

UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

NATÁLIA BIANCA ROSATTI

**PERDA DE ORIGINALIDADE E EXTINÇÕES
SIMULADAS DE ESPÉCIES ARBUSTIVO-ARBÓREAS
DE CERRADO**

SÃO CARLOS – SP

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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.

Orientador: Prof. Dr. Marco Antônio Batalha

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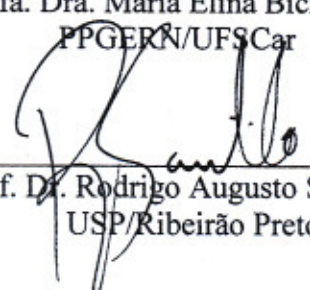
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RESUMO

A originalidade mede o quanto uma dada espécie é diferente das outras espécies em uma comunidade com relação à sua história filogenética e aos seus traços funcionais, podendo ser usada para atribuir prioridades de conservação. Este trabalho está dividido em dois capítulos. No primeiro capítulo, nosso objetivo foi introduzir as originalidades filogenética e funcional, medidas ainda pouco conhecidas. Justificamos as razões para o uso dessa abordagem e exemplificamos maneiras de utilizá-la para fins conservacionistas. No segundo capítulo, nosso objetivo foi avaliar a relação entre a originalidade filogenética e a originalidade funcional, a relação de ambas com variáveis ambientais, e suas perdas em cenários de extinções baseados na abundância, tolerância ao fogo e preferência por habitats, uma maneira objetiva para se tomar decisões com fins conservacionistas. Para isso, em uma reserva de cerrado no Brasil Central, lançamos 100 parcelas, amostramos o componente arbustivo-arbóreo e medimos para cada indivíduo 14 traços funcionais. Para cada parcela, coletamos variáveis ambientais de solo, topografia e histórico de fogo. As originalidades filogenética e funcional estiveram correlacionadas, e ambas aumentaram em direção a ambientes mais severos. Entretanto, nas simulações de extinções baseadas na abundância e na tolerância de fogo, a perda de originalidade funcional foi diferente da perda em extinções aleatórias, enquanto que a perda de originalidade filogenética não foi. Originalidade funcional parece ser uma medida mais apropriada para ser utilizada em estratégias de conservação, já que foi sensível a diferença entre as espécies com relação a suas abundâncias e tolerância ao fogo.

Palavras-chaves: conservação; filogenia; fogo; traços funcionais; savana

ABSTRACT

Originality measures how different a given species is from all other species regarding either their phylogenetic history or functional traits and may be used to assign conservation priorities. This dissertation is divided into two chapters. In the first chapter, we introduced and defined the phylogenetic and functional originalities, which are still underused. We discussed the advantages of using this approach and showed how it could be used in conservation plans. In the second chapter, we analysed the relationships between phylogenetic, and functional originalities, their relationships with the environment, and their losses under extinction scenarios based on species abundance, fire tolerance, and habitat preference. We placed 100 plots in a cerrado reserve located in central Brazil, sampled all woody plants within the plots, measured 14 functional traits, and measured soil, topography, and fire. We assembled a phylogenetic tree, and a functional dendrogram, with which we calculated the originalities. Phylogenetic- and functional-based originalities were correlated, and both increased towards harsher environments. 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. Functional originality seemed to be a better surrogate to be used in conservation strategies, because it was sensitive to differences in species abundances and fire tolerance.

Key words: conservation; fire; functional traits; phylogeny; savanna.

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Capítulo 1

Usando as originalidades filogenética e funcional na conservação da biodiversidade

Natalia Bianca Rosatti e Marco Antônio Batalha

1. Introdução

A ocupação do meio e o uso de recursos pelo homem estão colocando em risco a biodiversidade, pois as taxas de extinções atuais superam até mesmo as grandes extinções históricas. Ações conservacionistas enfrentam obstáculos devido a indefinições de como medir a biodiversidade e de como determinar prioridades (Pavoine *et al.* 2005). A biodiversidade é um conceito que inclui padrões espaço-temporais, entidades como espécies, traços e unidades evolutivas (Pavoine *et al.* 2010). Nesse cenário complexo, para conservar a biodiversidade – ou, ao menos, para minimizar sua perda – devemos quantificá-la. Frequentemente, essa quantificação é feita contando-se o número de espécies em uma dada área ou em um dado número de indivíduos (riqueza de espécies ou densidade), ou combinando o número de espécies com a distribuição de abundâncias (por exemplo, os índices de Shannon e de Simpson). Tais medidas assumem que todas as espécies são equivalentes ecológica e evolutivamente.

Porém, assumir essa equivalência entre as espécies não é adequado para viabilizar a conservação da biodiversidade (Vane-Wright *et al.* 1991). De acordo com suas características, as espécies têm funções ecológicas distintas, que influenciam diferentemente a comunidade sob dois principais aspectos. Primeiro, no que diz respeito à estabilidade. Uma maior diversidade de traços está diretamente relacionada à resistência e à resiliência das comunidades após perturbações, tornando as comunidades mais estáveis (Díaz & Cabido 2001). Segundo, no que diz respeito ao uso de recursos. Se as espécies possuem valores diferentes para os seus traços funcionais, elas são mais complementares, ocupando nichos distintos. Isso leva a um uso mais eficiente dos recursos e, conseqüentemente, a um melhor funcionamento da comunidade, cuja produtividade pode ser maior e cuja ciclagem de nutrientes pode ser mais rápida.

Assim, alterações na diversidade dos traços das espécies devem ter implicações na estabilidade e no funcionamento das comunidades, afetando inclusive a manutenção de serviços ecológicos, dos quais o bem-estar humano depende. Sob essa perspectiva, devemos considerar os valores e a variação dos traços que influenciam o funcionamento das comunidades em planos de conservação. Ademais, como as espécies possuem diferentes informações genéticas, devemos maximizar a preservação da história evolutiva em tais planos de conservação, tanto para que as espécies deem continuidade a seus processos evolutivos, quanto por questões éticas de preservarmos a história evolutiva da Terra. Dessa forma, temos que as espécies são diferentes entre si, quer funcional, quer filogeneticamente, e tais

diferenças devem ser consideradas em ações conservacionistas.

