Phylogenetic and phenotypic originality and abundance in a cerrado plant community

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Abstract The originality of a species is how much that species contributes to the rarity of traits in a community. Here we tested the relation between abundance and both phylogenetic and phenotypic originality. We measured nine traits associated with defence against herbivory, as well as phylogenetic information and abundance for woody plant species in a woodland cerrado in southeastern Brazil. About 90% of the species accounted for about 50% of the phylogenetic and phenotypic originality: most woody species had low originality. Abundance was related to tougher leaves, lower specific leaf area and lower originality based on nutritional quality. Our results suggest that herbivory may reduce the abundance of species with low resistance to herbivory and with different nutritional quality. Nevertheless, abundance was not related to either phylogenetic or phenotypic originality, so extinction of rare species may not endanger overall community function as long as more abundant species are retained. We argue that this is a consequence of the low complementarity of a large number of woody species.

Key words: community functioning, complementarity, herbivory, savanna.

INTRODUCTION

Complementarity is a property of communities that emerges when a set of species have different resource use requirements (Petchey 2003). Conversely, species are functionally redundant if they overlap completely in some aspect of their life-history, such as habitat or phenology (Petchey *et al.* 2007). Complementarity allows species to coexist in a community and use resources more efficiently (Petchey 2003; Petchey *et al.* 2007). Resource use efficiency depends on niche complementarity: complementary species have more ways of using resources and fill a greater portion of the available niche (Petchey 2003). Complementarity also increases community stability, as complementary species have functions acting at different times or under different local conditions (Questad & Foster 2008; Gonzalez & Loreau 2009). Thus, greater complementarity among species will result in higher community function (Petchey 2003).

Because the traits of a species correspond to the functions it performs and the conditions it needs (Cornelissen *et al.* 2003), differences in traits will establish niche partitions and functional divergence (Mason *et al.* 2008; Questad & Foster 2008). Species with uncommon traits may use different resources, increasing the probability of coexistence and sometimes even the growth of other species (Quintana-Ascencio &

Menges 2000; Lyons *et al.* 2005). Trait frequency ranges from exclusive (present in only one species) to very common (present in most species, Pavoine *et al.* 2005). The rarity of a trait is analogous to the rarity of a species and can be calculated by a decreasing function of its frequency (Pavoine *et al.* 2005). Species with rare and uncommon traits can perform original functions in the community and are called 'original species' (Pavoine *et al.* 2005, 2008). Because of their rare traits, original species are more complementary than others (Pavoine *et al.* 2005).

The originality of a species is how much that species contributes to rarity of traits in a community and is usually measured as an average value of difference in traits between a given species and all other species (Pavoine *et al.* 2005). If many species contribute with specific traits, originality will be well distributed, whereas if a few species contribute most of the rare traits, originality will be concentrated into few species (Pavoine *et al.* 2005). The importance of the traits in a community is also related to the abundance of species (Cadotte *et al.* 2010). Functionally diverse communities in heterogeneous habitats have high spatial turnover owing to trait variation among species (Questad & Foster 2008). In these communities, original species could be more abundant if they occupy different portions of the available niche, or less abundant if they need specific and rare environmental conditions (Petchey *et al.* 2007; Mouillot *et al.* 2008). The common species might be still the most original if their niches are narrow. Alternatively, common species

might be less original if the environment favours species with similar traits. Moreover, the abundance of original species has important implications for conservation (Mouillot *et al.* 2008). In any community, rare species are at higher risk of extinction (Purvis *et al.* 2000; Lyons *et al.* 2005). If the original species with key traits are rare, there is a high risk of the community losing important functions (Purvis *et al.* 2000; Lyons *et al.* 2005). Thus, the relationships between originality and abundance allow us not only to infer the predominant ecological processes of communities, but also to establish priorities for conservation of species.

