Loss of phylogenetic and functional originalities of woody cerrado species in simulated extinction scenarios

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Abstract   Originality measures how different a given species is from all other co-occurring species regarding either their phylogenetic history or functional traits. Since it is important to preserve the various aspects of diversity and original species carry more phylogenetic or functional information, originality may be used to assign conservation priorities. Our goal was to evaluate the relationships between phylogenetic and functional originalities, and their simulated losses under extinction scenarios based on abundance, fire tolerance and habitat preference. We placed 100 plots in a cerrado reserve located in central Brazil, sampled all woody plants species within the plots, measured 14 functional traits and measured fire history. We assembled a phylogenetic tree and a functional dendrogram, with which we calculated the originalities. Phylogenetic- and functional-based originalities were correlated. However, the loss of functional originality was different from random extinctions on the abundance and fire tolerance scenarios, whereas the loss of phylogenetic originality was not. When compared with phylogenetic originality, functional originality brought more information to be used in conservation strategies because it was sensitive to differences in species abundance and fire tolerance. Thus, the extinction of rare or fire-sensitive species would result in important functional changes due to loss of distinctive traits.

Key words: conservation, fire, functional originality, phylogenetic originality, savanna.

INTRODUCTION

Faced with intense loss of diversity, we should search for indices that maximize conservation in all aspects of biodiversity. Distinctiveness among species is a useful measure of diversity for conservation because attribute rarity and phylogenetic relatedness among species determine their role in community functioning (Vane-Wright *et al.* 1991; Pavoine *et al.* 2005; Petchey & Gaston 2006). Distinct species have complementary attributes, which we expect might increase stability and optimize resource use in a community (Petchey 2003). For example, plants with different heights and bark thicknesses may avoid or recover faster from fires; different leaf sizes are related to growth allocation or resource acquisition, optimizing the use of resources (Cornelissen *et al.* 2003). Originality measures the distinctiveness among species, that is, how different a given species is from all other co-occurring species, regarding phylogenetic history or functional attributes (Pavoine *et al.* 2005). Extinction of a highly original species results in loss of rare functional attributes and

can disrupt community functioning (Mouillot *et al.* 2008; O'Gorman *et al.* 2011).

The originality of a species can be based either on phylogenetic distances or functional differences (Pavoine *et al.* 2005; Petchey *et al.* 2007; Mouillot *et al.* 2008). Many studies on conservation priorities take into account only the phylogenetic information (for instance, Redding & Mooers 2006), but phylogenetically more related species may be functionally different. Although phylogeny accounts for some of the functional differences, environmental pressure can select similar attributes from distantly related species. If so, phylogenetically diverse community may be functionally similar (Batalha *et al.* 2011; Silva *et al.* 2012). Taken together, these measures could elucidate how environmental conditions affect biotic interactions, changing community composition and resource use (Pavoine & Bonsall 2011). For example, in sites with more resources, a dominant species may outcompete others, whereas in harsher environments facilitation may prevail (Tielbörger & Kadmon 2000).

Local extinctions are not random, but are the result of traits responding to environmental conditions and interspecific interactions (Purvis *et al.* 2000; Razafindratsima *et al.* 2013; Sasaki *et al.* 2014).

Simulations of realistic extinction scenarios allow the estimation of originality loss and the prediction of the consequences of change, being useful to guide future management actions to maintain key aspects of biological diversity. There is a risk of losing valuable functions, due to the loss of entire lineages or functionally unique species, when conservation plans ignore evolutionary distinctiveness and functional divergence (Maherali & Klironomos 2007; Redding *et al.* 2010). In this sense, one may use species originality as a criterion to establish conservation priorities (Pavoine *et al.* 2005). Proper systems to study originality loss include communities with high richness, endemic species, high heterogeneity and those threatened by human activities. The cerrado encompasses the richest savanna in the world, with many endemic species, and has been rapidly converted into croplands, pastures or urban areas, putting many species at risk. Thus, it is one of the 25 biodiversity hot spots in the world (Myers *et al.* 2000; Klink & Machado 2005). Here we simulated three extinction scenarios based on variables that may affect attempts to conserve the cerrado and assessed their consequences in originality loss.