Uma das principais dificuldades em ações conservacionistas são os recursos financeiros limitados. As reservas ambientais geralmente possuem um tamanho que não é suficiente para abrigar todas as espécies de uma região. A impossibilidade de protegermos simultaneamente todas as espécies implica a necessidade de atribuímos prioridades na conservação da biodiversidade. Essas prioridades podem ser baseadas no grau de ameaça (por exemplo, a lista vermelha da IUCN; do inglês *International Union for Conservation of Nature*), no grau de endemismo e no valor econômico das espécies. Mas, se quisermos garantir o funcionamento e a manutenção da diversidade a longo prazo, é importante conservarmos a maior amplitude de traços funcionais e o máximo de história evolutiva possíveis nas unidades de conservação (Redding & Mooers 2006). Uma maneira de se fazer isso é levando-se em consideração a raridade média dos traços das espécies que ocorrem em um dado local. Vane-Wright *et al.* (1991) foram os primeiros a propor uma medida de raridade média de traços das espécies com base em suas relações taxonômicas, que eles chamaram de *distinguíbilidade taxonômica* e que poderia ser usada para definir prioridades de conservação. Desde então, algumas outras medidas com o mesmo intuito foram propostas, incluindo aquela que discutiremos aqui, a *originalidade*.

2. Originalidades filogenética e funcional

Proposta por Pavoine *et al.* (2005), a originalidade utiliza a história filogenética das espécies para estimar a raridade média dos traços de cada espécie. Essa estimativa é possível, pois os ramos da árvore filogenética contêm o tempo de evolução de cada espécie e cada nó, o tempo de divergência evolutiva entre elas. Portanto, o comprimento dos braços compartilhados por duas espécies indica o número esperado de traços herdados de um ancestral comum, e a distância de duas espécies ao nó mais próximo, o tempo desde que elas começaram a evoluir independentemente e, portanto, a probabilidade de apresentarem traços únicos. Consequentemente, quanto mais isolada na árvore filogenética uma espécie estiver, maior a probabilidade de ela conter traços raros ou únicos (Pavoine *et al.* 2005). Dessa forma, a originalidade filogenética nos fornece uma estimativa de diferenças genotípicas, fenotípicas e funcionais entre as espécies. Assim, ao priorizarmos a conservação das espécies filogeneticamente mais originais, esperamos conservar uma maior diversidade de traços e de informações genéticas raras ou únicas e, portanto, uma maior diversidade de estados evolutivos e ecológicos (Pavoine *et al.* 2005).

O funcionamento de uma comunidade, porém, não é determinado necessariamente pela história evolutiva das espécies que abriga, mas sim pelos traços funcionais dessas espécies (Naeem & Wright 2003). Se os traços das espécies são conservados na filogenia, então podemos esperar que espécies filogeneticamente mais originais também sejam as mais originais funcionalmente. Nesse caso, a abordagem filogenética seria suficiente para medirmos a originalidade das espécies e, para isso, dependeríamos da identificação taxonômica das espécies e de informações das relações filogenéticas entre elas, evitando a coleta de dados funcionais, que demanda tempo e dinheiro.

Correlações entre a história evolutiva e traços funcionais foram encontradas em estudos recentes, como, por exemplo, no gênero de peixes *Sebastes*, em que as espécies mais isoladas na árvore filogenética também são as mais distintas morfológicamente (Magnuson-Ford *et al.* 2009). Porém, traços relacionados com funções ecologicamente relevantes podem ser convergentes. O processo de convergência de traços, resultado de adaptações independentes ao ambiente, permite que espécies distantes filogeneticamente apresentem traços semelhantes (Pavoine *et al.* 2010). Nesse caso, as espécies mais isoladas filogeneticamente não são necessariamente as mais distintas funcionalmente. Portanto, se priorizássemos em ações de conservação as espécies mais isoladas filogeneticamente, estaríamos preservando uma maior diversidade de informação genética, mas não traços funcionais raros ou únicos.

Como os índices baseados em árvores filogenéticas também podem ser aplicados em dendrogramas funcionais, podemos calcular a originalidade funcional das espécies (Pavoine *et al.* 2010). Aqui, em vez de usarmos a árvore filogenética, usamos o dendrograma funcional, obtido por meio da coleta dos traços funcionais das espécies em uma comunidade. Essa abordagem permite estimar a complementaridade nas funções ecológicas das espécies e identificar aquelas funcionalmente importantes. O uso de traços funcionais não exige o conhecimento taxonômico das espécies, o que é uma vantagem em locais com poucos estudos desse tipo. Porém, essa abordagem exige passos críticos como a escolha de traços realmente importantes a serem coletados e a coleta em si, que é bastante trabalhosa e custosa.

3. Aplicações

Como a proteção de áreas é a principal ferramenta utilizada para a conservação da diversidade, podemos maximizar a diversidade preservada ao escolher áreas que abriguem as espécies mais originais. Usando dados de carnívoros, Pavoine *et al.* (2005) aplicaram um algoritmo que indica a combinação de espécies que maximiza a quantidade de diversidade

preservada em função da originalidade. Nesse estudo, assumiu-se que apenas um quinto das espécies poderia ser preservado. Quando as espécies a serem conservadas foram sorteadas, 43% da história evolutiva foi preservada; porém, quando o método de maximização da originalidade foi usado, a proporção de história evolutiva preservada subiu para 55%. Essa abordagem é uma alternativa viável para o *dilema da Arca de Noé*, em que, a partir de um conjunto de espécies, devemos escolher aquelas que serão protegidas pelas ações de conservação e aquelas que ficarão desamparadas. A originalidade das espécies pode ser calculada no ambiente R com o pacote ‘ade4’ (R Development Core Team 2009). Além disso, Pavoine *et al.* (2005) disponibilizaram as instruções e as funções usadas nos apêndices do artigo.