The traits used to calculate functional originality are usually related to the dietary niche of a species (Petchey *et al.* 2007; Mouillot *et al.* 2008). Mouillot *et al.* (2008), for example, measured fish traits related to diet, food acquisition and position in the water. Petchey *et al.* (2007) measured avian traits related to quantity of resource consumed, feeding behaviour and activity period. However, any trait that characterizes some important aspect of niche, such as floral colour related to pollinator attraction (McEwen & Vamosi 2010), may be used (Petchey *et al.* 2007). Here, we measured traits associated with plant resistance and defence against herbivory (Cornelissen *et al.* 2003; Agrawal & Fishbein 2006). The presence of the same defence traits in many species would indicate defence against background herbivory, whereas the presence of these traits in few species would indicate specific herbivory (Nyman 2010).

Species extinctions are not random (Purvis *et al.* 2000; Vamosi & Wilson 2008): they are based on traits and may be biased by phylogeny (Purvis *et al.* 2000; Purvis 2008). Thus, the loss of some species may result in greater loss of functionality or evolutionary history than others, particularly if endangered species also have relatives at risk (Vamosi & Wilson 2008). For that reason, phenotypic and phylogenetic originality should be considered when determining priorities for conservation (e.g., Redding *et al.* 2010). How much the loss of a given number of species results in a 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). The effect of extinctions on community function can be tested by examining the correlation between originality and abundance.

We evaluated the originality of woody species in cerrado, with special attention to the vulnerability of the plant community to extinctions of rare species, by estimating phenotypic originality of functional traits associated with plant defence against herbivory. In cerrado, resources are limited and plants concentrate their investments in defences against herbivory (Fine *et al.* 2006; Gottsberger & Silberbauer-Gottsberger 2006) because replacing damaged tissues requires additional resources (Coley & Barone 1996). Thus, these traits represent important dimensions of the plant niche and contribute to the maintenance of overall cerrado functions. We addressed the following questions:

1. Is phylogenetic and phenotypic originality concentrated in few species?
2. Is species abundance related to either phenotypic or phylogenetic originality?

METHODS

Study area and sampling

We studied a woodland cerrado on the northeastern portion of 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). The regional climate is seasonal, with dry winters and wet summers (Cwa, Köppen 1931). The cerrado site, which is located on an Oxisol (Santos *et al.* 1999), was divided into a permanent 50×50 m grid, with 100 contiguous plots of 5×5 m, in which all individuals belonging to the woody component were identified (Silva & Batalha 2011). We determined species abundance by counting individuals of each species in a plot; we found 61 woody species in the study area.

We measured nine leaf traits related to defence against herbivory (Silva & Batalha 2011): carbon–nitrogen ratio, specific leaf area, water content, latex presence, trichome density, toughness, presence of alkaloids, presence of terpenoids and presence of tannins. These traits decrease herbivory rate, herbivore performance or herbivore preference (Cornelissen *et al.* 2003; Agrawal & Fishbein 2006). Even low specific leaf area and low water content, which are associated with environmental characteristics, can be also considered as defence traits, because they are related to palatability and are inversely related to structural defences (Cornelissen *et al.* 2003; Coley *et al.* 2006).

We used an elemental CHNS-O analyser (CE Instruments/EA 1110) to determine carbon and nitrogen leaf concentration from two to five individuals of each species, 20 mg of leaves per individual. We divided leaf area by dry mass to obtain specific leaf area, from two to 10 individuals of each species with two leaves per individual (Cornelissen *et al.* 2003). We assigned leaf water content by the difference between fresh and dry mass, divided by leaf area from two to 10 individuals of each species with two leaves per individual (Agrawal & Fishbein 2006). We determined the presence of latex by observing exudation after cutting the base of the leaves from two to 10 individuals of each species with one leaf per individual. We assigned trichome density by counting the number of trichomes in a 28 mm^2 circle, delimited near the leaf tip, on both top and bottom, with a dissecting microscope from one to five individuals of each species with one leaf per individual (Agrawal & Fishbein 2006). We used a penetrometer (dynamometer DFE 010, Chatilon, with a cone tip) to measure leaf toughness from two to 10 individuals of each species with two leaves per species. 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 the procedures of Falkenberg *et al.* (2003) from 20 mg of leaves per species.