Abundance is an important aspect of diversity and must be taken into account when estimating extinction risk because the risk increases when population size decreases (Purvis *et al.* 2000; Morris & Doak 2002). In the cerrado, population sizes decrease due to an intense anthropic pressure, and so species that are less abundant are under higher risk of extinction. If rare species are more endangered and if original species are rare, then these species are likely to be lost first and many functions in the community may be compromised. Although dominant species have important functions (Grime 1998), subordinate species also play a role in main functions (Mariotte 2014), and rare species contribute to some functions disproportionally to their abundance (Lyons *et al.* 2005). Besides, in high-diversity communities, the most distinct combinations of attributes are supported predominantly by rare species (Mouillot *et al.* 2013).

Another consequence of the human occupation of the cerrado region is the increase in fire frequency (França *et al.* 2007). Fires tend to burn cerrado sites every 3 years due to biomass accumulation (Coutinho 1990), but cattle ranchers and farmers use fires every dry season to promote grass regrowth and to prepare land for cultivation. Anthropogenic fires spread easily from farmlands to natural areas and result in catastrophic burnings (França *et al.* 2007). Cerrado woody species usually have adaptations against fire, such as thick bark and resprouting ability, but if fire frequency is too high, even these plants may die (Hoffmann 1999). As a matter of fact, higher fire frequency decreases tree densities (Hoffmann 1999), whereas lower fire frequency increases the occurrence of fire-sensitive species (Moreira 2000). Thus, an increase in fire frequency may lead to a loss of both phylogenetic and functional originalities in cerrado plant communities.

A third way human activities are endangering cerrado species is the conversion into agriculture. Open cerrado physiognomies are more vulnerable to the process of loss and fragmentation because they are more easily converted into agriculture and pasture than closed ones (Tubelis & Cavalcanti 2000). Open and closed cerrado physiognomies have different floristic compositions, and a given species tends to occur more in open or closed physiognomies according to specific requirements (Angelo & Angelini 2007). If open physiognomies are at higher risk of extinction and if they contain more original species, then they should be prioritized in conservation efforts. In this case, based on species habitat preference, one could predict the consequences of open physiognomies conversion.

Here we calculated phylogenetic and functional originalities of woody cerrado species and simulated what would happen to the communities under three extinction scenarios. We tested whether (i) phylogenetic and functional originalities were correlated; and (ii) the losses of originalities based on abundance, fire tolerance and habitat preference were different from what would be expected solely by chance. We intend to provide guidelines to management strategies when one wants to minimize biodiversity loss and to maintain current functioning in the cerrado and savannas in general.

STUDY SITE AND METHODS

Study site and sampling

We carried out this study in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49′–18°28′S and 52°39′–53°10′W), under a humid tropical climate, with wet summers and dry winters (Aw, Köppen 1931). Annual rainfall varies from 1200 to 2000 mm concentrated from October to March (Ramos-Neto & Pivello 2000). In the ENP, open cerrado physiognomies are predominant, occupying 68.1% of the total area, and closed cerrado physiognomies occupy 25.1% (Ramos-Neto & Pivello 2000). Up to 1984, farmers used ENP for cattle ranching and used fire to promote grass regrowth (Ramos-Neto & Pivello 2000). After 1984, the reserve was fenced, and a fire policy was established. Initially, a policy of complete fire exclusion was adopted, which resulted in catastrophic burnings every 3 years due to the accumulation of dry biomass (França *et al.* 2007). After 1994, natural fires were no longer stopped inside the reserve, and anthropogenic burnings were avoided by preventive firebreaks, burned annually during the dry season (Ramos-Neto & Pivello 2000). Despite these precautions, another catastrophic fire burned 93% of the reserve in August 2010.

