no sudeste do Brasil. Testamos a correlação entre todos os pares de traços e agrupamos as espécies em síndromes de defesa de acordo com os traços. A maioria das correlações par a par dos traços foi complementar. Plantas com menores áreas foliares específicas apresentaram também folhas duras, com menos nitrogênio, com mais tricomas e com taninos. Encontramos cinco síndromes: duas com baixos valores de defesa e alta qualidade nutricional, duas com altos valores de defesa e baixa qualidade nutricional e uma com traços compensando uns aos outros. Houve duas estratégias de defesa contra herbivoria predominantes no cerrado: as síndromes de “tolerância” e de “baixa qualidade nutricional”. Filogenia não determinou o conjunto de traços que as espécies apresentaram; então, postulamos que a herbivoria atua como um fator biótico selecionando esses traços.

A complementaridade permite a coexistência das espécies e um uso mais eficiente do nicho. Originalidade de uma espécie é o quanto aquela espécie contribui para a raridade de traços. Testamos a relação entre abundância e as originalidades filogenética e fenotípica e comparamos a extinção baseada na abundância com extinções aleatórias. A abundância não esteve relacionada com as originalidades, que por sua vez, não estiveram relacionadas entre si. Extinções baseadas na abundância não diferiram do acaso. Entretanto, as originalidades estiveram concentradas em poucas espécies e quatro das mais originais estavam entre as mais raras. Essas espécies contribuíram para a raridade de traços mais do que as espécies comuns e podem contribuir para dinâmicas compensatórias e manutenção da estabilidade da comunidade. Logo, a abundância das espécies pode não ser um fator predominante na manutenção das funções no cerrado.

Abstract

Plants have traits against herbivory that may occur together and increase defense efficiency. We tested whether there are defense syndromes in a cerrado community and, if so, whether there is a phylogenetic signal in them. We measured nine defense traits from a woodland cerrado community in southeastern Brazil. We tested the correlation between all pairs of traits and grouped the species into defense syndromes according to their traits. Most pairwise correlations of traits were complementary. Plants with lower specific leaf area also presented tougher leaves, with low nitrogen, more trichomes, and tannins. We found five syndromes: two with low defenses and high nutritional quality, two with high defenses and low nutritional quality, and one with traits compensating each other. There were two predominant strategies against herbivory in cerrado: “tolerance” and “low nutritional quality” syndromes. Phylogeny was not determining the suite of traits species presented; so, herbivory could be regarded as a biotic factor selecting these traits.

Complementarity allows species coexistence and more efficient use of niche. Originality of a species is how much that species contributes to rarity of traits. Here we (1) tested the relation between abundance and both phylogenetic and phenotypic originalities and (2) compared abundance-based extinctions to random ones. We measured nine defense traits, phylogenetic information and abundance from a woodland cerrado community in southeastern Brazil. Abundance was not related to neither phylogenetic nor functional originalities; phylogenetic and phenotypic originalities were not related. Abundance-based extinctions were not different from random. However, the originalities were concentrated in few species and four of the more original species were among the rarest. These species contribute to rarity of traits more than common ones and they may contribute to compensatory dynamics and to maintenance of community stability. Thus, species abundance may not be a predominant factor to the maintenance of functions in cerrado.

Introdução Geral

Conjuntos de traços de defesas contra tipos diversos de herbívoros tendem a ser favorecidos, pois reduzem o custo da defesa, de modo que, respostas mais gerais devem estar presentes em toda a comunidade (Núñez-Farfán et al. 2007). Por outro lado, defesas para herbívoros específicos são mais custosas e podem reduzir a resistência a outros herbívoros e patógenos, assim tendem a ser induzidas apenas na presença destes herbívoros (Núñez-Farfán et al. 2007, Thaler et al. 1999, Fordyce & Malcom 2000). A presença de um determinado traço de defesa nas espécies pode covariar com a presença de outros traços, formando conjuntos de traços que se podem definir como “síndromes de defesa” (Agrawal & Fishbein 2006). Como a pressão de seleção da comunidade de herbívoros está sendo exercida sobre toda a comunidade vegetal, as mesmas síndromes de defesas devem ocorrer em várias espécies. Como as plantas de cerrado estão crescendo em solos pobres (Haridasan 2000) a reposição de folhas perdidas por herbivoria é mais custosa (Fine et al. 2006). Por isso, o dano causado pela herbivoria no cerrado é reduzido devido tanto à fenologia – o período de produção de novas folhas é distinto do pico de herbívoros – quanto a alguns traços das folhas, como dureza, baixos teores de nitrogênio e água e alto teor de fenóis (Marquis et al. 2002). A herbivoria possui um papel importante para o cerrado, tanto diretamente pela influência no crescimento e reprodução das plantas, quanto pela interação com fatores abióticos (Marquis et al. 2002). Esperamos, pois, que a herbivoria seja um filtro ambiental muito forte no cerrado, selecionando espécies com grande investimento em traços de defesa.

No primeiro capítulo, testamos a correlação entre os traços de defesa contra herbivoria e sua interação com a filogenia do componente arbóreo-arbustivo de uma área de cerrado sensu stricto no estado de São Paulo. Procuramos responder as seguintes perguntas: (1) As plantas do cerrado apresentam conjunto de traços similares que caracterizam síndromes de

defesa?; (2) Se sim, Quais são essas síndromes?; e (3) Há sinal filogenético nas síndromes de defesa contra herbivoria?

No segundo capítulo, utilizamos os traços de defesa contra herbivoria e as relações filogenéticas das espécies do capítulo anterior. Com esses dados, determinamos as originalidades filogenéticas e fenotípicas das espécies. Originalidade de uma espécie é uma medida de quanto aquela espécie contribui para a raridade de traços na comunidade (Pavoine et al. 2005). Espécies originais, devido a seus traços raros, são mais complementares às outras espécies (Pavoine et al. 2005). Complementaridade permite a coexistência das espécies e o uso mais eficiente do nicho (Petchey 2003). Nesse capítulo, testamos a relação entre a abundância e a originalidade. Procuramos responder as seguintes perguntas: (1) As espécies mais abundantes são filogeneticamente mais originais?; (2) As espécies mais abundantes são fenotipicamente mais originais?; (3) As medidas de originalidade filogenética e fenotípica estão relacionadas?; (4) Os valores de originalidades estão concentrados em poucas espécies?; (5) Extinções simuladas das espécies baseadas nas suas abundâncias são diferentes do acaso?

Capítulo 1

Defense syndromes against herbivory in cerrado plant community

Danilo Muniz da Silva & Marco Antônio Batalha

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Defense syndromes against herbivory in cerrado plant community

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Defense syndromes against herbivory in cerrado plant community

Abstract

Plants have traits against herbivory that may occur together and increase defense efficiency. We tested whether there are defense syndromes in a cerrado community and, if so, whether there is a phylogenetic signal in them. We measured nine defense traits from a woodland cerrado community in southeastern Brazil. We tested the correlation between all pairs of traits and grouped the species into defense syndromes according to their traits. Most pairwise correlations of traits were complementary. Plants with lower specific leaf area also presented tougher leaves, with low nitrogen, more trichomes, and tannins. We found five syndromes: two with low defenses and high nutritional quality, two with high defenses and low nutritional quality, and one with traits compensating each other. There were two predominant strategies against herbivory in cerrado: “tolerance” and “low nutritional quality” syndromes. Phylogeny was not determining the suite of traits species presented; so, herbivory could be regarded as a biotic factor selecting these traits.

Key-words: defense traits, herbivores, savanna, trade-off

Introduction

Plants have two defense strategies against herbivory: tolerance, the ability to maintain fitness independently of herbivory damage, and resistance, the possession of traits that avoid or deter herbivory (Mauricio 2000). It is difficult for plants growing in poor soils to replace biomass lost to herbivores, so resistance should be the predominant defense strategy in such situations (Fine et al. 2006). Defense traits can be structural (such as trichomes, spines, and leaf toughness), chemical, or nutritional (Agrawal and Fishbein 2006, Hanley et al. 2007).

Structural defenses are morphological or anatomical traits that are advantageous to the plant by avoiding that herbivores feed upon them, from protuberances to increased cell wall toughness (Craine et al. 2003, Hanley et al. 2007). Nutritional defenses are traits that impose difficulties for absorption of nutrients by herbivores, especially nitrogen, due to poor nutritional materials (While 1993, Agrawal and Fishbein 2006). Chemical defenses are toxic or repulsive compounds or enzyme inhibitors (Thaler et al. 1999, Craine et al. 2003). Structural and chemical traits have investment costs along with defense benefits, and, thus, are under selection (Craine et al. 2003, Hanley et al. 2007, Núñez-Farfán et al. 2007). These traits may occur together and be complementary to each other, increasing defense efficiency; for example, chemical and physical traits provide a greater level of defense when they occur together (Berenbaum 1991). Thus, we expect some defense traits against herbivory to co-occur in a given species.

Since suites of traits against several kinds of herbivores tend to be favored to reduce costs associated to defense, general responses should be present in the whole community (Núñez-Farfán et al. 2007). Moreover, defense against specific herbivores is more costly and can reduce resistance against other herbivores and pathogens, defenses tend to be induced only in the presence of the specific herbivore (Thaler et al. 1999, Fordyce and Malcon 2000, Núñez-Farfán et al. 2007). Two or more traits may be positively correlated, resulting in suites of covarying traits that may define “defense syndromes” (Agrawal and Fishbein 2006). As long as the herbivore community implies selective pressure over the whole plant community, the same defense syndromes should be present on most species.