Originality

We constructed a phylogenetic dendrogram for the species using the Phylomatic module of the Phylocom software (Webb & Donoghue 2005; Webb *et al.* 2008). The lengths of the branches were estimated from ages of dated nodes (Wikström *et al.* 2001) and the topology from the current Phylomatic tree (tree R20080147; Webb *et al.* 2008). We fixed the root and all dated nodes and then extrapolated branch lengths, placing non-dated nodes evenly between dated nodes or between dated nodes and terminals (species), using the bladj algorithm in the Phylocom software (Webb *et al.* 2008). We tested whether the traits tended to be phylogenetically conserved (that is, to show a phylogenetic signal) with a test based on the variance of phylogenetically independent contrasts (PICs, Blomberg *et al.* 2003). We also constructed a functional dendrogram using the nine defence traits. We did a hierarchical clustering of species based on these traits, using Euclidean distance and average–linkage clustering (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 in the dendrograms. Next, we measured originality as the frequency distribution that maximizes quadratic entropy (QE-based index, Pavoine *et al.* 2005). In doing so, we calculated two originality indices: phylogenetic originality based on the phylogenetic dendrogram, and phenotypic originality based on the functional dendrogram. To measure the degree of concentration of originality, we arranged the species in decreasing order of originality and calculated the cumulative sum of originalities. Then, we determined the number of species needed to achieve at least 50% of the total originality

for both originality measures. We also summed up the proportion of individuals of these species.

We separated the defence traits into three categories: nutritional quality and palatability (carbon–nitrogen ratio, specific leaf area and water content); mechanical defences (trichome density, latex presence and toughness); and chemical defences (presence of alkaloids, terpenoids and tannins). For each category, we recalculated the dendrogram and phenotypic originality to assess trait specific associations and the proportional contribution of each category of traits to originality. That is, we assessed whether the highly original species were original in many categories of traits, or just very different in one category.

Statistical analyses

To assess whether traits had positive or negative abundance–originality relationships, we tested the correlation between each trait and abundance. To test whether the originality of a species was related to its abundance, we tested the correlation between abundance and either phylogenetic or phenotypic originality. We repeated this test using originality based on categories of traits. We log-transformed the data in all analyses to achieve the requirements of the test and to decrease effects of extreme values (Zar 1999). We carried out all analyses in R (R Development Core Team 2009) with the 'ade4' package (Dray & Dufour 2007).

RESULTS

In general, most species, including many rare species, showed low originality (Appendix S1; Fig. 1). About 90% of the species accounted for about 50% of the phylogenetic and phenotypic originality (Appendix S1). Only a few rare species showed high values of
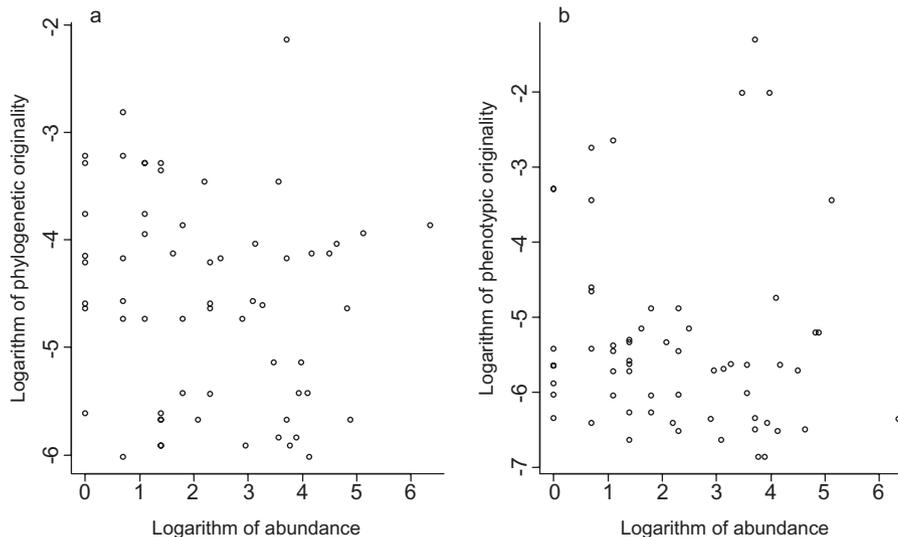

Fig. 1. Dispersion diagram between (a) abundance and phylogenetic originality, (b) abundance and phenotypic originality in a woodland cerrado, southeastern Brazil (approximately 21°58′05.3″S, 47°52′10.1″W). All data were log-transformed.

originality. Nine species comprised 52% of the phylogenetic originality, accounting for 4.75% of total abundance, whereas three species comprised 54% of the phenotypic originality, accounting for 6.11% of total abundance (Appendix S1). Thus, most of the woody species in cerrado were functionally redundant.