Outra abordagem possível prioriza medidas de manejo contra espécies exóticas. Se partirmos da premissa de que espécies aparentadas compartilham nichos ecológicos semelhantes, bem como inimigos naturais, então, quanto mais distintas filogeneticamente e funcionalmente as espécies exóticas forem em relação às espécies nativas, isto é, quanto mais originais elas forem, maior o potencial invasor (Strauss *et al.* 2006). Dessa forma, ações de manejo que combatam as espécies exóticas mais distintas filogeneticamente e funcionalmente deveriam ser priorizadas (Strauss *et al.* 2006).

Mouillot *et al.* (2008) testaram se as reservas biológicas realmente beneficiam as espécies funcionalmente mais originais e, portanto, promovem a manutenção de uma maior diversidade de traços. Nesse estudo, as espécies mais originais tornaram-se mais abundantes quando delimitada a reserva biológica e cessada a pressão antrópica. Eles sugeriram que as espécies mais originais podem atuar como indicadoras dos efeitos de ações conservacionistas em ambientes que sofreram perturbações. Isso sustentaria o funcionamento e promoveria a resiliência da comunidade, proporcionando serviços ecológicos mais eficientes e capacidade da comunidade se manter frente às pressões, como aquelas resultantes das mudanças climáticas globais e modificações no uso da terra (Mouillot *et al.* 2008).

4. Conclusões

O uso das originalidades das espécies para guiar planos de conservação pode nos ajudar a preservar uma maior diversidade de história evolutiva e de atributos funcionais em uma comunidade. Com a aplicação desses índices, haveria uma mudança de foco da conservação das espécies para as unidades evolutivas e funcionais, que devem estar diretamente relacionadas ao funcionamento e à estabilidade das comunidades. Esses índices podem ser

usados em diversos contextos, entre os quais: (1) determinação de prioridades de conservação, (2) detecção de mudanças devido a impactos ambientais e (3) simulações de extinções para prever as consequências da perda de espécies na diversidade ecológica e evolutiva das comunidades. No entanto, apesar da versatilidade, o conceito de originalidade ainda é subutilizado. A consolidação dessa nova abordagem para a mensuração da diversidade e as relações dessa medida com os processos ecológicos, como funcionamento e estabilidade, aumentam as chances de maximizarmos a preservação da biodiversidade e serviços ecológicos em ações conservacionistas e, portanto, estudos que a usem devem ser encorajados.

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Capítulo 2

Loss of phylogenetic and functional originalities of woody cerrado species in simulated extinction scenarios based on abundance, fire tolerance, and habitat preference

Natalia Bianca Rosatti, Danilo Muniz da Silva and Marco Antônio Batalha

Abstract

Originality measures how different a given species is from all other species regarding either their phylogenetic history or functional traits and may be used to assign conservation priorities. Our goal was to evaluate the relationships between phylogenetic and functional originalities, their relationships with the environment, and their losses under several extinction scenarios. 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 soil features, topography, and fire history. We assembled a phylogenetic tree and a functional dendrogram, with which we calculated the originalities. Phylogenetic- and functional-based originalities were correlated, and both increased towards harsher environments. 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. Functional originality seemed to be a better surrogate to be used in conservation strategies, because it was sensitive to differences in species abundances and fire tolerance.

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

1. Introduction

Faced with intense loss of diversity, the main goal of conservation plans is to preserve as much diversity as possible. An important question in this context is how to measure diversity. For the purpose of conservation, a useful measure is the distinctiveness among species (Vane-Wright et al. 1991). Trait distinctiveness and phylogenetic relatedness among species determine their role in community functioning (Pavoine et al. 2005; Petchey and Gaston 2006). The more distinct is the species, the more complementary are its traits, and complementarity among traits increases stability and optimises resource use in a community (Petchey 2003).

Originality measures the distinctiveness among species, that is, how different a given species is from all other species, regarding phylogenetic history or functional traits, and can be used to predict changes in community functioning (Pavoine et al. 2005; Petchey et al. 2007). For example, extinction of a highly original species results in loss of unique or rare functional traits and can disrupt community functioning (Mouillot et al. 2008; O’Gorman et al. 2010). The originality of a species can be based either on phylogenetic distances or functional differences (Mouillot et al. 2008; Pavoine et al. 2005; Petchey et al. 2007). Indeed, many studies on conservation priorities take into account only the phylogenetic information, considering that the traits are conserved and, thus, species with fewer close relatives should be more functionally unique (for instance, Redding and Mooers 2006). Although phylogeny accounts for some of the functional differences, environmental pressure can select convergent traits from distantly related species, therefore, phylogenetically dispersed community may be functionally convergent (Batalha et al. 2011; Silva et al. 2011). Since plants traits can be conserved or convergent, phylogenetic and functional relationships among species may provide complementary information (Pavoine and Bonsall 2010). Taken together, these measures could improve the understanding of how ecological processes affect community composition and functioning (Pavoine and Bonsall 2010).

Since environmental filters may act on either convergent or conserved traits and since different environmental filters may act in different habitats, the distribution of lineages and functions may have, accordingly, spatial signals (Pavoine et al. 2011). In sites with more resources, a dominant species may outcompete others, whereas, in harsher environments, facilitation may prevail (Tielbörger and Kadmon 2000). Thus, species complementarity is expected to be influenced by environmental conditions and, if so, originalities should be related to the environmental variation.

Local extinctions are not random, but are the result of traits responding to environmental conditions and interspecific interactions (Purvis et al. 2000). Simulations of realistic extinction scenarios allow estimates of originality losses, to predict the consequences of change, and, consequently, are useful to guide future management actions when trying to maintain key aspects of biological diversity. When conservation plans ignore evolutionary distinctiveness and functional divergence, there is a risk of losing valuable functions, because of the loss of entire lineages or functionally unique species (Maherali and Klironomos 2007; Redding et al. 2010). Communities with high richness, endemic species, high heterogeneity, and threatened by human activities are proper systems to study the originality as a surrogate of biodiversity loss. The Brazilian cerrado vegetation presents a wide physiognomic range, going from grasslands to woodlands, but with most of its physiognomies within the definition of tropical savanna (Coutinho 1990). The cerrado encompasses the richest savanna in the world, with many endemic species, and is being rapidly converted into croplands, pastures, or urban areas, putting many species at risk. Thus, it is one of the 25 biodiversity hotspots in the world (Klink and Machado 2005; Myers et al. 2000). In this sense, one may use species originality as a criterion to establish conservation priorities (Pavoine et al. 2005) for the cerrado and, occasionally, for other savannas. Here we simulated three extinction scenarios based on variables that may affect attempts to conserve the cerrado, assessing their consequences in originality loss.