Since cerrado (Brazilian savanna) plants grow in poor soils (Haridasan 2000), leaf replacement demands more costs to them (Fine et al. 2006). Therefore, herbivory damage is minimised in cerrado by both leaf phenology – that is, new leaves in periods distinct from herbivore peaks – and leaf traits, such as toughness, low levels of nitrogen and water, and high levels of phenolic compounds (Marquis et al. 2002). Herbivory has an important role in

cerrado ecology, either directly, by influencing plant growth and reproduction, or indirectly, by the interaction with abiotic factors (Marquis et al. 2002). Herbivory restricts plant distribution, acting as an environmental filter (Harley 2003). Environmental filters tend to select species with similar traits that allow them to survive certain pressures (Fukami et al. 2005). We expect, then, herbivory to be a strong environmental filter in cerrado, selecting species with high investment on defense traits.

Functional traits generally present phylogenetic conservatism on plant lineages (Ackerly 2003). If so, phylogenetic proximity allows two species to respond similarly to environmental processes, due to traits inherited from common ancestry (Webb et al. 2002, Núñez-Farfán et al. 2007). However, strong selection pressure can also lead two less related species to respond similarly due to adaptative convergence (Webb et al. 2002, Núñez-Farfán et al. 2007). At higher phylogenetic scales, defense traits seem to be more conserved, whereas, at lower scales, they seem to be convergent (Agrawal and Fishbein 2006, Fine et al. 2006). For example, different genera tend to present different suites of defense traits, indicating phylogenetic clustering (Fine et al. 2006). However, in the genus *Asclepias*, defense traits are not congruent to phylogeny, indicating “phylogenetic overdispersion” (Agrawal and Fishbein 2006). We expect, then, at community level, defense syndromes to be conserved.

Although there are studies on defense syndromes at genus level (Agrawal and Fishbein 2006, Becerra 2007) and among pairs of genera in forest communities (Fine et al. 2006), there are no studies at community level. Particularly in the Brazilian cerrado, herbivory surveys are restricted to only one species (*e.g.*, Varanda and Pais 2006) or only a defense trait, such as presence of extra-floral nectaries to ant association (*e.g.*, Oliveira 1997, Oliveira and Freitas 2004) or latex presence (*e.g.*, Diniz et al. 1999). Field mensurative experiments of defense syndromes in cerrado plant communities could test the extrapolation of syndrome theory, as well as relate defense traits to ecological and evolutionary constraints of savanna areas.

If defense syndromes are phylogenetically convergent, then one may suggest that herbivory as a selective force is common and widespread; if, however, they are phylogenetically conserved, then one may suggest that there is a phylogenetic signal and that common ancestry can explain the association (Agrawal and Fishbein 2006). We expect cerrado plants to present high investment in structural defenses, constituted primarily by carbohydrates, and low investment in chemical defense, especially nitrogen compounds, because the cerrado is a nutrient-limited community (Haridasan 2000, Craine et al. 2003).

The aim of this study was to test, in a cerrado disjunct site, the correlation of defense traits and their interaction with phylogeny of woody plants. We addressed the following questions: *i*) Do cerrado plant species present similar suites of traits that characterise defense syndromes?; *ii*) If so, which are these syndromes?; and *iii*) Is there a phylogenetic signal in defense syndromes against herbivory?

Methods

Study area and sampling

We carried out this study at the Federal University of São Carlos, southeastern Brazil (21°58'05.3"S, 47°52'10.1"W, 815-890 m a.s.l.; Santos et al. 1999). Regional climate is seasonal, with dry winter and wet summer, defined as Cwa (Köppen 1931). The study site is located at northeastern portion of the campus and is covered by woodland cerrado, a savanna with dense tree cover (Sarmiento 1984, Santos et al. 1999). The study site presents poor soils, with low pH, low content of organic matter and nitrogen, low cation exchange capacity, high aluminum saturation and high proportion of sand (Table A1) and are classified as Oxisol (Santos et al 1999).

We placed a 50 m x 50 m grid, with 100 5 m x 5 m contiguous plots, in which we sampled

all individuals belonging to the woody component, that is, woody individuals with stem diameter at soil level equal to or higher than 3 cm (SMA 1997). We identified them to species level, by using identification keys based on vegetative characters (Batalha and Mantovani 1999) and comparing vouchers to herbarium collections. We checked species names and taxonomic information with Plantminer software (Carvalho et al. 2009). For each species in the sample, we drew randomly ten individuals to measure the traits (Cornelissen et al. 2003). When, for a given species, there were not ten individuals at the sample, we searched for additional individuals nearby the plots, making an extra effort to reach ten individuals for each species.

Defense traits

From each sampled individual, we collected mature leaves, that is, fully expanded and hardened leaves, with as less damage as possible (Cornelissen et al. 2003). We kept the leaves in a cooler to avoid water loss or deterioration, and took them as soon as possible to the laboratory, where we measured the following traits: nutritional quality, specific leaf area, water content, latex content, trichome density, toughness, presence of alkaloids, terpenoids, and tannins (Agrawal and Fishbein 2006).

We measured carbon (C) and nitrogen (N) concentration in leaves and calculated C:N ratio as an indicator of plant nutritional quality. We collected leaf samples from five replicates from each species. Analyses were conducted at University of São Paulo, using an elemental CHNS-O analyser (CE Instruments/EA 1110) to determine carbon and nitrogen concentration. Nutritional quality may influence herbivore attacks to plant tissue; that is, an elevated C:N ratio imposes difficulties for nitrogen acquisition by herbivores (Agrawal and Fishbein 2006). In some cases, herbivores avoid plants with low nutritional quality, whereas, in others, they increase herbivory rates to compensate for low nitrogen (Mattson 1980).

Specific leaf area is positively related to growth rate and to maximum photosynthetic rate (Cornelissen et al. 2003). Low values of specific leaf area are related to high investments on structural leaf defenses (Cornelissen et al. 2003), whereas high values indicate fast growing and high palatability (Agrawal and Fishbein 2006). Similarly, leaf water content increases palatability, and so a leaf with less water should be more resistant to herbivory (Agrawal and Fishbein 2006). To measure specific leaf area and water content, we collected two leaves from each individual, kept them in a cooler and weighted their fresh masses. We scanned the leaves and determined leaf area using the ImageJ 1.33 software (Rasband 2004). Then, we oven-dried them at 75°C during 72 h to obtain dry mass. Dividing leaf area by dry mass, we obtained specific leaf area (Cornelissen et al. 2003). We assigned leaf water content by the difference between fresh and dry mass, divided by leaf area (Agrawal and Fishbein 2006).

Latex is an important physical defense strategy against herbivory (Agrawal and Fishbein 2006). To measure latex content, we cut a leaf at the base and collected the latex with a filter paper until the flow stopped. We oven-dried the samples at 75°C during 24 h, then we weighted them. Trichomes are also important structural defenses (Agrawal and Fishbein 2006). We assigned trichome density by counting the number of trichomes in a 28 mm² circle, delimited near the leaf tip, on both top and bottom, with a dissecting microscope (Agrawal and Fishbein 2006). Toughness is related to defense and nutritional constituents, and should influence herbivore activities (Agrawal and Fishbein 2006). We used a penetrometer (dynamometer DFE 010, Chatillon, with a cone tip) to measure leaf toughness. We pushed the probe of the penetrometer through the leaf and recorded the maximum force required to penetrate it. We measured the toughness at each side of the mid-rib and used the mean as a single data point per plant (Agrawal and Fishbein 2006).

We determined presence of chemical compounds in leaves following Falkenberg et al. (2003). We assigned the presence of alkaloids, terpenoids, and tannins, which are chemical compounds frequently found in Brazilian plants that may work as defense against herbivores

(Lima 2000). We oven-dried the leaves, extracting them with methanol and filtering the extract after 48 h (Falkenberg et al. 2003). To alkaloids tests, we mixed 2 ml of hydrogen chloride and 2 ml of the methanol extract; we then heated the mixture for 10 minutes, waited until it cooled off and filtered it again (Falkenberg et al. 2003). After that, we used a series of three assays, Mayer, Dragendorff, and Wagner reactions, to determine the presence of alkaloids and, then, we considered as positive those samples that reacted to at least two out of the three (Falkenberg et al. 2003). To terpenoids tests, we first evaporated 2 ml of the methanol extract and to the residue we added 5 ml of chloroform. Then we used Liebermann-Burchard and Salkowisk reactions to test the presence of terpenoids (Falkenberg et al. 2003). To tannin tests, we first evaporated 5 ml of the methanol extract and to the residue we added 10 ml of distilled water. Then we used a ferric chloride reaction to determine the presence of tannins (Falkenberg et al. 2003).

We constructed a matrix with the mean of each continuous trait and presence or absence of binary traits for each species; when necessary, we log-transformed the variables to achieve normality; we standardised all defense traits to zero mean and unit variance. We also constructed a matrix with the phylogenetic independent contrast (PIC) of traits, which corrects each variable for phylogenetic dependence, by scaling its contrasts by its standard deviation related to phylogenetic distances, assuming a Brownian model of evolution (Felsenstein 1985). We applied a correlation test with Spearman's coefficient to all pairs of traits and to all pairs of phylogenetic independent contrast of traits.

We constructed an Euclidean distance matrix based on average values for the species. We then used K-means multivariate clustering (Legendre and Legendre 1998) to group the species into defense syndromes, such that species within each syndrome would have defense traits more similar to one another than to species in the other groups. We searched for species clustering from two to five groups, and we selected the best clustering number with the pseudo-statistics F (Calinski-Harabasz 1974). We did a principal component analysis and

constructed an ordination diagram to view the groups in relation to the traits (Legendre and Legendre 1998). We carried out all analyses in R (R Core Development Team 2008).