Table 1. Plant traits used to calculate functional originality and their functional relevance (see Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013) for more details)

Trait	Details (data type, unit)	Functional relevance
Basal area	Continuous, m^2	Space occupation, resource uptake, total mass
Height	Continuous, m	Competitive vigour, fecundity, growth time between disturbances, positively correlated with above-ground biomass, root depth, and leaf area
Height of first bifurcation	Continuous, m	Resistance
Resprouting capacity	Binary	Competitive vigour, persistence after environmental disturbance
Bark thickness	Continuous, mm	Bud and meristem protection
Wood density	Continuous, mg mm^{-3}	Resistance, lifespan, carbon storage
Leaf toughness	Continuous, N	Leaf tissue density, negatively correlated with growth rate, positively correlated with leaf lifespan
Leaf size	Continuous, mm^2	Energy and water balance, allometric factors, nutrient stress and disturbance
Specific leaf area	Continuous, mm^2 mm^{-1}	Leaf lifespan, leaf defence, positively correlated with growth rate and maximum photosynthetic rate
Leaf nutrients (N, P, K)	Continuous, mg g^{-1}	Maximum photosynthetic rate, nutrient stress
Pollination system	Categorical	Reproductive success
Dispersal mode	Categorical	Colonizing abilities and resistance to disturbances

We used a stratified sampling by dividing the study site into 10 strata according to fire history, using satellite images from 1973 to 2009. Then, we randomly placed 10 plots with 5 m × 5 m in each stratum. We sampled all woody plants in each plot with stem diameter at soil level equal to or higher than 3 cm. We identified all plants to the species level by comparing vouchers to ENP's reference collection (Batalha & Martins 2002). We used Plantminer (Carvalho *et al.* 2010) to check for synonyms and species authors, and to place them in families according to current classifications. We measured 14 functional traits related to environmental filters, such as drought, fire and nutrient-depleted soils (Cornelissen *et al.* 2003; Table 1): basal area, height, height of first bifurcation, resprouting capacity, bark thickness, wood density, leaf toughness, leaf size, specific leaf area, leaf nitrogen content, leaf phosphorus content, leaf potassium content, pollination system and dispersal mode. The importance of these traits and the way we measured them are described in detail by Pérez-Harguindeguy *et al.* (2013).
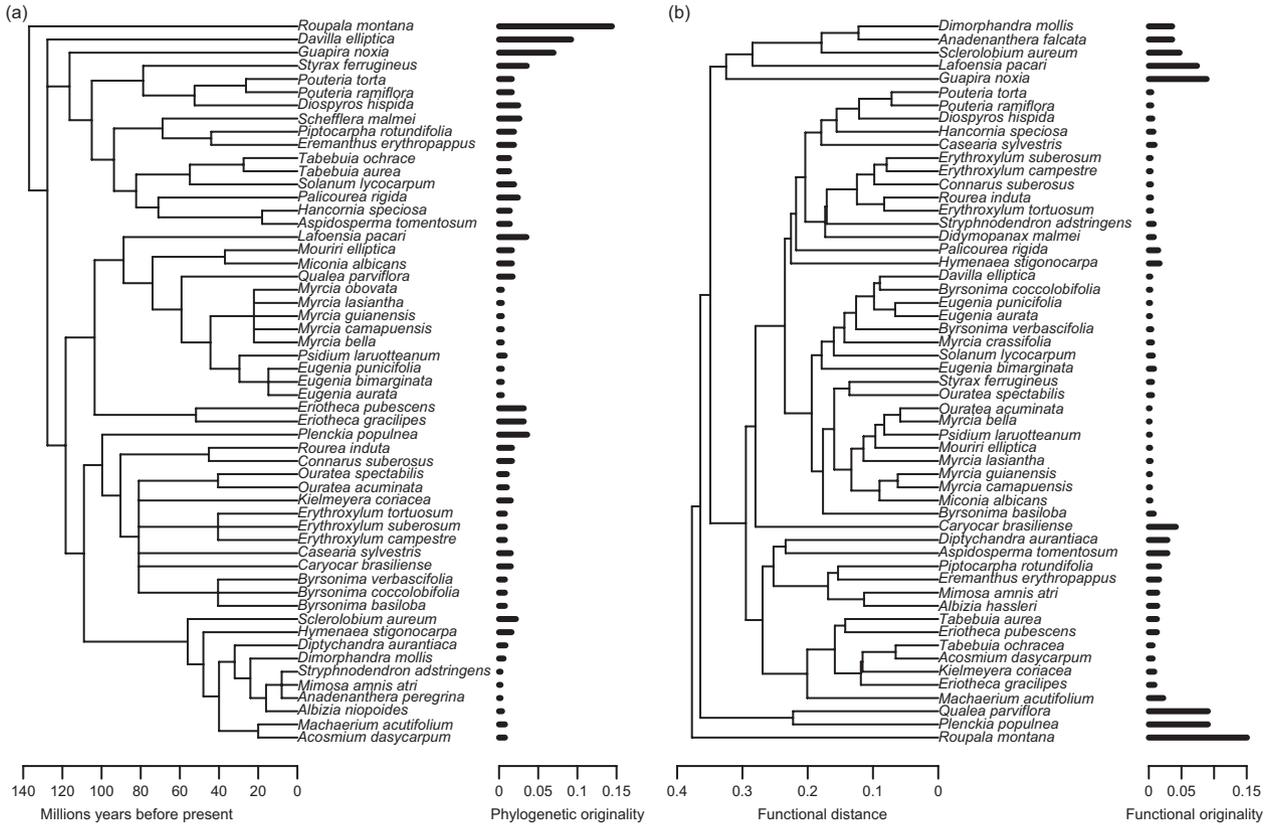
Phylogenetic and functional originalities