Abundance is an important aspect of diversity and must be taken into account when estimating extinction risk, since the risk increases with decreasing population (Morris and Doak 2002; Purvis et al. 2000). In the cerrado, the intense anthropic pressure further decreases population sizes, increasing the chances of loss. 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.

Other 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 three 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 barks and resprouting ability, but if fire frequency is too high, even these plants may die (Hoffman 1999). As a matter of fact, higher fire frequency decreases tree densities (Hoffman 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.

Presence of open or closed physiognomy depends on soil, water availability, and fire frequency (Pivello and Coutinho 1996). Different physiognomies have different floristic compositions, and a given species tend to occur in a given physiognomy according to its requirements (Angelo and Angelini 2007). 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 and Cavalcanti 2000). If a given physiognomy is at a higher risk of extinction and if it contains more original species, then this physiognomy must be prioritised in conservation efforts.

Here, we calculated phylogenetic and functional originalities of woody cerrado species and simulated what would happen to the communities under three extinction scenarios. So, we tested whether: (1) phylogenetic and functional originalities were correlated; (2) both originalities were related to environmental variables, such as topography, fire regime, and soil; and (3) the losses of originalities based on abundance, fire tolerance, and habitat preference were different from what would be expected solely by chance. We intended to provide guidelines to management strategies when one wants to minimise biodiversity loss in the cerrado and other savannas.

2. Material and methods

2.1. 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 1,200 to 2,000 mm concentrated from October to March (Ramos-Neto and 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 and Pivello 2000). Up to 1984, farmers used ENP for cattle ranching and used fire to promote grass regrowth (Ramos-Neto and 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 three years due to the accumulation of dry biomass (França et al. 2007). After 1994, natural fires were allowed inside the reserve, and anthropogenic burnings were avoided by

preventive firebreaks, burned annually during the dry season (Ramos-Neto and Pivello 2000). Despite these precautions, another catastrophic fire burned 93% of the reserve in August 2010.

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 x 5 m plots in each stratum. We sampled all woody plants in each plot with stem diameter at soil level equal to or higher than 3 cm (SMA 1997). We identified all plants to the species level by comparing vouchers to ENP's reference collection (Batalha and 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; Pausas and Paula 2005; 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 Cornelissen et al. (2003). In each plot, we measured altitude and slope as surrogates for water availability. In ENP, the higher the altitude and the flatter the terrain, the lower the water availability. We also measured several soil features following Silva and Batalha (2008): pH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminium, sum of bases, cation exchange capacity, base saturation, aluminium saturation, sand proportion, silt proportion, and clay proportion. Based on satellite images from 1984 to 2010, we determined mean interval between fires and time since last fire.

2.2. Phylogenetic and functional originalities

We assembled a phylogenetic tree for the sampled species using the Phylocom software and the latest reference tree (R20091110; Webb and 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 the Phylocom software (Webb et al. 2008). To construct the functional dendrogram, we used a matrix with functional traits in rows, species in columns, and average values in entries. We standardised continuous traits to zero mean and unit variance. Then, using Gower distance and average-

linkage clustering, we assembled a functional dendrogram (Petchey and Gaston 2002; Petchey and Gaston 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 maximised quadratic entropy (QE-based index; Pavoine et al. 2005). So, we obtained two originality indices for each species: phylogenetic originality, based on the phylogenetic tree, and functional originality, based on the functional dendrogram.

2.3. Statistical analyses

We tested whether the phylogenetic and functional originalities of each species were correlated using the Spearman's rank correlation, because the data were not normally distributed (Zar 1999). To test whether topography, soil, and fire history predicted originality, first we removed variables that were correlated to each other ($-0.7 > R > 0.7$) and then did two multiple regressions (Jongman et al. 1995), one for phylogenetic originality and another for functional originality. In each one, the sum of originality species present per plot was the response variable, and altitude, slope, pH, organic matter, nitrogen, phosphorus, potassium, aluminium, sum of bases, cation exchange capacity, base saturation, silt, clay, fire interval, and time since last fire were the explanatory variables. Using the Akaike Information Criterion (Akaike 1973), we ranked the models and selected the best. For it, we compared the models based on $\Delta AICc$, $AICcW_i$, and the coefficient of determination (Burnham and Anderson 2002). The $\Delta AICc$ is the difference between each model's $AICc$ and the "best model", that is, the one with the lowest $AICc$. Models with $\Delta AICc$ values lower than two may be considered as good as the "best model". The Akaike weight ($AICcW_i$) provides evidence that the model is the best in the model set.

2.4. Simulated extinction

We simulated three extinction scenarios. The first scenario was based on abundances, 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 et al. 1999). 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, using the vegetation physiognomy as a surrogate for habitat. Since open cerrado physiognomies are more susceptible to the process of loss and fragmentation (Tubelis and Cavalcanti 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. The higher the volume, the closer the physiognomy. We multiplied the cylindrical volume vector by the matrix of species abundances 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 extinction trajectory with random ones, in which, at each step, we did 1,000 randomisations, excluding species at random and calculating the remaining originality. We calculated the mean and the 95% confidence intervals of the randomisations and compared both observed and random extinction trajectories. We did all analyses in R (R Development Core Team 2009).

3. Results

We sampled 531 individuals, belonging to 55 species and 26 families (Appendix). The richest families were Fabaceae (10 species) and Myrtaceae (9 species). We assessed the phylogenetic and functional originalities these 55 species (Figures 1 and 2). The most original species according to evolutionary history were *Roupala montana*, *Davilla elliptica*, *Guapira noxia*, *Styrax ferrugineus*, and *Diospyros hispida* (Figure 1), whereas the most original species regarding functional traits were *R. montana*, *Qualea parviflora*, *Plenckia populnea*, *G. noxia*, and *Lafoensia pacari* (Figure 2). We found a weak, but significant and positive, correlation between both originality indices ($\rho = 0.38$, $P < 0.01$).