The abundance was positively related to toughness ($R = 0.32$, $P = 0.01$), but negatively related to specific leaf area ($R = -0.32$, $P = 0.01$) and originality based on nutritional quality ($R = -0.39$, $P < 0.01$). However, abundance was not related to any other trait ($R < 0.22$ and $P > 0.08$ in all cases), to originality based on physical defences ($R = 0.01$, $P = 0.94$), or to originality based on chemical defences ($R = -0.01$, $P = 0.95$). Abundance was also not related to either phylogenetic originality ($R = -0.21$, $P = 0.10$; Fig. 1a) or phenotypic originality ($R = -0.18$, $P = 0.16$; Fig. 1b).

Five of the nine traits (carbon–nitrogen content, specific leaf area, water content, latex presence and trichome density) presented a significant phylogenetic signal ($P < 0.05$, mean variance of observed PICs = 0.0366, mean variance of random PICs = 0.022). The variances of the other traits were not different from expected by chance ($P > 0.05$, mean variance of observed PICs = 0.020, mean variance of random PICs = 0.022).

DISCUSSION

The originality of woody plants in the cerrado was not concentrated in rare species. Although a few plant species retained a large proportion of the community's originality, most of the rare species had low phenotypic and phylogenetic originality. Consequently, extinctions of species with low abundance may not endanger the overall functioning of this plant community, as long as the most abundant species are retained. We argue that this is a consequence of the low complementarity of a large number of woody species.

We estimated the phenotypic originality of plants considering only functional traits of defence against herbivory, which are expected to be related to important dimensions of the niche in cerrado (Coley & Barone 1996; Fine *et al.* 2006). However, phylogenetic originality is a good surrogate for general phenotypic originality, as phylogenetic differences imply generally functional differences (Pavoine *et al.* 2005). Accordingly, the low complementarity in defence traits as well as in phylogenetic information in cerrado species may reflect the general functional redundancy of the plant community. This redundancy may be caused by environmental filtering for functionally similar plant species. Environmental filters assemble species on the basis of their tolerances to abiotic conditions (Webb *et al.* 2002). The cerrado experiences several environmental filters, such as drought, poor-nutrient soils and frequent fires (Gottsberger & Silberbauer-Gottsberger 2006), which may limit local communities to species with similar abiotic tolerances (Silva & Batalha 2010).

Phenotypic clustering of species in communities assembled by environmental filters is accompanied by phylogenetic clustering when functional traits are conserved in plant lineages (Webb *et al.* 2002; Verdú & Pausas 2007). We found phylogenetic signals in some defence traits, including traits that are also associated with abiotic factors (specific leaf area and water content, Cornelissen *et al.* 2003). We have also found phylogenetic signals in fire-related traits in cerrado species (Silva & Batalha 2010). The presence of a large number of species with low phylogenetic originality (i.e. closely related plant species) may be also due to the environmental filters in the cerrado, even though phylogenetic clustering has not been observed in other cerrado sites (Silva & Batalha 2009, 2010).

A few species showed a great originality in cerrado. *Kielmeyera coriacea*, *Kielmeyera grandiflora* and *Tocoyena formosa*, for example, encompassed more than half of the phenotypic originality. Similar results were found in a fish community, in which five fish species comprised 52% of the phenotypic originality (Mouillot *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). These results suggest that the restricted presence of highly original species in a community may be an overall ecological pattern. Although we could not identify specific mechanisms from this pattern, environmental filtering may again be important by making most species in local communities functionally similar. However, whether these few original species are rare keystone species, having larger impacts in the community functioning than common species (Lyons *et al.* 2005), is a question that deserves more attention in further studies.