Phylogenetic analysis

We constructed a phylogenetic tree for the species in the sample using the Phylomatic software (Webb and Donoghue 2005). The lengths of the branches were estimated from maximum ages determined for genus, families, orders, and superior clades (Davies et al. 2004). We fixed the root and all dated nodes, and then we extrapolated branches length placing the non-dated nodes evenly between dated nodes or between dated nodes and terminals (species), using the Bladj algorithm in the Phylomatic software (Webb and Donoghue 2005). We calculated phylogenetic distances among all pairs of species using the Phylocom 4.01b software (Webb et al. 2008). We did a Mantel correlogram with 999 randomisations, correlating the trait matrix to the phylogenetic distance matrix. We calculated Mantel statistic for each distance class and we tested for significance by permutations, using Bonferroni's correction to test for the global significance (Legendre and Fortim 1989).

Results

We found 2,062 individuals, belonging to 61 species and 29 families, obtaining defense traits for each species (tables 1 and 2). Spearman's coefficient between the pairs of traits and between PICs were low, with the highest values around 0.6 (table 3). We found significant negative correlations between: C:N and specific leaf area; specific leaf area and water; specific leaf area and trichomes; specific leaf area and toughness; specific leaf area and tannins; and latex and trichomes (table 3). We found significant positive correlations between C:N and

toughness, water and latex, and water and toughness (table 3). We found the same pattern for PICs, except that the correlations of latex were not significant, tannins were correlated to alkaloids and not to specific leaf area, and C:N and trichomes were positively correlated (table 3).

We found five groups of defense traits (table 2, figure 1). The first group was related to latex; the second group was more related to high values of specific leaf area and low ratios of C:N; the third group was related to low trichome densities and C:N ratios; and the fifth group was related to high values of trichomes and alkaloids; the fourth group was more related to low values of specific leaf area, to high values of C:N, and to the presence of chemical defenses (figure 1). The number of species varied among the groups (2, 28, 4, 26, and 1, respectively). We did not find relationships between trait distances and phylogenetic distances (figure 2).

Discussion

Most pairwise correlations of traits were complementary. For instance, plants with lower specific leaf area also presented tougher leaves, lower nitrogen content, more trichomes, and tannins. These traits are probably acting together to defend the plant against herbivory, as predicted by syndrome theory (Agrawal & Fishbein 2006). Nevertheless, there were also some trade-offs. Leaves with more water content were tougher and had lower specific leaf area. Although two correlations with latex and one with alkaloids also indicated trade-offs, there were only two species with latex and one with alkaloids. Relationships among traits are usually synergistic or present no trade-off (Steward & Keeler 1988, Agrawal & Fishbein 2006). Leaf trait relationships may suffer constraints by morphometry, that is, the range a given trait can assume depends on the variation on other traits. However, herbivory might also press selection over traits with multiple functions (Steward & Keeler 1988). Even if a trait

is related or evolved in response to other functions, it might contribute to anti-herbivore resistance of a given syndrome (Agrawal & Fishbein 2006).

We found the three types of syndromes proposed by the “defense syndrome triangle” theory (Agrawal & Fishbein 2006). Two syndromes found here (groups 2 and 3) corresponded to the “tolerance” syndrome. Species within these syndromes had low values of all defense traits and high values of nutritional quality. Leaves with low levels of defense are more consumed both in field and in laboratory conditions (Pérez-Harguindeguy et al. 2003). Thus, although we did not measure the amount of damage caused by herbivores, these species are expected to have tolerance to herbivory. Two other syndromes (groups 4 and 5) corresponded to the “low nutritional quality” syndrome. They had traits that deter herbivory and offer little nutrients. Species with these characteristics are expected to be less attacked by herbivores (Pérez-Harguindeguy et al. 2003). A last syndrome could correspond to the “nutrition and defense” syndrome, with tougher leaves and latex compensating high water content and absence of trichomes. Species in this syndrome should be attacked only by few herbivores that can overcome specific (latex) barriers and should be avoided by generalist herbivores (Pérez-Harguindeguy et al. 2003). Three of the syndromes presented one or few species and differed one from other by one trait (presence of alkaloids, absence of tannins, or presence of latex). Thus, there were basically two predominant strategies of defense against herbivory in the cerrado woody species we sampled.

As long as we did not find a phylogenetic signal, phylogeny was not determining the suite of traits the species presented and so herbivory could be regarded as a biotic factor selecting for these traits (Agrawal & Fishbein 2006). Furthermore, as the two predominant strategies were present in most species, these suites of traits are expected to respond well to several herbivores (Núñez-Farfán et al. 2007). Suites of diverse herbivores from different phylogenetic groups and guilds attack the same phenotypic hosts (Maddox & Root 1990). Since the selective pressure by herbivory is caused by suites of high diverse herbivores, the

response evolved against a species can act against another (Maddox & Root 1990). Moreover, the community of herbivores is expected to be generalist, acting on the whole plant community and not only on some phylogenetic groups (Agrawal & Fishbein 2006).

We should be careful to extrapolate these results to other savannas, because predominant herbivores in cerrado are leaf-cutter ants and other insects, whereas in other savannas they are large mammals living in big herds (Costa et al. 2008). Nevertheless, herbivory in cerrado is greater than or comparable to other terrestrial communities (Costa et al. 2008). It can decrease reproductive fitness or even lead to mortality of plants (Mundim 2009). Although almost half of species presented tolerance syndrome, the impact of herbivory, together with the nutrient-poor soils, makes tolerance strategy something unexpected as a defense against herbivory for cerrado species (Fine et al. 2006). Tolerance strategy can have evolved as a response to fire, which removes leaves less selectively than herbivores (Bond and Keeley 2005). Furthermore, cerrado plants may adjust their leaf phenology to escape in time from insects attack (Marquis et al. 2001). The few strategies we found may be the result from series of environmental filters, reducing the species pool sequentially, only to remain those with phenotypic conditions to survive all of them, that is, drought, fire, poor soils, and, finally, herbivory.

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Table 1 Numbers of sampled individuals of woody species in cerrado *sensu stricto* at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). In parenthesis the number of individuals sampled outside of the plots (see Methods).

Family	Species	Individuals
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	10 (9)
Annonaceae	<i>Annona coriacea</i> Mart.	10 (8)
Annonaceae	<i>Annona crassiflora</i> Mart.	10 (9)
Annonaceae	<i>Xylopia frutescens</i> Aubl.	10 (8)
Araliaceae	<i>Schefflera macrocarpa</i> (Cham. & Schltdl.) Frodin	10 (6)
Araliaceae	<i>Schefflera vinosa</i> (Cham. & Schltdl.) Frodin & Fiaschi	10 (0)
Asteraceae	<i>Gochnatia pulchra</i> Cabrera	10 (0)
Asteraceae	<i>Piptocarpha rotundifolia</i> (Less.) Baker	10 (0)
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	10 (0)
Celastraceae	<i>Plenckia populnea</i> Reissek	10 (0)
Clusiaceae	<i>Kielmeyera coriacea</i> Mart. & Zucc.	10 (1)
Clusiaceae	<i>Kielmeyera grandiflora</i> (Wawra) Saddi	10 (0)
Connaraceae	<i>Connarus suberosus</i> Planch.	10 (9)
Dilleniaceae	<i>Davilla elliptica</i> A. St.-Hil.	10 (6)
Dilleniaceae	<i>Davilla rugosa</i> Poir.	10 (9)
Ebenaceae	<i>Diospyros hispida</i> A. DC.	10 (0)
Erythroxylaceae	<i>Erythroxylum cuneifolium</i> (Mart.) O.E. Schulz	10 (4)
Erythroxylaceae	<i>Erythroxylum suberosum</i> A. St.-Hil.	10 (0)
Erythroxylaceae	<i>Erythroxylum tortuosum</i> Mart.	10 (0)
Euphorbiaceae	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	10 (1)
Fabaceae	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	10 (0)
Fabaceae	<i>Acosmium subelegans</i> (Mohlenbr.) Yakovlev	10 (6)
Fabaceae	<i>Bauhinia rufa</i> (Bong.) Steud.	10 (0)
Fabaceae	<i>Dalbergia miscolobium</i> Benth.	10 (0)
Fabaceae	<i>Dimorphandra mollis</i> Benth.	10 (3)
Fabaceae	<i>Machaerium acutifolium</i> Vogel	10 (6)
Fabaceae	<i>Stryphnodendron adstringens</i> (Mart.) Coville	10 (0)
Fabaceae	<i>Stryphnodendron obovatum</i> Benth.	10 (1)
Lacistemataceae	<i>Lacistema</i> sp. Sw.	10 (9)
Lauraceae	<i>Ocotea pulchella</i> (Nees) Mez	10 (0)
Malpighiaceae	<i>Banisteriopsis megaphylla</i> (A. Juss.) B. Gates	10 (9)
Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth	10 (0)
Malpighiaceae	<i>Byrsonima verbascifolia</i> (L.) DC.	2 (0)
Malpighiaceae	<i>Heteropterys umbellata</i> A. Juss.	10 (6)
Melastomataceae	<i>Leandra lacunosa</i> Cogn.	10 (7)
Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana	10 (0)
Melastomataceae	<i>Miconia ligustroides</i> (DC.) Naudin	10 (0)
Melastomataceae	<i>Miconia rubiginosa</i> (Bonpl.) DC.	10 (9)
Myrsinaceae	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.	10 (4)
Myrsinaceae	<i>Myrsine umbellata</i> Mart.	10 (0)
Myrtaceae	<i>Campomanesia adamantium</i> (Cambess.) O.Berg	10 (0)
Myrtaceae	<i>Myrcia bella</i> Cambess.	10 (0)
Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	10 (0)