Phylogenetic originality was positively related with altitude, slope, potassium, aluminium,

and fire interval and negatively related with pH, sum of bases, silt, clay, and time since last fire (Table 2). Functional originality was positively related with altitude, aluminium, and fire interval and negatively related with pH, nitrogen, clay, and time since last fire (Table 3). 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 (Figures 3b and 3d, Appendix), but the losses of phylogenetic originality were not different from the expected by chance (Figures 3a and 3c, Appendix). On the other hand, in the habitat preference scenario, the losses of both originalities were indistinguishable from random (Figure 3e and 3f, Appendix).

4. Discussion

Phylogenetic and functional originalities were positively correlated, pointing out that, in general, the more isolated the species in the phylogeny, the more functionally unique it was, a pattern also found elsewhere (Magnuson-Ford et al. 2009). For instance, *R. montana* was the most isolated species in the 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. 2011). Whereas it is generally assumed that traits are retained during the evolution of plant species lineages (Arkerly 2003), phylogenetic signal is absent for many traits of the plant species (Cavender-Bares et al. 2004). In a study carried out with ten out of 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.

Phylogenetic and functional originalities responded similarly to topography, soil, and fire regime. They increased in higher altitudes, acid, sandy, nutrient-poor, and aluminium-rich soils, and in recently burned sites. High aluminium content and low clay proportion decrease soil fertility (Goodland 1971; Larcher 1995), whereas high altitude and low clay proportion decrease water availability (Eiten 1972; Larcher 1995). Fire has direct, negative effects on the growth rate of plants, increasing seedling mortality and hindering full development of plants to reproductive size (Hoffman 2002; Hoffman et al. 2009), but has indirect, positive effects on nutrient availability (Kauffman et al. 1994). Thus, overall, phylogenetic and functional

originalities increased towards harsher environments. In these environments, differences in species abilities to explore the limited resources are essential to allow their coexistence (Petchey 2003). Communities with high originality presented both more species and highly original species. In these communities, complementarity among species may result in facilitation (Quintana-Ascencio and Menges 2000), because original plants will not compete for the same resources or, at least, will use them in different manners. Thus, they can respond differently to the environment and carry out different ecological functions (McEwen and Vamosi 2010; Mouillot et al. 2008; Tielbörger and Kadmon 2000). High originality in harsh environments leads to higher complementarity among species and, consequently, to communities that may operate better (Mouillot et al. 2008; O’Gorman et al. 2010; Pavoine et al. 2005).

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 traits and resulted in high loss of functional originality. Rare species contribute to the use of resources and to resilience disproportionately to their abundances (Lyons et al. 2005). The unique or rare traits related to the nutritional stresses and disturbances of rare species may provide environmental requirements and tolerances different from those provided by the abundant species (Walker et al. 1999). In addition, these unique or rare traits are at the base of food chains, which should strong influence on higher levels trophic (Bracken and Low 2012) If so, losing these rare species may result in lower stability of the community and subsequent extinction of other species (O’Gorman et al. 2010). Similarly, fire tolerance-based extinction trajectory was close to the lower confidence intervals based on random simulations and, at some points, below the lower limit. Losing fire-sensitive species led to loss of unique or rare functional traits and resulted in high loss of functional originality. Most cerrado species are adapted to fire and some even depend on it (Coutinho 1990; Gottsberger and Silberbauer-Gottsberger 2006), but these fire-sensitive species must have unique or 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. This consideration is reinforced by fact that functional originality increased towards environments with higher fire interval, that is, lower fire frequency. Conversely, habitat-based extinctions were not different from random extinctions, that is, unique and rare traits were randomly distributed throughout the physiognomies. If so, all cerrado physiognomies should be conserved, including the open

ones, which are often neglected and more easily turned into pastures or crop fields.

Phylogenetic and functional originalities were positively correlated, responded to the same environmental variables, and followed similar trajectories in the habitat-based extinction scenario. This set of results indicated that either phylogenetic or functional originality could be used interchangeably, at least to define conservation priorities. As long as phylogenetic originality is easier to be calculated, because there is no need to measure functional traits, which is time and resource consuming, it would be the best choice if one wanted to preserve both evolutionary history and trait diversity. However, taking into account extinction scenarios based on species abundances and fire tolerance, losses of phylogenetic originality were random, which contrasted with losses of functional originality that were higher than expected by chance. Taking these results into account, functional originality seems to be a more accurate descriptor of the maintenance of community functioning. 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 prioritised in management actions.

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Table 1. Plant traits used to calculate functional originality and their functional relevance (see Cornelissen et al. 2003 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 vigor, fecundity, growth time between disturbances, positively correlated with above-ground biomass, root depth, and leaf area
Height of first bifurcation	Continuous, m	Resistance and resource disponibilitiy
Resprouting capacity	Binary	Resistance and resource disponibilitiy
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 mg ⁻¹	Leaf lifespan, leaf defense, 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	Colonising abilities and resistance to disturbances

Table 2. Values calculated for the model selection of multiple regression analysis, using phylogenetic originality per plot as response variable and soil, topography, and fire history as explanatory variables. alt = altitude, slo = slope, OM = organic matter, N = nitrogen, P = phosphorus, K = potassium, Al = aluminium, SB = sum of bases, CEC = cation exchange capacity, V = base saturation, silt = silt proportion, clay = clay proportion, interval = fire interval, lastfire = time since last fire.