We assembled a phylogenetic tree for the sampled species using the Phylocom software and the reference tree R20120829 (Webb & Donoghue 2005; Webb *et al.* 2008). We dated nodes based on fossil data (Wikström *et al.* 2001) to estimate tree branch lengths. We fixed the root and all dated nodes, and then we interpolated branch lengths, placing the undated nodes evenly between dated nodes with the 'bladj' algorithm in Phylocom (Webb *et al.* 2008). To construct the functional dendrogram, we used Gower distance based on traits and average-linkage clustering (Petchey & Gaston 2002, 2006; Podani & Schmera 2006).

We calculated the originality of each species based on both the phylogenetic tree and the functional dendrogram. First, we calculated the distances connecting each pair of species by summing the branches necessary to link the pairs in the tree or the dendrogram. Then, we calculated originalities as the frequency distribution that maximized quadratic entropy (QE-based index; Pavoine *et al.* 2005) with the 'originality' function of the ade4 package in R (R Development Core Team 2014). So, we obtained two originality indices for each species: phylogenetic originality, based on the phylogenetic tree; and functional originality, based on the functional dendrogram. We tested whether the phylogenetic and functional originalities of each species were correlated using Spearman's rank correlation because the data were not normally distributed (Zar 1999).

Simulated extinction

We simulated three extinction scenarios. The first scenario was based on abundance, assuming that rare species are more likely to become extinct (Gaston 1994). We ranked the species by their relative abundance and excluded them in increasing order, calculating at each step the remaining originality. If two or more species presented the same relative abundance, the order of extinctions was random. The second scenario was based on fire tolerance, assuming that if fire frequency increases, fire-sensitive species are more likely to become extinct (Pausas 1999). In each plot, we determined the mean interval between fires based on satellite images from 1984 to 2010. We assigned a value to each species corresponding to the lowest fire interval it experienced, which represented the fire frequency the species was able to tolerate. We ranked the species by their fire tolerance and excluded them in increasing order, calculating at each step the remaining originality. If two or more species presented the same fire tolerance, the order of extinctions was random. The third scenario was based on habitat preference, considering the vegetation physiognomy. Since open cerrado physiognomies are more susceptible to the process of loss and fragmentation (Tubelis & Cavalcanti

Fig. 1. (a) Phylogenetic tree assembled for the cerrado species sampled in Emas National Park, central Brazil (17°49′–18°28′S and 52°39′–53°10′W) with phylogenetic originalities. The relationship among species was based on the current Phylomatic tree (tree R20120829; Webb & Donoghue 2005). (b) Functional dendrogram assembled for the cerrado species sampled in Emas National Park, central Brazil (17°49′–18°28′S and 52°39′–53°10′W) with functional originalities.