Family	Species	Individuals
Myrtaceae	<i>Myrcia</i> sp. DC. ex Guill	10 (6)
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	10 (3)
Myrtaceae	<i>Myrcia tomentosa</i> (Aubl.) DC.	10 (6)
Myrtaceae	<i>Psidium laurotteanum</i> Cambess. in A.St.-Hil.	9 (7)
Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell	10 (7)
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	10 (7)
Ochnaceae	<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	10 (7)
Phyllanthaceae	<i>Phyllanthus acuminatus</i> Vahl	10 (8)
Rubiaceae	<i>Palicourea coriacea</i> (Cham.) K.Schum.	10 (8)
Rubiaceae	<i>Rudgea viburnoides</i> (Cham.) Benth.	10 (0)
Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	10 (0)
Rutaceae	<i>Fagara rhoifolia</i> (Lam.) Engl.	10 (7)
Salicaceae	<i>Casearia sylvestris</i> Sw.	10 (4)
Styracaceae	<i>Styrax ferrugineus</i> Nees & Mart.	10 (1)
Thymelaeaceae	<i>Daphnopsis</i> sp. Mart.	10 (6)
Verbenaceae	<i>Aegiphila lhotskiana</i> Cham.	10 (0)
Verbenaceae	<i>Lippia velutina</i> Schauer	10 (9)
Vochysiaceae	<i>Vochysia tucanorum</i> Mart.	10 (0)

Table 2 Defense traits (mean \pm sd, presence/absence for chemical defenses) for sampled species in cerrado *sensu stricto* at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). Group = group from K-means partitioning, Water = water content (mg cm⁻²), SLA = specific leaf area (cm² g⁻¹), Toughness (N), Trichomes = trichome density (trichomes cm⁻²), Latex (mg), C:N = carbon:nitrogen ratio.

Group	Species	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tanins
1	<i>Kielmeyera coriacea</i> Mart. & Zucc.	28 \pm 5	77 \pm 13	31 \pm 3	5 \pm 5	1 \pm 1	1.1 \pm 0.2	0	1	1
1	<i>Kielmeyera grandiflora</i> (Wawra) Saddi	34 \pm 9	77 \pm 13	41 \pm 9	9 \pm 3	0 \pm 0	1.9 \pm 0.4	0	0	1
2	<i>Acosmium subelegans</i> (Mohlenbr.) Yakovlev	17 \pm 3	82 \pm 14	17 \pm 5	0 \pm 0	56 \pm 123	1.0 \pm 0.2	0	1	1
2	<i>Aegiphila lhotskiana</i> Cham.	15 \pm 2	104 \pm 15	27 \pm 5	0 \pm 0	841 \pm 193	0.7 \pm 0.2	0	1	1
2	<i>Banisteriopsis megaphylla</i> (A. Juss.) B. Gates	15 \pm 3	127 \pm 28	18 \pm 6	0 \pm 0	617 \pm 331	0.4 \pm 0.2	0	0	1
2	<i>Byrsonima coccolobifolia</i> Kunth	22 \pm 3	97 \pm 16	20 \pm 0	0 \pm 0	14 \pm 12	0.8 \pm 0.1	0	0	1
2	<i>Casearia sylvestris</i> Sw.	16 \pm 3	124 \pm 20	10 \pm 0	0 \pm 0	143 \pm 114	0.7 \pm 0.2	0	0	1
2	<i>Dalbergia miscolobium</i> Benth.	18 \pm 3	76 \pm 10	20 \pm 0	0 \pm 0	11 \pm 10	0.8 \pm 0.3	0	0	1
2	<i>Daphnopsis</i> sp. Mart.	24 \pm 6	132 \pm 44	17 \pm 5	0 \pm 0	1 \pm 1	1.2 \pm 0.2	0	0	1
2	<i>Davilla elliptica</i> A. St.-Hil.	29 \pm 3	129 \pm 43	16 \pm 5	0 \pm 0	216 \pm 158	0.9 \pm 0.3	0	0	1
2	<i>Davilla rugosa</i> Poir.	28 \pm 3	188 \pm 40	11 \pm 3	0 \pm 0	228 \pm 134	0.8 \pm 0.3	0	0	1
2	<i>Dimorphandra mollis</i> Benth.	13 \pm 1	102 \pm 15	12 \pm 4	0 \pm 0	623 \pm 173	0.3 \pm 0.1	0	0	1
2	<i>Erythroxylum cuneifolium</i> (Mart.) O.E. Schulz	18 \pm 2	160 \pm 42	11 \pm 3	0 \pm 0	1 \pm 2	0.4 \pm 0.2	0	1	1
2	<i>Erythroxylum suberosum</i> A. St.-Hil.	18 \pm 3	90 \pm 13	19 \pm 3	0 \pm 0	0 \pm 1	1.3 \pm 0.4	0	1	1
2	<i>Erythroxylum tortuosum</i> Mart.	20 \pm 1	91 \pm 14	20 \pm 0	0 \pm 0	2 \pm 1	0.9 \pm 0.4	0	0	1
2	<i>Fagara rhoifolia</i> (Lam.) Engl.	17 \pm 3	106 \pm 15	13 \pm 5	0 \pm 0	247 \pm 101	0.5 \pm 0.2	0	1	1
2	<i>Gochnatia pulchra</i> Cabrera	21 \pm 6	103 \pm 23	10 \pm 0	0 \pm 0	2700 \pm 803	0.8 \pm 0.1	0	1	1
2	<i>Guapira noxia</i> (Netto) Lundell	10 \pm 1	104 \pm 24	31 \pm 7	0 \pm 0	17 \pm 25	0.9 \pm 0.2	0	1	1
2	<i>Guapira opposita</i> (Vell.) Reitz	11 \pm 1	120 \pm 28	19 \pm 7	0 \pm 0	38 \pm 55	0.8 \pm 0.2	0	1	1
2	<i>Heteropterys umbellata</i> A. Juss.	17 \pm 4	118 \pm 22	11 \pm 3	0 \pm 0	27 \pm 45	0.4 \pm 0.1	0	0	1
2	<i>Lacistema</i> sp. Sw.	28 \pm 8	157 \pm 43	10 \pm 0	0 \pm 0	519 \pm 86	0.6 \pm 0.2	0	0	1
2	<i>Leandra lacunosa</i> Cogn.	29 \pm 3	126 \pm 26	22 \pm 4	0 \pm 0	257 \pm 35	0.8 \pm 0.3	0	0	1
2	<i>Machaerium acutifolium</i> Vogel	11 \pm 2	92 \pm 11	14 \pm 5	0 \pm 0	214 \pm 123	0.9 \pm 0.2	0	0	1
2	<i>Miconia ligustroides</i> (DC.) Naudin	27 \pm 3	97 \pm 22	19 \pm 3	0 \pm 0	5 \pm 7	0.6 \pm 0.1	0	0	1
2	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.	20 \pm 1	126 \pm 21	12 \pm 4	0 \pm 0	308 \pm 93	0.5 \pm 0.1	0	1	1
2	<i>Phyllanthus acuminatus</i> Vahl	28 \pm 1	207 \pm 41	10 \pm 0	0 \pm 0	0 \pm 0	0.3 \pm 0.1	0	0	1
2	<i>Plenckia populnea</i> Reissek	21 \pm 5	106 \pm 12	12 \pm 4	0 \pm 0	0 \pm 0	0.7 \pm 0.2	0	1	1
2	<i>Stryphnodendron adstringens</i> (Mart.) Coville	18 \pm 1	81 \pm 15	22 \pm 4	0 \pm 0	24 \pm 48	0.7 \pm 0.1	0	0	1
2	<i>Stryphnodendron obovatum</i> Benth.	18 \pm 3	121 \pm 30	17 \pm 7	0 \pm 0	5 \pm 2	0.4 \pm 0.1	0	0	1