Explanatory variables	R²	AICc	AICc	AICcWt
alt + slo + pH + OM + N + P + K + Al + SB + CEC + V + silt + clay + interval + lastfire	0.345	-372.542	13.397	0.001
alt + slo + pH + N + P + K + Al + SB + CEC + V + silt + clay + interval + lastfire	0.353	-375.410	10.529	0.003
alt + slo + pH + N + P + K + Al + SB + CEC + silt + clay + interval + lastfire	0.360	-378.211	7.728	0.011
alt + slo + pH + N + P + K + Al + SB + silt + clay + interval + lastfire	0.367	-380.901	5.038	0.044
alt + slo + pH + P + K + Al + SB + silt + clay + interval + lastfire	0.369	-382.797	3.142	0.114
alt + slo + pH + K + Al + SB + silt + clay + interval + lastfire	0.371	-384.594	1.345	0.280
alt + pH + K + Al + SB + silt + clay + interval + lastfire	0.370	-385.939	0.000	0.548

Table 3. Values calculated for the model selection of multiple regression analysis, using functional originality per plot as response variable and soil, topography, and fire history as explanatory variables. alt = altitude, slop = slope, OM = organic matter, N = nitrogen, P = phosphorus, K= potassium, Al = aluminium, SB = sum of bases, CEC = cation exchange capacity, V = base saturation, silt = silt proportion, clay = clay proportion, interval = fire interval, lastfire = time since last fire.

Explanatory variables	R²	AICc	AICc	AICcWi
alt + slo + pH + OM + N + P + K + Al + SB + CEC + V + silt + clay + interval + lastfire	0.329	-322.465	18.234	0.000
alt + slo + pH + N + P + K + Al + SB + CEC + V + silt + clay + interval + lastfire	0.337	-325.370	15.329	0.000
alt + slo + pH + N + P + K + Al + CEC + V + silt + clay + interval + lastfire	0.344	-328.168	12.531	0.001
alt + pH + N + P + K + Al + CEC + V + silt + clay + interval + lastfire	0.350	-330.696	10.003	0.003
alt + pH + N + P + Al + CEC + V + silt + clay + interval + lastfire	0.353	-332.663	8.036	0.009
alt + pH + N + P + Al + CEC + silt + clay + interval + lastfire	0.359	-335.066	5.633	0.029
alt + pH + N + P + Al + silt + clay + interval + lastfire	0.363	-337.128	3.571	0.082
alt + pH + N + Al + silt + clay + interval + lastfire	0.360	-338.194	2.505	0.139
alt + pH + N + Al + clay + interval + lastfire	0.359	-339.344	1.355	0.248
alt + pH + N + Al + clay + lastfire	0.359	-340.699	0.000	0.488

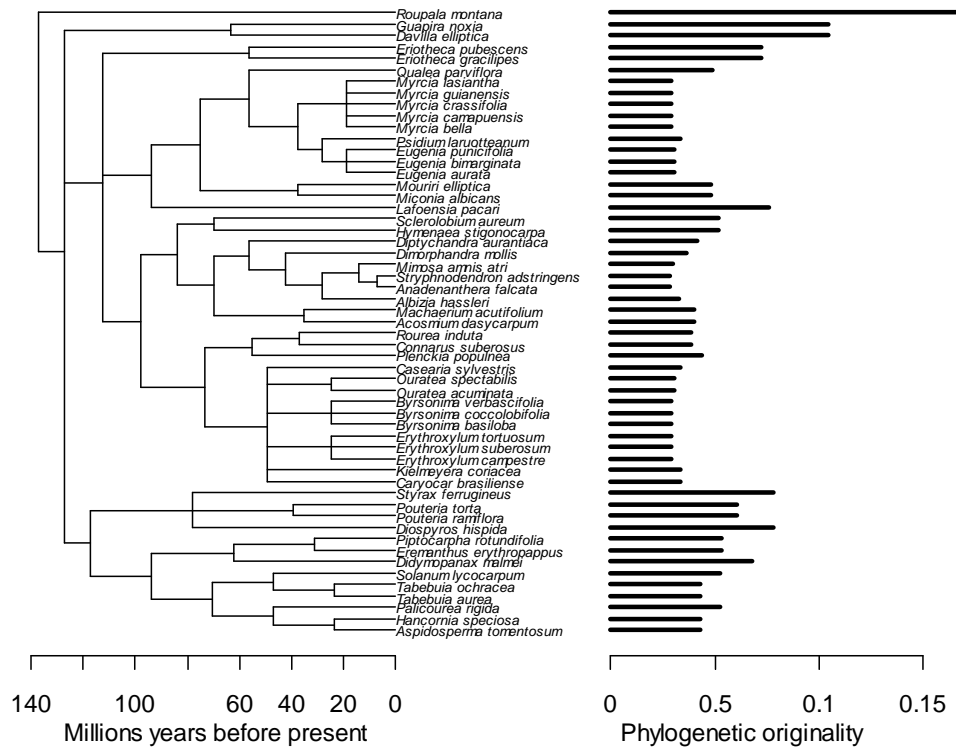


Figure 1. Phylogenetic tree assembled for the cerrado species sampled in Emas National Park, central Brazil (17°49'-18°28'S and 52°39'-53°10'W) with phylogenetic originalities. The relationship among species was based on the current Phylomatic tree (tree R20091110; Webb and Donoghue, 2005).