Synergistic interactions among defence traits are predicted to provide a greater level of defence than would be possible if the traits were present independently (Berenbaum *et al.* 1991; Stapley 1998). If these interactions brought advantages for woody species in such a way that those plants with several distinct defence strategies were less attacked by herbivores, highly original species would also be the most abundant. However, we did not observe positive correlations between abundance and either phenotypic or phylogenetic originalities. Therefore, herbivory alone may not be strong enough to determine the abundance of woody species in cerrado, and other environmental filters, such as fire, drought and nutrient-poor soils, could also be important. Nevertheless, we found a negative correlation between abundance and nutritional quality. So, herbivory may act as a biotic filter, assembling predominantly species with similar palatability. Besides, abundant plants had more resistance against herbivory, with tougher leaves and lower

specific leaf area. Fire, drought and nutrient-poor soils could also favour species with these characteristics (Cornelissen *et al.* 2003), that is, favour sclerophyllous species (Gottsberger & Silberbauer-Gottsberger 2006). Notwithstanding, our results support that herbivory is also an important filter, assembling predominantly species with high mechanical resistance and low nutritional quality.

We observed a tendency of the highly original species to present specific defence strategies. When we grouped the traits into categories associated with nutritional, physical and chemical characteristics of the traits, we observed that *Tocoyena formosa*, for example, was the most original in chemical defences, because it was the only species that possessed alkaloids, followed by four species, *Vochysia tucanorum*, *Palicourea coriacea*, *Lippia velutina* and *Annona crassiflora* that did not have tannins (Silva & Batalha 2011). *Kielmeyera grandiflora* and *K. coriacea* were the most original species in physical defences owing to presence of latex, followed by *Annona coriacea*, *Ouratea spectabilis*, with high toughness, and *Miconia albicans*, with greatest number of trichomes (Silva & Batalha 2011). Variations in plant traits represent a multidimensional resource map with discontinuities to which herbivores have to adapt (Nyman 2010). Phenotypic dissimilarities among plant species correspond to herbivores' tolerance to dietary variation (Nyman 2010). As a result, less original species are expected to share herbivores, whereas more original species are expected to have specialist herbivores. Thus, the specific defences of the highly original species may be adaptations to specific herbivores (Nyman 2010). When this is not the case, specific defences may at least decrease the abundance of herbivores (Diniz *et al.* 1999).

Both rare and common species had very low originality and, consequently, abundance did not predict originality. The most phenotypically original species were generally neither the most nor the least abundant ones, implying that extinctions of rare species would have little effect on trait diversity. Low originality of most species showed that a large number of cerrado woody species share functional traits, presenting low overall complementarity. When a large number of species, including the more abundant ones, are functionally similar, the community shows a great resilience (Gunderson 2000; Wohl *et al.* 2004), as the stochastic extinctions may exclude species from the community without excluding functional traits (Pavoine *et al.* 2005). Thus, the cerrado seems to be very resilient to the natural perturbations, at least when defence traits are considered. It is worth noticing that other ecological aspects of the plants in cerrado (e.g. regenerative functions associated with dispersion traits, or stock functions associated with basal area and height) are also important to species spatial distribution, persistence, and abundance (Cornelissen *et al.* 2003). Thus, the abundance of the woody species in cerrado may be related to other functional traits. Further studies should seek relationships between abundance and originality based on regenerative and reproductive functional traits, as the functions associated with these traits are also important in environments under several environmental constraints (Cornelissen *et al.* 2003).

Most of the relative abundance was concentrated in few species in cerrado. This pattern of few common and many rare species is found worldwide in many types of communities (Stohlgren *et al.* 2005). In general, common species contribute more to biomass and, consequently, to stock function, whereas rare species contribute to nutrient use efficiency and regulatory functions disproportionally to their abundance (Lyons *et al.* 2005). Here we did not find significant relationships between abundance and specific functions associated with defence against herbivory and between abundance and more general functions associated with phylogeny. Thus, species abundance seems not be critical to the maintenance of functions in cerrado. If a significant relationship between abundance and originality based on regenerative and reproductive functional traits is also not found, then one could argue that there is a high functional redundancy of cerrado woody species that may prevent stochastic extinctions from reducing the functioning of the plant community.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supporting information of 61 woody species in a woodland cerrado, southeastern Brazil (approximately 21°58′05.3″S, 47°52′10.1″W).