Group	Species	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tanins
2	<i>Xylopia frutescens</i> Aubl.	21 ± 2	197 ± 34	10 ± 0	0 ± 0	140 ± 131	0.4 ± 0.1	0	1	1
3	<i>Annona crassiflora</i> Mart.	25 ± 5	117 ± 25	20 ± 0	0 ± 0	380 ± 82	0.7 ± 0.1	0	0	0
3	<i>Lippia velutina</i> Schauer	17 ± 3	164 ± 60	14 ± 5	0 ± 0	926 ± 130	0.5 ± 0.1	0	0	0
3	<i>Palicourea coriacea</i> (Cham.) K.Schum.	18 ± 5	112 ± 21	29 ± 5	0 ± 0	2 ± 4	0.9 ± 0.4	0	1	0
3	<i>Vochysia tucanorum</i> Mart.	21 ± 3	107 ± 16	24 ± 5	0 ± 0	9 ± 14	1.2 ± 0.2	0	1	0
4	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	17 ± 3	79 ± 9	20 ± 5	0 ± 0	1040 ± 334	1.2 ± 0.2	0	0	1
4	<i>Annona coriacea</i> Mart.	28 ± 4	86 ± 17	27 ± 7	0 ± 0	204 ± 72	2.1 ± 0.5	0	0	1
4	<i>Bauhinia rufa</i> (Bong.) Steud.	19 ± 2	67 ± 5	16 ± 5	0 ± 0	954 ± 227	1.1 ± 0.2	0	1	1
4	<i>Byrsonima verbascifolia</i> (L.) DC.	40 ± 7	74 ± 7	25 ± 7	0 ± 0	2056 ± 793	0.7 ± 0.1	0	0	1
4	<i>Campomanesia adamantium</i> (Cambess.) O.Berg	28 ± 3	81 ± 14	13 ± 5	0 ± 0	604 ± 401	1.1 ± 0.2	0	1	1
4	<i>Connarus suberosus</i> Planch.	30 ± 6	65 ± 6	20 ± 0	0 ± 0	1403 ± 561	1.4 ± 0.2	0	1	1
4	<i>Diospyros hispida</i> A. DC.	33 ± 5	62 ± 7	23 ± 5	0 ± 0	708 ± 278	1.0 ± 0.3	0	1	1
4	<i>Miconia albicans</i> (Sw.) Triana	31 ± 7	91 ± 17	17 ± 5	0 ± 0	65100 ^a	0.7 ± 0.2	0	0	1
4	<i>Miconia rubiginosa</i> (Bonpl.) DC.	38 ± 4	64 ± 7	20 ± 0	0 ± 0	281 ± 52	0.7 ± 0.1	0	0	1
4	<i>Myrcia bella</i> Cambess.	33 ± 6	89 ± 12	17 ± 5	0 ± 0	1020 ± 308	1.2 ± 0.2	0	1	1
4	<i>Myrcia guianensis</i> (Aubl.) DC.	29 ± 4	64 ± 8	20 ± 0	0 ± 0	661 ± 370	1.3 ± 0.3	0	0	1
4	<i>Myrcia</i> sp. DC. ex Guill	28 ± 2	78 ± 8	12 ± 5	0 ± 0	1095 ± 504	0.9 ± 0.2	0	0	1
4	<i>Myrcia splendens</i> (Sw.) DC.	39 ± 5	104 ± 24	10 ± 0	0 ± 0	1067 ± 385	0.8 ± 0.1	0	0	1
4	<i>Myrcia tomentosa</i> (Aubl.) DC.	25 ± 3	87 ± 13	16 ± 5	0 ± 0	419 ± 138	1.1 ± 0.3	0	1	1
4	<i>Myrsine umbellata</i> Mart.	31 ± 3	84 ± 20	20 ± 0	0 ± 0	0 ± 0	1.1 ± 0.3	0	0	1
4	<i>Ocotea pulchella</i> (Nees) Mez	30 ± 6	70 ± 12	14 ± 5	0 ± 0	1445 ± 710	1.4 ± 0.2	0	1	1
4	<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	32 ± 7	63 ± 12	22 ± 5	0 ± 0	0 ± 0	2.3 ± 0.5	0	1	1
4	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	31 ± 2	74 ± 9	20 ± 0	0 ± 0	0 ± 0	0.9 ± 0.2	0	0	1
4	<i>Piptocarpha rotundifolia</i> (Less.) Baker	28 ± 8	96 ± 22	20 ± 0	0 ± 0	1304 ± 419	1.1 ± 0.3	0	1	1
4	<i>Psidium laurotteanum</i> Cambess. in A.St.-Hil.	38 ± 6	74 ± 14	18 ± 4	0 ± 0	1583 ± 133	1.3 ± 0.1	0	1	1
4	<i>Rudgea viburnoides</i> (Cham.) Benth.	25 ± 4	81 ± 14	33 ± 5	0 ± 0	687 ± 258	1.2 ± 0.2	0	0	1
4	<i>Schefflera macrocarpa</i> (Cham. & Schltdl.) Frodin	31 ± 5	52 ± 17	36 ± 11	0 ± 0	2392 ± 450	1.0 ± 0.3	0	0	1
4	<i>Schefflera vinosa</i> (Cham. & Schltdl.) Frodin & Fiaschi	27 ± 5	62 ± 5	28 ± 6	0 ± 0	1572 ± 1038	0.9 ± 0.2	0	1	1
4	<i>Styrax ferrugineus</i> Nees & Mart.	36 ± 4	70 ± 19	20 ± 5	0 ± 0	437 ± 12	1.5 ± 0.3	0	1	1
4	<i>Tabebuia ochracea</i> (Cham.) Standl.	20 ± 3	77 ± 13	21 ± 3	0 ± 0	620 ± 148	1.3 ± 0.4	0	0	1
4	<i>Tapirira guianensis</i> Aubl.	34 ± 4	75 ± 11	20 ± 0	0 ± 0	18 ± 31	0.7 ± 0.1	0	0	1
5	<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	27 ± 6	86 ± 11	20 ± 5	0 ± 0	1627 ± 959	0.8 ± 0.3	1	1	1

^a measure without standard deviation, because it was based on a single leaf due to elevated number of trichomes

Table 3 Pairwise correlations of defense traits among cerrado species at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). SLA = Specific leaf area. Lower diagonal are based on raw data, upper diagonal are phylogenetic independent contrast (PIC).

	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tanins
C:N		-0.41**	0.21	0.15	0.26*	0.38**	0.01	-0.19	0.14
SLA	-0.47***		-0.54***	-0.01	-0.09	-0.60***	-0.11	-0.05	-0.15
Water	0.20	-0.53***		0.23	-0.16	0.57***	0.11	-0.13	-0.19
Latex	0.16	-0.15	0.30*		-0.12	0.13	0.00	-0.06	0.19
Trichomes	0.22	-0.28*	-0.05	-0.26*		-0.15	0.10	-0.09	-0.05
Toughness	0.39**	-0.61***	0.49***	0.22	0.08		-0.06	0.05	0.07
Alkaloids	0.02	-0.04	0.06	-0.02	0.19	-0.04		0.07	-0.28*
Terpenoids	-0.09	-0.12	0.01	0.02	0.10	0.23	0.14		0.03
Tanins	0.17	-0.26*	-0.15	0.05	0.06	0.07	0.03	-0.03	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 1 Biplot of principal component analysis with defense traits of species in cerrado *sensu stricto* at the Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). Each species is represented by the number of its group. Water = water content (mg cm⁻²), SLA = specific leaf area (cm² g⁻¹), Toughness (N), Trichomes = trichome density (trichomes cm⁻²), Latex (mg), C:N = carbon:nitrogen ratio

Fig. 2 Mantel correlogram between the trait and the phylogenetic distances matrices for cerrado species. No correlation was significant at $\alpha' = 0.004$ (Bonferroni correction)