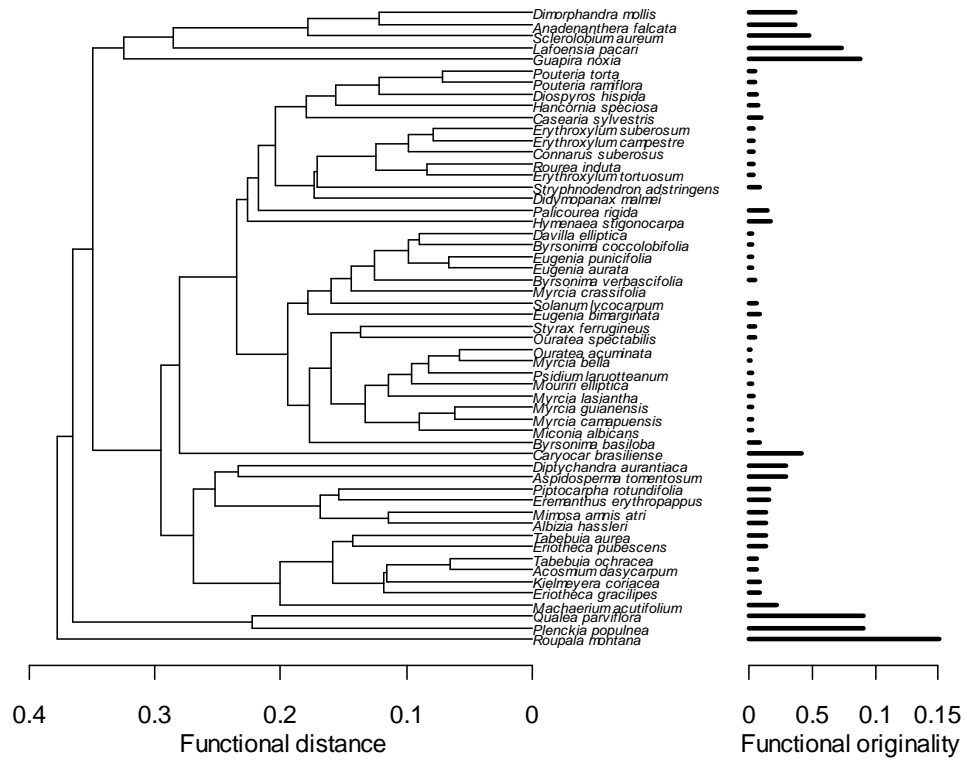


Figure 2. Functional dendrogram assembled for the cerrado species sampled in Emas National Park, central Brazil (17°49'-18°28'S and 52°39'-53°10'W) with functional originalities.

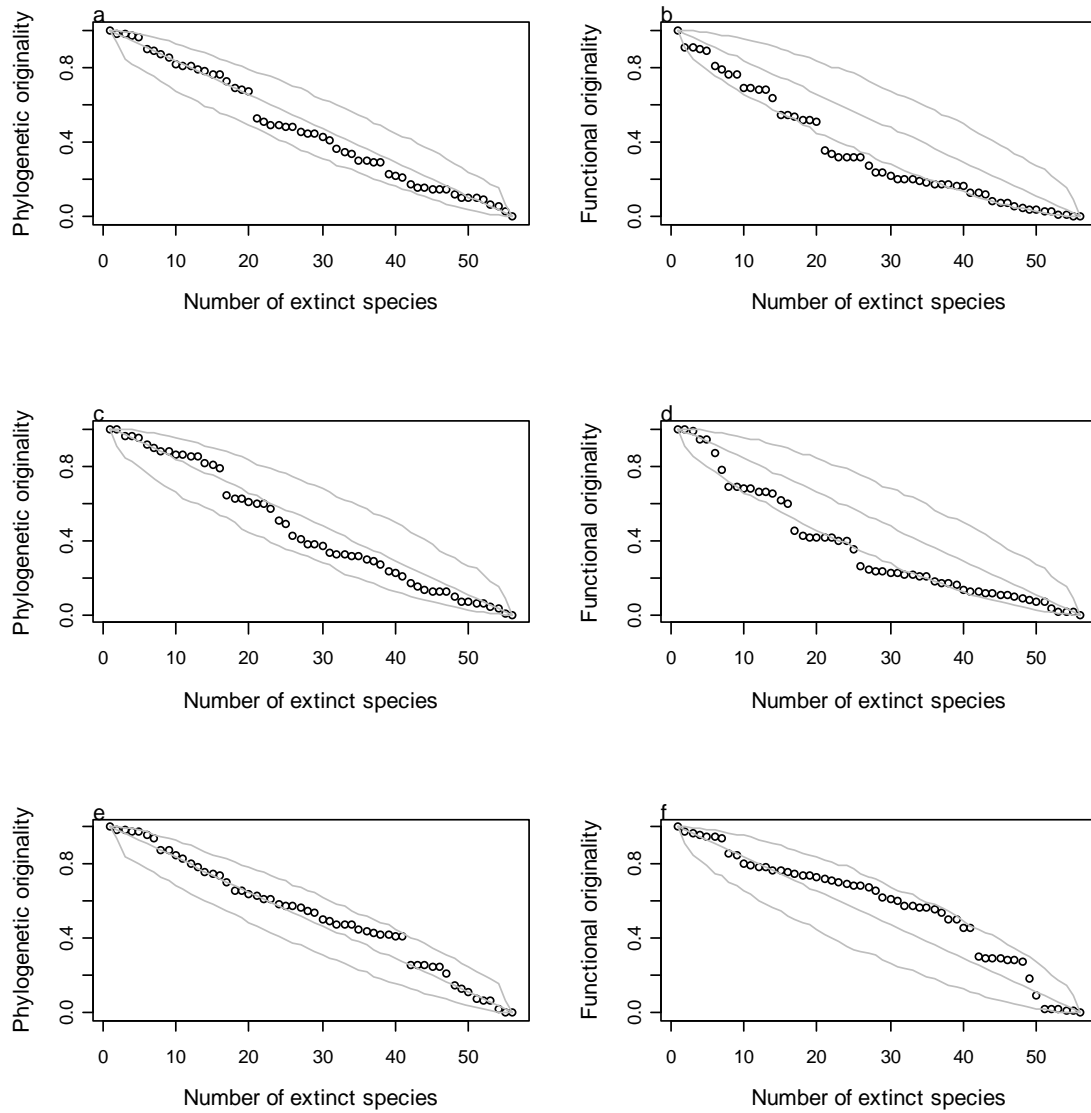


Figure 3. Filled circles represent the extinction trajectory following traits, gray lines represent mean and 95% confidence intervals of 1,000 random extinction trajectories. Abundance-based extinction trajectory: (a) phylogenetic originality and (b) functional originality. Fire-tolerance-based extinction trajectory: (c) phylogenetic originality and (d) functional originality. Habitat-preference-based extinction trajectory: (e) phylogenetic originality and (f) functional originality.

Appendix. Relative abundance, fire tolerance, and habitat preference for the 55 cerrado species sampled in Emas National Park, central Brazil (17°49'–18°28'S and 52°39'–53°10'W). Fire tolerance is based on the lowest fire interval, in years, a given species had experienced. Habitat preference reflects the occurrence of a given species in open or closed physiognomies. The higher the value, the closer the physiognomy.