2000), we assumed that species occurring in open physiognomies were more likely to become extinct. First, we calculated cylindrical volume of each individual (basal area times height), and then summed up the cylindrical volumes of all individuals in a given plot. Higher volumes indicated closer physiognomies. We multiplied the cylindrical volume vector by the matrix of species abundance per plot. We then estimated habitat preference as the sum of the columns, obtaining a value for each species that indicated its preference for open or closed physiognomies. We ranked the species by this value and excluded them in increasing order, calculating at each step the remaining originality. In each scenario, we compared the extinction trajectory with random ones, in which, at each step, we did 1000 randomizations, excluding species at random and calculating the remaining originality. We calculated the mean and the 95% confidence intervals of the randomizations and compared both observed and random extinction trajectories. We also calculated the worst and best scenarios, excluding the most original species, respectively, first and last. In each scenario, we also plotted the inverse extinction scenario (excluding species in reverse order) to be compared with the observed trajectory. We did all analyses in R (R Development Core Team 2014).

RESULTS

We sampled 531 individuals, belonging to 55 species and 26 families. The richest families were Fabaceae (10 species) and Myrtaceae (9 species, Appendix S1). The species richness varied from 2 to 10 species per plot with a coefficient of variation of 0.56. We assessed the phylogenetic and functional originality of these 55 species (Fig. 1). The most original species according to evolutionary history were *Roupala montana*, *Davilla elliptica*, *Guapira noxia*, *Styrax ferrugineus* and *Diospyros hispida* (Fig. 1a), whereas the most original species regarding functional attributes were *R. montana*, *Qualea parviflora*, *Plenckia populnea*, *G. noxia* and *Lafoensia pacari* (Fig. 1b). The least phylogenetically original species were Myrtaceae and Fabaceae species, whereas the least functionally original species were *Ouratea acuminata* and six Myrtaceae species. We found a weak but significantly positive correlation between the two originality indices ($\rho = 0.38$, $P < 0.01$). Phylogenetic originality was concentrated, with the 10 most original species comprising 50% of the

originality and the 21 least original species comprising only 10%. Functional originality was even more concentrated, with the five most original species comprising 50% of the originality and the 29 least original species comprising 10% of originality.

Abundance was relatively concentrated, with the six most abundant species comprising 54% of the abundance and the 33 least abundant species comprising only 10% (Appendix S1). The fire tolerance ranged from intervals of 5.75 years for *Schefflera malmei* and *Myrcia guianensis*, to intervals of 1.18 years for *Mimosa amnis-atri* and *Pouteria torta* (Appendix S1). Most species had preference for open habitats and most plots had open physiognomies (Appendix S1).

Species extinction scenarios are shown in Figure 2. In the abundance and fire tolerance extinction scenarios, the losses of functional originality were higher than expected by chance, at least at some points of the trajectories (Fig. 2b,d), but the losses of phylogenetic originality were not different from those expected by chance (Fig. 2a,c). In the habitat preference scenario, the losses of both originalities were indistinguishable from random (Fig. 2e,f).

DISCUSSION

Phylogenetic and functional originalities were positively correlated, that is, more isolated species in the phylogeny were more functionally unique, a pattern also found elsewhere (Magnuson-Ford *et al.* 2009). For instance, *R. montana* was the most isolated species in the phylogenetic tree and also the most functionally distinct. Less functionally original species were within lineages with many species, such as Myrtaceae. Functional originality was more uneven than phylogenetic originality, that is, fewer species contributed more to trait diversity. This pattern was similar to that found when evaluating traits related to protection against herbivory in another cerrado community (Silva *et al.* 2012). Whereas it is generally assumed that traits are retained during the evolution of plant species lineages (Ackerly 2003), a positive phylogenetic signal – the tendency of related species to share similar attributes – is absent for many traits of the plant species (Cavender-Bares *et al.* 2004). In a study carried out with 10 out of the 14 traits we sampled, phylogenetic signal was absent for basal area, bark thickness and leaf toughness (Batalha *et al.* 2011). The combination of conserved and non-conserved traits probably led to the weak correlation we found.