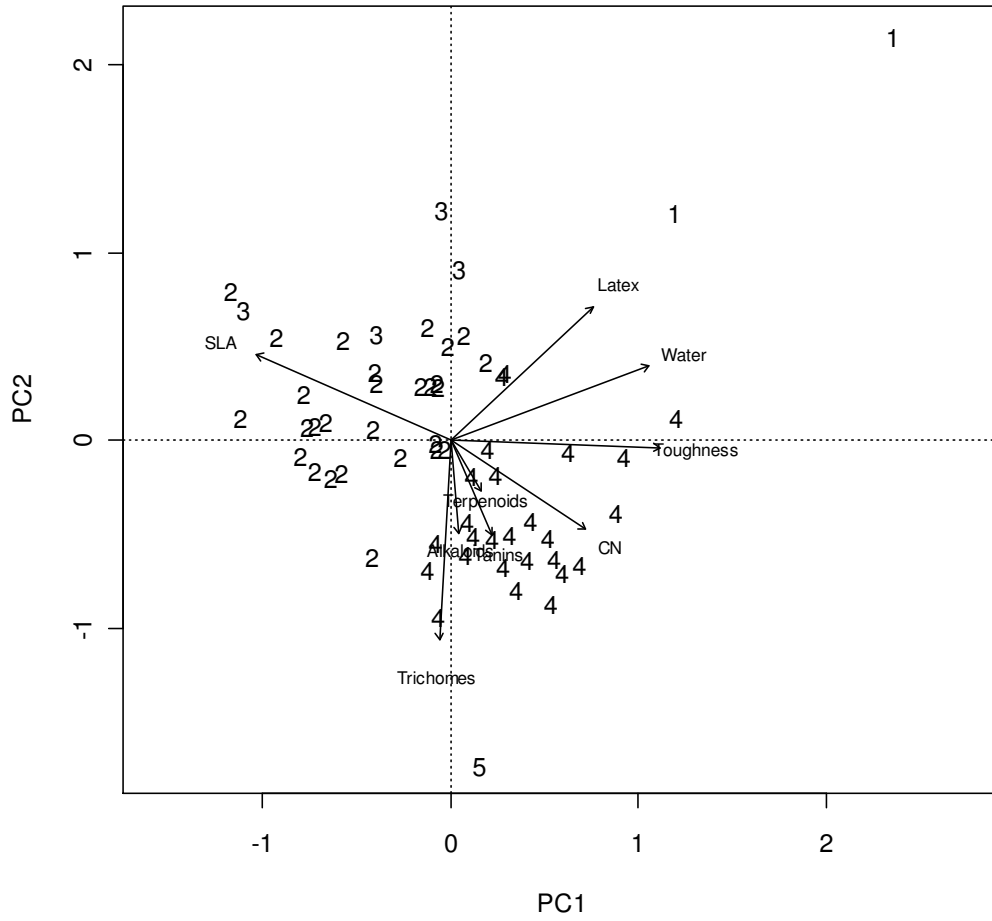


Fig. 1

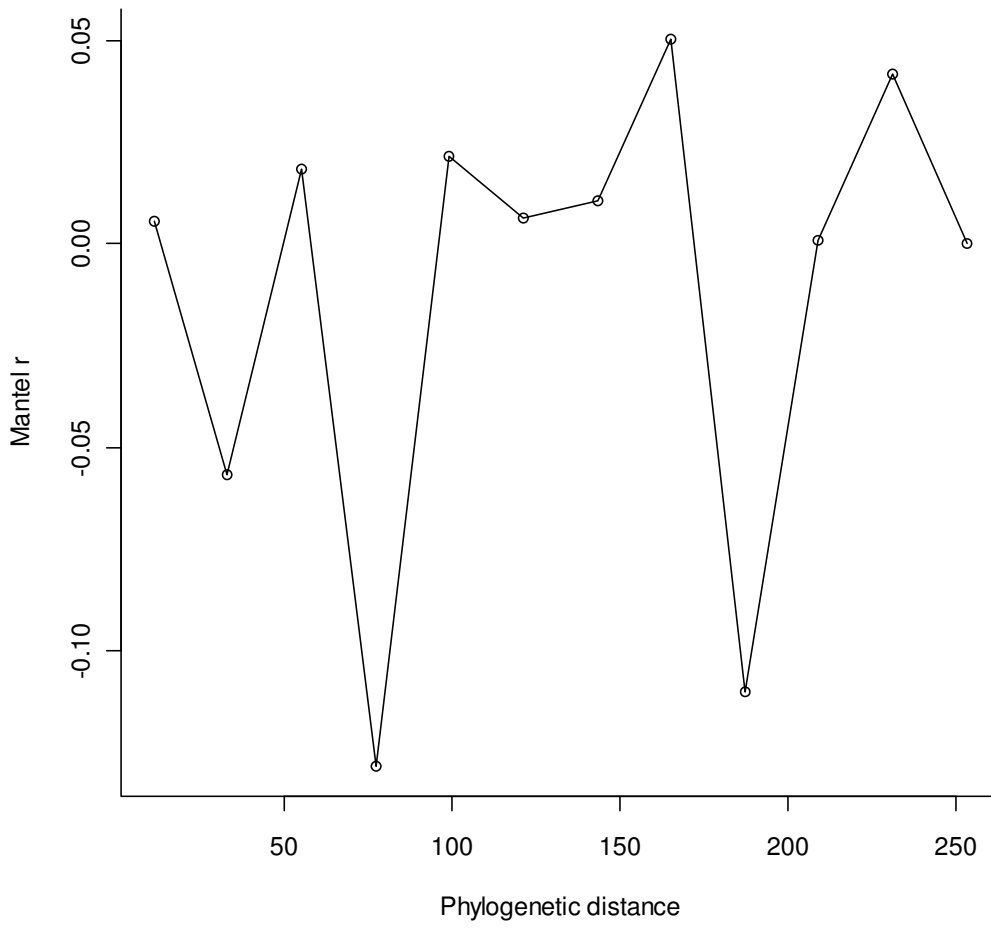


Fig. 2

Appendix

Table A1 Soil features (mean \pm sd) in cerrado *sensu stricto* at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). OM = organic matter (g kg⁻¹), P= available phosphorus (mg kg⁻¹), N= total nitrogen concentration (mg kg⁻¹), K= exchangeable K⁺ (mmol kg⁻¹), Ca= exchangeable Ca²⁺ (mmol kg⁻¹), Mg= exchangeable Mg²⁺ (mmol kg⁻¹), Al= exchangeable Al³⁺ (mmol kg⁻¹), SB= sum of bases (mmol kg⁻¹), CEC= cation exchange capacity (mmol kg⁻¹), V= base saturation (%), m= aluminum saturation (%), Sand, Silt and Clay (%)

Soil feature	mean \pm sd
pH	3.6 \pm 0.1
OM	43 \pm 8
P	5 \pm 2
N	1740 \pm 294
K	1.3 \pm 0.4
Ca	3 \pm 1
Mg	2 \pm 1
Al	17 \pm 4
SB	6.6 \pm 2.0
CEC	87 \pm 17
V	8 \pm 3
M	72 \pm 8
Sand	68 \pm 2
Silt	4 \pm 1
Clay	28 \pm 2

Capítulo 2

Phylogenetic and phenotypic originalities in a cerrado plant community

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Phylogenetic and phenotypic originalities in a cerrado plant community

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Short running title: Originality in cerrado plants

Phylogenetic and phenotypic originalities in a cerrado plant community

Abstract

Complementarity allows species coexistence and more efficient use of niche. Originality of a species is how much that species contributes to rarity of traits. Here we (1) tested the relation between abundance and both phylogenetic and phenotypic originalities and (2) compared abundance-based extinctions to random ones. We measured nine defense traits, phylogenetic information and abundance from a woodland cerrado community in southeastern Brazil. Abundance was not related to neither phylogenetic nor functional originalities; phylogenetic and phenotypic originalities were not related. Abundance-based extinctions were not different from random. However, the originalities were concentrated in few species and four of the more original species were among the rarest. These species contribute to rarity of traits more than common ones and they may contribute to compensatory dynamics and to maintenance of community stability. Thus, species abundance may not be a predominant factor to the maintenance of functions in cerrado.

Key words: complementarity, functionality, savanna, simulated extinction, species abundance.

Introduction

Complementarity allows species coexistence, and more efficient use of niche (Petchey 2003). Resource use efficiency depends on how much a community can make use of the available niche, that is, if the niche is plentiful filled, more ways of resource use will result in higher values of functioning (Petchey 2003). Complementarity also plays a role in stability in space or time, when complementary species have different functions acting at different periods or local conditions (Questad & Foster 2008; Gonzalez & Loreau 2009). As the traits of a species correspond to functions it performs and conditions it needs (Cornelissen *et al.* 2003), differences in traits will establish niche partition and functioning divergence (Mason *et al.* 2008; Questad & Foster 2008). Species with uncommon traits may use different niches, increasing the probability of coexistence and even increasing the conditions for the growth of other species in a process of facilitation (Quintana-Ascencio & Menges 2000; Lyons *et al.* 2005). The frequency of traits ranges from exclusive traits, present in one species only, to very common traits, present in most species (Pavoine *et al.* 2005). Some species may have a very rare trait or an amount of rare and uncommon traits; these species can thus perform original functions and they are called “original species” (Pavoine *et al.* 2005; 2008). Because of its rare traits, original species are more complementary to other species (Pavoine *et al.* 2005).

Originality is usually measured as an average value of difference in traits among a given species and all other species (Pavoine *et al.* 2005; 2008). The originality of a species is how much that species contribute to rarity of traits in a community (Pavoine *et al.* 2005). If many species contribute with specific traits each, then the

originality will be well distributed (Pavoine *et al.* 2005). If the opposite, few species with many rare traits, the originality will be concentrated into few species and all the others will have low originality (Pavoine *et al.* 2005). Functionally diverse communities in heterogeneous habitats present high spatial turnover due to trait variation among species for exploiting environmental heterogeneity (Questad & Foster 2008). Original species could be more abundant if they occupy different portions of the niche, or less abundant if they need specific and rare environmental conditions at small scale (Pavoine *et al.* 2005; Petchey *et al.* 2007). If common species are the more original ones, there is niche partitioning by narrowing species niches to distinct portions. Otherwise, if biotic factors act as environmental filters, favouring species with similar traits (Webb *et al.* 2002), common species would be the less original ones, presenting common traits. Moreover, if original species, with key traits, are rare, there would be implications for conservation. The role of rare species on functioning is underestimated and needs more studies, because rare species are at higher risk of extinction (Pruvis *et al.* 2000; Lyons *et al.* 2005). Thus, relationships between originality and abundance may allow us to infer ecological process and establish conservation priorities.

The comparison between originality based on phylogenetic distances and originality based on phenotypic distances may allow us to relate evolutionary history to traits: phylogenetic distances represent time of divergence, which is a period of isolated evolution and possibility of evolving new traits, whereas phenotypic distances represent a divergence in traits themselves (Pavoine *et al.* 2005; Mouliott *et al.* 2008). In addition, it is possible to infer about functional redundancy when comparing phenotypic originality to phylogenetic originality. Species may have similar traits, or share similar phylogenetic history, or both.

Nonetheless, the real condition of functionally similar species to become redundant is when their abilities to survive to different perturbations are different from each other (Laliberté *et al.* 2009). Then, if the measures of phenotypic and phylogenetic originality are not related, there may be insurance by redundancy. That is, species with different resistances – for example, defences against herbivory – share evolutionary history and may have the same functions. Thus, if one species is lost, other could play the same role (Lyons *et al.* 2005; Laliberté *et al.* 2009). Probability of traits shared by related plants due to common ancestor decreases with their phylogenetic distance (Pavoine *et al.* 2005). Also, some traits may converge occurring in non-related plants, especially if they allow species to survive to a given environmental filter (Webb *et al.* 2002). We expect, as a rule of thumb, the traits to be conserved in the phylogeny and, consequently, the two measures to be related. However, if traits are convergent, the two measures will not be related.

Species extinctions are not random (Pruvis *et al.* 2000; Vamosi & Wilson 2008). They are based on traits and may be biased on phylogeny (Pruvis *et al.* 2000; Pruvis 2008). Thus, the loss of some species may result in greater loss of functionality or evolutionary history than others, particularly if endangered species have relatives also at risk (Vamosi & Wilson 2008). Moreover, how much the loss of a given number of species results on loss of traits, depends on which species are lost: loss of evolutionary distinct species or of phylogenetic clumps results in greater loss of traits and evolutionary history (Isaac *et al.* 2007; Vamosi & Wilson 2008). Originality can be used to identify priority species for conservation and to maximise conservation actions (Pavoine *et al.* 2005). It is difficult to determine the exact minimum viable size of populations (Brook *et al.*

2006), but it is assumed that species with lower abundances have higher risk of extinction (Lyons *et al.* 2005). To assess the effect of extinctions on traits, we could compare the loss of originality in abundance-based extinction trajectory to random species loss.

The aim of this study was to test the relation of abundance and originality. We addressed the following questions: (1) Are species abundance and phylogenetic originality related?; (2) Are species abundance and phenotypic originality related?; (3) Are the phylogenetic originality and phenotypic originality related?; (4) Are phylogenetic and phenotypic originalities concentrated in few species?; (5) Are simulated extinction of species based on their abundances different from random?

Methods

Study area and sampling

We carried out this study at the Federal University of São Carlos, southeastern Brazil (21°58'05.3"S, 47°52'10.1"W, 815-890 m a.s.l.; Santos *et al.* 1999). Regional climate is seasonal, with dry winter and wet summer, defined as Cwa (Köppen 1931). The study site is located at the northeastern portion of the campus and is covered by woodland cerrado, on Oxisol (Santos *et al.* 1999). In this area, there is a permanent 50 m x 50 m grid, with 100 5 m x 5 m contiguous plots, in which all individuals belonging to the woody component were identified. We considered a list of leaf traits related to defence against herbivory: nutritional quality, specific leaf area, water content, latex content, trichome density, toughness, presence of alkaloids, presence of terpenoids, and presence of tannins.