Family	Species	Relative Abundance	Fire tolerance	Habitat preference
Fabaceae	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	0.0226	2.250	0.097
Fabaceae	<i>Albizia hassleri</i> (Spruce ex Benth.) Burkart	0.0019	3.500	1.000
Fabaceae	<i>Anadenanthera falcata</i> (Benth.) Reis	0.0282	1.700	0.289
Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.	0.0019	2.120	0.000
Malpighiaceae	<i>Byrsonima basiloba</i> A. Juss.	0.0056	2.370	0.338
Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth	0.0094	2.250	0.211
Malpighiaceae	<i>Byrsonima verbascifolia</i> (L.) DC.	0.0019	4.400	0.310
Caryocaraceae	<i>Caryocar brasiliense</i> A. St.-Hil.	0.0019	4.400	0.310
Salicaceae	<i>Casearia sylvestris</i> Sw.	0.0075	2.370	0.024
Connaraceae	<i>Connarus suberosus</i> Planch.	0.0791	2.000	0.129
Dilleniaceae	<i>Davilla elliptica</i> A. St.-Hil.	0.0113	2.570	0.403
Fabaceae	<i>Dimorphandra mollis</i> Benth.	0.0019	3.000	0.177
Ebenaceae	<i>Diospyros hispida</i> A.DC.	0.0151	2.000	0.105
Fabaceae	<i>Diptychandra aurantiaca</i> Tul.	0.0151	2.710	0.211
Asteraceae	<i>Eremanthus erythropappus</i> (DC.) MacLeish	0.0056	1.700	0.128
Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A.Robyns	0.0640	2.120	0.180
Malvaceae	<i>Eriotheca pubescens</i> (Mart. And Zucc.) Schott and Endl.	0.0075	3.330	0.102
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St.-Hil.	0.0019	1.700	0.019
Erythroxylaceae	<i>Erythroxylum suberosum</i> A. St.-Hil.	0.0038	1.700	0.226
Erythroxylaceae	<i>Erythroxylum tortuosum</i> Mart.	0.0320	2.710	0.141
Myrtaceae	<i>Eugenia aurata</i> O. Berg	0.0019	2.370	0.047
Myrtaceae	<i>Eugenia bimarginata</i> DC.	0.0075	2.250	0.022
Myrtaceae	<i>Eugenia puniceifolia</i> (Kunth) DC.	0.0019	2.710	0.572
Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell	0.0038	2.420	0.040
Apocynaceae	<i>Hancornia speciosa</i> Gomes	0.0019	2.000	0.116
Fabaceae	<i>Hymenaea stigonocarpa</i> Mart. Ex Hayne	0.0019	2.420	0.162
Calophyllaceae	<i>Kielmeyera coriacea</i> Mart. and Zucc.	0.0056	2.000	0.196

Lythraceae	<i>Lafoensia pacari</i> A.St.-Hil.	0.0301	4.400	0.422
Fabaceae	<i>Machaerium acutifolium</i> Vogel	0.0019	2.250	0.246
Melastomataceae	<i>Miconia albicans</i> (Sw.) Steud.	0.0038	2.000	0.081
Fabaceae	<i>Mimosa amnis atri</i> Barneby	0.0075	1.180	0.150
Melastomataceae	<i>Mouriri elliptica</i> Mart.	0.0320	2.710	0.970
Myrtaceae	<i>Myrcia bella</i> Cambess.	0.0019	2.710	0.373
Myrtaceae	<i>Myrcia camapuensis</i> N.Silveira	0.0132	2.000	0.555
Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	0.0038	5.750	0.395
Myrtaceae	<i>Myrcia lasiantha</i> DC.	0.0019	4.400	0.310
Myrtaceae	<i>Myrcia obovata</i> (O. Berg) Nied.	0.0019	3.330	0.102
Ochnaceae	<i>Ouratea acuminata</i> (DC.) Engl.	0.0019	2.250	0.361
Ochnaceae	<i>Ouratea spectabilis</i> (Mart. Ex. Engl.) Engl.	0.0471	4.200	0.238
Rubiaceae	<i>Palicourea rigida</i> Kunth	0.0094	2.570	0.054
Asteraceae	<i>Piptocarpha rotundifolia</i> (Less.) Baker	0.0038	1.270	0.084
Celastraceae	<i>Plenckia populnea</i> Reissek	0.0358	4.400	0.422
Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.	0.0019	1.880	0.231
Sapotaceae	<i>Pouteria torta</i> (Mart.) Radlk.	0.1827	1.180	0.063
Myrtaceae	<i>Psidium laruotteanum</i> Cambess.	0.0885	1.270	0.108
Vochysiaceae	<i>Qualea parviflora</i> Mart.	0.0621	4.400	0.422
Proteaceae	<i>Roupala montana</i> Aubl.	0.0019	2.710	0.316
Connaraceae	<i>Rourea induta</i> Planch.	0.0038	4.200	0.035
Araliaceae	<i>Schefflera malmei</i> (Harms) Frodin	0.0019	5.750	0.395
Fabaceae	<i>Sclerolobium aureum</i> (Tul.) Bail.	0.0038	2.570	0.047
Solanaceae	<i>Solanum lycocarpum</i> A. St.-Hil.	0.0019	2.370	0.039
Fabaceae	<i>Stryphnodendron adstringens</i> (Mart.) Coville	0.0603	2.000	0.122
Styracaceae	<i>Styrax ferrugineus</i> Neess and Mart.	0.0075	2.370	0.573
Bignoniaceae	<i>Tabebuia aurea</i> (Silva Manso) S. Moore	0.0056	2.710	0.115
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	0.0395	2.250	0.121

CONCLUSÃO GERAL

O uso das originalidades em simulações de extinções para prever as consequências da perda de espécies na diversidade ecológica e evolutiva das comunidades é uma abordagem promissora para a determinação de prioridades de conservação. A maior perda de originalidade funcional do que o acaso na simulações realizadas nos levou a concluir que distâncias filogenéticas podem não captar diferenças entre as espécies em relação a suas funções na comunidade e que, portanto, medidas funcionais devem ser melhores descritores do funcionamento e manutenção de comunidades, pelo menos em comunidades vegetais de cerrado. Devido à maior vulnerabilidade das espécies raras e das espécies sensíveis ao fogo e, sendo elas mais originais, tais espécies deveriam ser priorizadas em ações de conservação.