When simulating scenarios of species loss, it is important to follow an ecological realistic order of extinction because the shape of these trajectories reveals community properties (Sasaki *et al.* 2014). In the cerrado, the species abundance, the fire regime and the openness of the habitat are parameters for species

risk of extinction because of ecological factors and human-induced impacts. An extinction scenario that is worse than random may be an indicative of communities to be prioritized in conservation efforts (Sasaki *et al.* 2014). Here trajectories of phylogenetic originality loss were not different from random in any scenario; however, there were two trajectories of functional originality that showed faster decline than expected by chance. These two scenarios should be taken into account for planning biodiversity conservation.

The abundance-based extinction trajectory was close to the lower limit of the random simulations, and at some sections resulted in higher loss of functional originality than expected by chance. Losing rare species led to loss of unique or rare functional attributes and resulted in high loss of functional originality. Rare species contribute to the use of resources and to resilience disproportionally to their abundance (Lyons *et al.* 2005). In rich communities, rare species have the least redundant combination of attributes (Mouillot *et al.* 2013), and consequently should have higher priority for conservation. Since most of the species in the present study were rare, functionality in cerrado may be compromised if those species are made locally extinct by human-induced impacts.

Similarly, the fire tolerance-based extinction trajectory was close to the lower confidence interval based on random simulations, and at some points below the lower limit. Losing fire-sensitive species led to loss of rare functional attributes and resulted in high loss of functional originality. Most cerrado species are adapted to fire and some even depend on it (Coutinho 1990; Gottsberger & Silberbauer-Gottsberger 2006), but these fire-sensitive species must have rare attributes that increase functional originality. Thus, conservation plans directed to maintain the highest possible plant diversity in cerrado reserves should consider the implementation of a mosaic of different fire regimes, including regimes with low fire frequency. Conversely, habitat-based extinctions were not different from random extinctions, that is, rare attributes were randomly distributed throughout the physiognomies.