We used an elemental CHNS-O analyser (CE Instruments/EA 1110) to determine carbon and nitrogen concentration, with which we calculated C:N ratio as an indicator of plant nutritional quality. We divided leaf area by dry mass, to obtain specific leaf area (Cornelissen *et al.* 2003). We assigned leaf water content by the difference between fresh and dry mass, divided by leaf area (Agrawal & Fishbein 2006). To measure latex content, we cut a leaf at the base and collected the latex with a filter paper. We oven-dried the samples at 75°C during 24 h, then we weighted them. We assigned trichome density by counting the number of trichomes in a 28 mm² circle, delimited near the leaf tip, on both top and bottom, with a dissecting microscope (Agrawal & Fishbein 2006). We used a penetrometer (dynamometer DFE 010, Chatillon, with a cone tip) to measure leaf toughness. We pushed the probe of the penetrometer through the leaf and recorded the maximum force required to penetrate it. We determined the presence of alkaloids, terpenoids, and tannins in leaves following Falkenberg *et al.* (2003). We also determined species abundances by counting the number of individuals for each species in the plots.

Originality

We constructed a phylogenetic dendrogram for the species using the Phylomatic software (Webb & Donoghue 2005). The lengths of the branches were estimated from maximum ages determined for genus, families, orders, and superior clades according to Davies *et al.* (2004). We fixed the root and all dated nodes, and then we extrapolated branch lengths, placing the non-dated nodes evenly between dated nodes or between dated nodes and terminals (species), using the Bladj

algorithm in the Phylomatic software (Webb & Donoghue 2005). We also constructed a functional dendrogram using the defence traits. We did a hierarchical clustering of species based on the traits, using Euclidean distance and average method (Legendre & Legendre 1998).

For both dendrograms, we calculated the originality of each species following the procedures proposed by Pavoine *et al.* (2005). First, we calculated the distance of each pair of species, by summing the branches necessary to link the pairs into the dendrograms. Then, we measured originalities as the frequency distribution that maximises quadratic entropy (QE-based index, Pavoine *et al.* 2005). In this way, we obtained two originality indices: phylogenetic originality, based on the phylogenetic dendrogram, and phenotypic originality, based on the functional dendrogram. We carried out all analyses in R (R Core Development Team 2009) with the package “ade4” (Dray & Dufour 2007).

Statistical analyses

To test whether the originality of a species was related to its abundance, we used a parametric Pearson correlation tests between abundances and both phylogenetic and phenotypic originalities. We also tested for correlation between both originality indices. We determine the number of species and individuals necessary to achieve at least 50% of the whole originality for both originality measures.

We ordered species by their abundances and then we simulated extinctions, excluding species from the less to the most abundant. At each step, we summed up the originality of remaining species. Then, we did 1,000 randomisations, excluding

species at random and summing up the originality of the remaining species at each step. We then calculated the mean and 95% confidence intervals of the randomisations. We carried out all analyses in R (R Core Development Team 2009).

Results

We did not find significant correlation between abundance and phylogenetic originality ($r = -0.028$, $P = 0.83$), between abundance and phenotypic originality ($r = -0.001$, $P = 0.99$), and between phylogenetic and phenotypic originalities ($r = -0.047$, $P = 0.72$). Nine species comprised 52% of the phylogenetic originality, accounting for 4.75% of total abundance, whereas other three species comprised 54% of the phenotypic originality, accounting for 6.11% of total abundance (Table 1). The common species (58% of total abundance) comprised only 7.5 and 4.9% of the phylogenetic and phenotypic originalities, respectively (Table 2). Four species, that is, *Xylopia frutescens*, *Annona coriacea*, *Annona crassiflora*, and *Davilla rugosa* were among the nine species with higher phylogenetic originality and also were among the rare species, with one or two individuals in the plots. Species with higher phenotypic originality were among neither the less nor the most abundant species.

The extinctions following abundance were not different from random extinctions, when considering the trajectory of loss of either phylogenetic originality (Fig. 1a) or phenotypic originality (Fig. 1b).

Discussion

There was a degree of redundancy among species, since the phenotypic and phylogenetic originalities were not related. Most of the originalities were concentrated in a few rare species, indicating that these species present a higher susceptibility to extinctions. The loss of the originalities was not different from random and so species abundance may not be a predominant variable to the maintenance of functions in cerrado.

The rare species were the more phylogenetically original ones. Although there was no relation between abundance and phylogenetic originality, four of the most original species were the less abundant ones. Rare species are usually underestimated, although in some communities they perform keystone process in the functioning (Lyons *et al.* 2005). As these rare species were isolated in the phylogenetic tree, they may have a series of phylogenetic related traits contributing more than common species to the rarity of traits (Pavoine *et al.* 2005). More distinct species are expected to compensate the reduction of the population size of the dominant species caused by environmental changes, because they may be adapted to different conditions (Gonzalez & Loureau 2009). Besides, rare species may have populations increased after disturbances or catastrophes, with higher survival and growth rates, recolonising open areas and stabilising the environmental conditions until populations of superior competitors stabilise (Quintana-Ascencio & Menges 2000; Lyons *et al.* 2005). We know little about the role rare species play in communities, and given that they are at high risk of extinction, they should have a special conservation attention (Lyons *et al.* 2005). The loss of one of these phylogenetically original species implies great loss of

genetic information, and, consequently, decreases possible responses to environmental changes in cerrado.

Only three species encompassed more than half of the phenotypic originality, implying that few species contributed to rarity of traits, even though these species were not the most abundant and represented only about 6% of the total abundance. Similar results were found in a fish community, in which five fish species comprised 52% of the phenotypic originality (Moulliot *et al.* 2008) and in a carnivore phylogeny, in which 12 out of 70 carnivore species comprised 50% of the phylogenetic originality (Pavoine *et al.* 2005). If this pattern is maintained in many community types, one may postulate that originality is concentrated in a small number of species and, probably, of individuals. The concentration of traits in species with low abundances indicates a degree of susceptibility of the community to stochastic extinctions. If these few species were lost, there would be loss of many functions in the community.

As long as we used defence traits against herbivory to estimate the phenotypic originality, this measure was related to specific capacities to resist against herbivores. In this context, more original species could be expected to have specific defences and, consequently, specific herbivores. Variations in plant traits represent a multidimensional resource map with discontinuities to which herbivores have to adapt (Nyman 2009). As each plant lineage will inherit most of its traits from its immediate ancestor, herbivores will have to overcome smaller differences, and in a smaller number of traits, to attack related plants (Nyman 2009). Thus, common and widespread plants with many relatives tend to have more associated herbivores than rare, taxonomically isolated ones (Nyman 2009). Likewise, phenotypic dissimilarities among species (for example, morphological features,

concentrations of nutrients, and presence of chemical defensive compounds) correspond to herbivores tolerance to dietary variation, which is determined by its physiological capabilities (Nyman 2009). Thus, less original species – clumped in the phenotypic dendrogram – should share herbivores, whereas more original species – isolated in the phenotypic dendrogram – should have specialist herbivores.

Most of the relative abundance was concentrated in few species. This pattern, in which there are few common and many rare species, is found worldwide in many types of communities (Stohlgren *et al.* 2005). Common species contribute more to biomass and, consequently, to stock function, but rare species may contribute to nutrient use efficiency and regulatory functions disproportionately to their abundances (Lyons *et al.* 2005). In communities that experience environmental changes in time, less abundant species are important to compensatory dynamics, especially if they have traits that allow them to survive different perturbations (Gonzalez & Loreau 2009). This is the case in the Brazilian cerrado, which presents many seasonal perturbations, such as fire and drought, which modify the structure of the vegetation and increment light, nutrient, and the availability of open patches (Gottsberger & Silberbauer-Gottsberger 2006). Moreover, the spatial variation of rarity and dominance highlights the importance of rare species, with their unique traits, to the maintenance of the community stability (Stohlgren *et al.* 2005).

Since the two originality indices were not related, the species isolated in the phylogenetic tree had defence traits similar to the average of other species and some species had rare traits, which were not present in their relatives. For a given group of phylogenetic related plants, there were different resistance strategies against herbivory; hence, functions performed by this group could be kept under

different herbivory pressures. If some less abundant species were functionally similar to some dominant species, but with different requirements and tolerances, they could increase the resilience of the community under perturbations, such as an increasing herbivory (Lyons *et al.* 2005). This resilience may occur in the cerrado, because the most abundant species were less original ones, being similar to many species, and their phenotypic originality was not related to their phylogenetic originality.

The simulated extinction based on abundances showed that the loss of originality was not different from random, because most species had very low originalities and their abundances did not predict their originalities. The most phenotypically original species were generally neither the most abundant nor the less abundant species, implying that the extinctions expected for rare species would have low effect on the trait diversity. Besides, the general low levels of originality and independence from the abundance indicated, to a certain extent, a high functional similarity among rare and common species. Thus, the decline in abundance of common species could be compensated by the increase of rare competitor species adapted to different conditions (Gonzalez & Loreau 2009). For each lost species, there will be a loss of originality: if species were extinct by their abundance, the loss of phylogenetic originality would be predictable and phenotypic originality would experience a great loss with a high number of extinct species.

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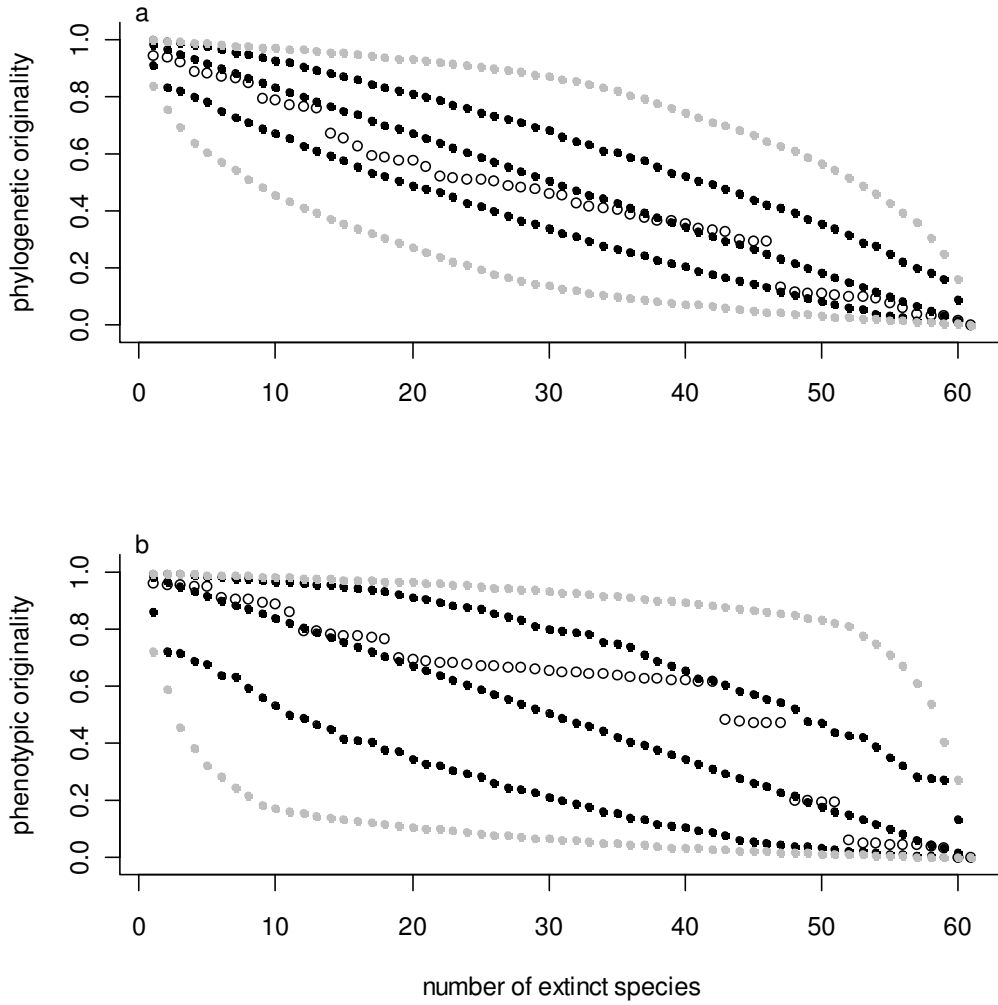
Table 1 Woody species with higher values of phylogenetic and phenotypic originalities, cumulative proportion of originality (f), and cumulative proportion of abundance (n) in a woodland cerrado at Federal University of São Carlos (approximately, 21°58'05.3"S, 47°52'10.1"W)

	Phylogenetic originality	f (%)	n (%)
<i>Ocotea pulchella</i> (Nees) Mez	0.160	16	1.99
<i>Xylopia frutescens</i> Aubl.	0.087	25	2.09
<i>Annona coriacea</i> Mart.	0.057	31	2.13
<i>Annona crassiflora</i> Mart.	0.057	36	2.23
<i>Davilla elliptica</i> A. St.-Hil.	0.033	40	2.28
<i>Davilla rugosa</i> Poir.	0.033	43	2.47
<i>Diospyros hispida</i> A. DC.	0.030	46	4.17
<i>Styrax ferrugineus</i> Nees & Mart.	0.030	49	4.61
<i>Guapira opposita</i> (Vell.) Reitz	0.029	52	4.75
	Phenotypic originality		
<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	0.273	27	1.99
<i>Kielmeyera coriacea</i> Mart. & Zucc.	0.134	41	3.54
<i>Kielmeyera grandiflora</i> (Wawra) Saddi	0.135	54	6.11

Table 2 Most abundant species, cumulative proportion of abundance (n), cumulative proportion of phylogenetic originality, and cumulative proportion of phenotypic originality in a woodland cerrado at Federal University of São Carlos (approximately, 21°58'05.3"S, 47°52'10.1"W)

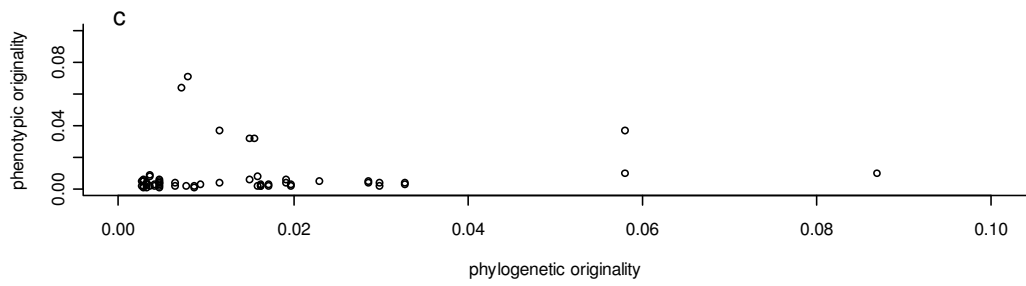
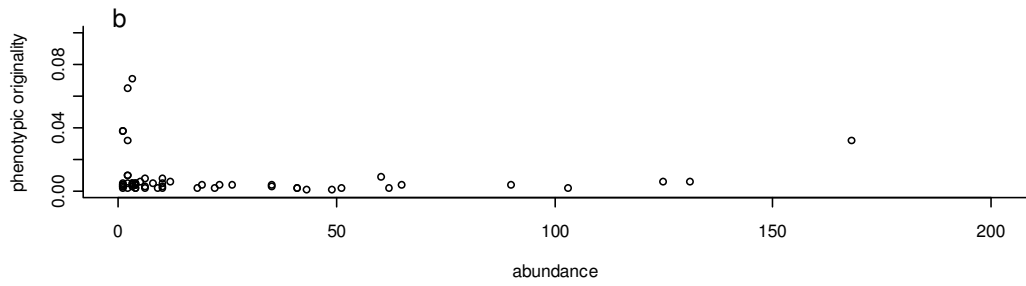
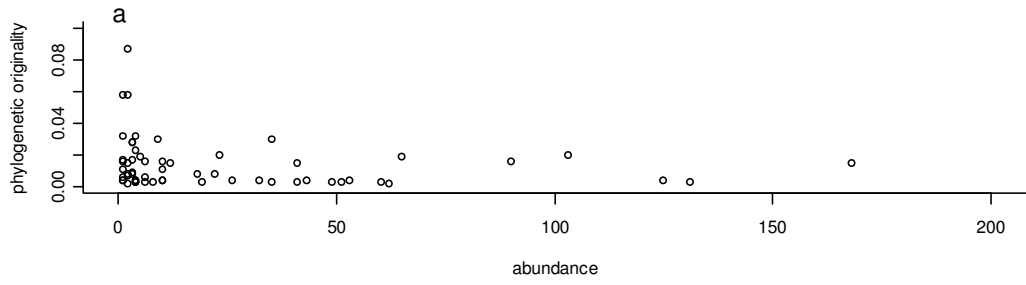
	n (%)	Phylogenetic originality (%)	Phenotypic originality (%)
<i>Myrsine umbellata</i> Mart.	28	1.6	0.2
<i>Vochysia tucanorum</i> Mart.	36	3.2	3.4
<i>Myrcia guianensis</i> (Aubl.) DC.	42	3.5	3.9
<i>Miconia albicans</i> (Sw.) Triana	48	4.0	4.5
<i>Piptocarpha rotundifolia</i> (Less.) Baker	53	6.0	4.6
<i>Tabebuia ochracea</i> (Cham.) Standl.	58	7.5	4.9

Fig. 1 Effects of abundance-based extinctions on (a) phylogenetic originality and (b) phenotypic originality in a woodland cerrado at Federal University of São Carlos (approximately, 21°58'05.3"S, 47°52'10.1"W). Open circles show extinction trajectory following abundance, black circles show mean and 95% confidence intervals of 1,000 random extinction trajectory, and gray circles show the worst case (lower line) and best case (upper line) scenarios



Supplementary material

Fig. S 1 Dispersion diagram between (a) abundance and phylogenetic originality, (b) abundance and phenotypic originality and (c) phylogenetic originality and phenotypic originality in a woodland cerrado at Federal University of São Carlos (approximately, 21°58'05.3"S, 47°52'10.1"W).



Conclusão geral

Houve basicamente duas estratégias predominantes de defesa contra a herbivoria nas espécies arbóreas de cerrado: “tolerância”, espécies com baixos valores de defesa e altos valores nutricionais; e “baixa qualidade nutricional”, espécies com altos valores de defesa e com baixos valores nutricionais. Como nós não encontramos um sinal filogenético, a filogenia não foi o fator determinando o conjunto de traços que as espécies apresentaram, logo, a herbivoria pode ser o fator selecionando tais traços. As poucas estratégias que encontramos podem ser resultado de uma série de filtros ambientais, reduzindo o banco de espécies sequencialmente, entre eles a herbivoria.

Houve um grau de redundância na comunidade vegetal de cerrado, já que a originalidade filogenética e originalidade fenotípica não estiveram relacionadas. A maior proporção de originalidade esteve concentrada em poucas espécies, indicando um grau de suscetibilidade a perda dessas poucas espécies. A abundância não foi o fator predominante para a manutenção das funções no cerrado.