The scenarios of abundance- and fire-dependent extinctions should be considered together for management purposes. Less abundant species may be capable of buffering community functions against perturbations because they are usually functionally different from the dominant ones (Mariotte 2014). For example, if some rare species have thicker barks, then they could resprout shortly after fire, providing a higher stability to the community (Hoffmann 2002; Hoffmann *et al.* 2009). Also, in areas with low disturbance, less abundant species may provide different resources for other trophic levels (Bracken & Low 2012; Mariotte 2014). For example, rare species may
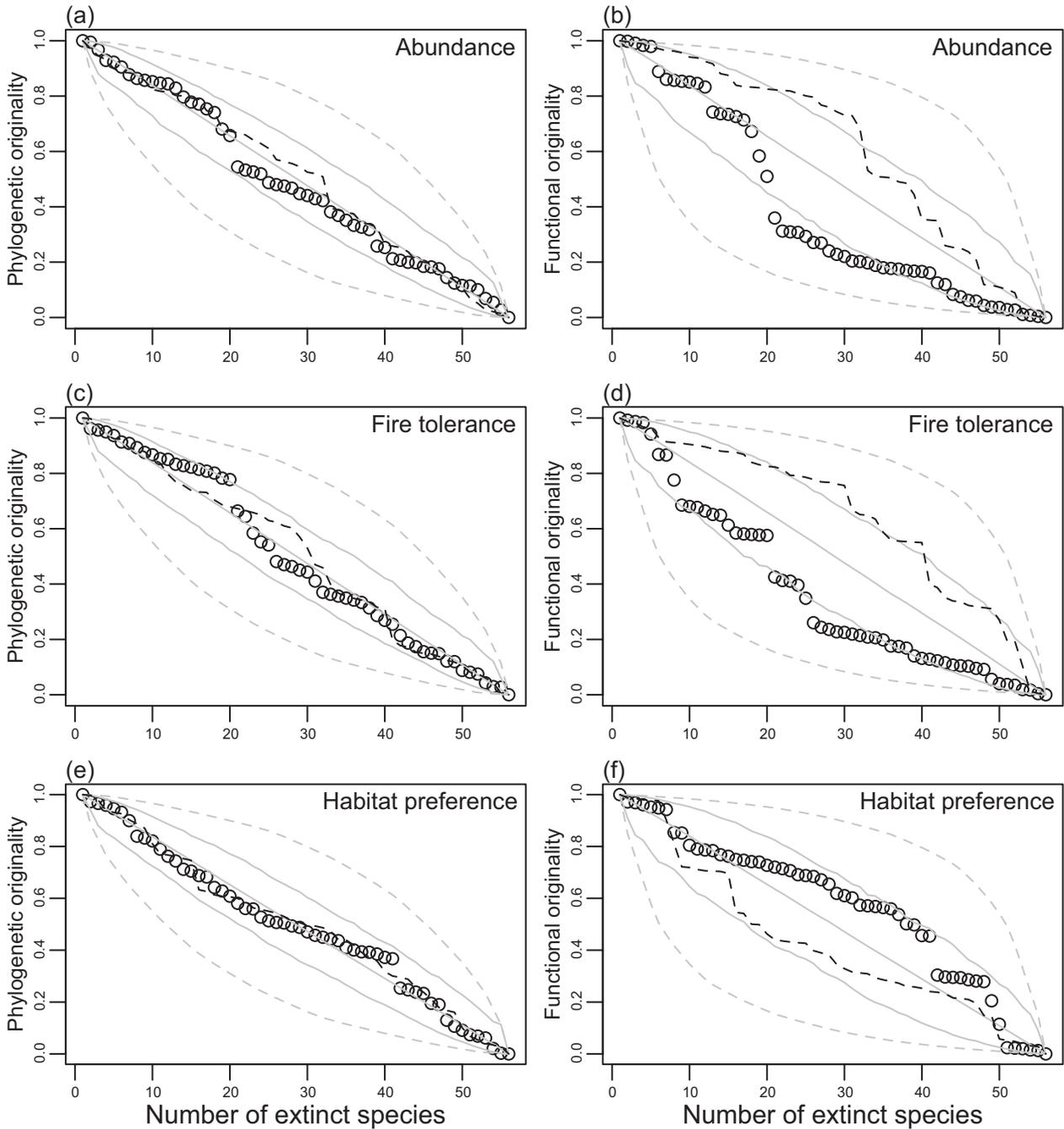
Fig. 2. Species extinction trajectories based on three different scenarios. Circles represent the extinction trajectory, solid grey lines represent mean and 95% confidence intervals of 1000 random extinction trajectories, dashed grey lines represent best and worst trajectories, and dashed black lines represent reverse extinction trajectory. Abundance-based extinction trajectory: (a) phylogenetic originality and (b) functional originality. Fire-tolerance-based extinction trajectory: (c) phylogenetic originality and (d) functional originality. Habitat-preference-based extinction trajectory: (e) phylogenetic originality and (f) functional originality.

have different dispersal or pollination systems. In sum, the conservation of rare species is important because of community functioning (Mouillot *et al.* 2013).

Functional originality seemed to be a more accurate descriptor of the maintenance of community function-ing than phylogenetic originality because, taking into account extinction scenarios based on species abun-dance and fire tolerance, losses of phylogenetic origi-nality were random, which contrasted with losses of functional originality that were higher than expected

by chance. Rare and fire-sensitive species are intrinsically more vulnerable. If they become extinct, many ecological functions will be lost, potentially leading to decreases in community stability and resilience, and occasionally to cascade extinctions due to loss of key interactions. If so, these species should be prioritized in management actions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Relative abundance, fire tolerance and habitat preference for the 55 cerrado species sampled in Emas National Park.