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# Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: [www.elsevier.de/ppees](http://www.elsevier.de/ppees)

## Research article

# The influence of fire on phylogenetic and functional structure of woody savannas: Moving from species to individuals

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## ARTICLE INFO

### Article history:

Received 22 May 2010

Received in revised form 28 October 2011

Accepted 26 November 2011

### Keywords:

Community assembly  
Environmental filtering  
Intraspecific variability  
Plant traits

## ABSTRACT

Fire is a key determinant of tropical savanna structure and functioning. High fire frequencies are expected to assemble closely related species with a restricted range of functional trait values. Here we determined the effect of fire on phylogenetic and functional diversity of woody species and individuals in savanna communities under different fire frequencies. We found phylogenetic signals for one third of the functional traits studied. High numbers of fires simultaneously led to phylogenetic overdispersion and functional clustering when communities were represented by mean trait values with all traits that putatively should be affected or respond to fire. This finding is important, because it shows that the relationship between ecological processes and the phylogenetic structure of communities is not straightforward. Thus, we cannot always assume that close relatives are more similar in their ecological features. However, when considering a different set of traits representing different plant strategies (fire resistance/avoidance, physiological traits and regeneration traits), the results were not always congruent. When asking how communities are assembled in terms of individuals (not species) the outcome was different from the species-based approach, suggesting that the realised trait values – rather than mean species trait values – have an important role in driving community assembly. Thus, intraspecific trait variability should be taken into account if we want fully to improve our mechanistic understanding of assembly rules in plant communities.

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## Introduction

A fundamental goal in ecology is to understand the process by which local communities are assembled (Weiher and Keddy, 1999; Pavoine and Bonsall, 2011). In recent years, community assembly rules have received increased attention from ecologists. A wide variety of processes may play important roles, including mutualism, facilitation, dispersal limitation and random colonisation-extinction events (see Leibold et al., 2004; Pausas and Verdú, 2010; Pavoine and Bonsall, 2011).

Two processes in particular have received much attention: environmental filtering and competitive interactions among species (Webb et al., 2002; Kraft et al., 2007; Vamosi et al., 2009; Mouchet et al., 2010; Pausas and Verdú, 2010). These processes have opposing (but not exclusive) effects on functional similarity and phylogenetic relatedness of co-occurring species. Environmental

filters select those species that can persist within a community on the basis of their tolerance to the prevailing abiotic conditions. The result is an assembly of species with similar characteristics and niches (Fukami et al., 2005; Pausas and Verdú, 2010). Consequently, a restricted range of species trait values is viewed as evidence of environmental filtering (Weiher et al., 1998; Pausas and Verdú, 2008). Competitive interactions, by contrast, are predicted to result in co-occurring species with dissimilar traits, and this can be interpreted as evidence for limiting similarity (niche differentiation among species) (Weiher et al., 1998; Webb et al., 2002). The predicted effects of these two processes on phylogenetic relatedness depend on how functional traits evolved in species lineages. Phylogenetic signal in functional traits (i.e., traits are more similar among closely related species; sensu Losos, 2008) and environmental filtering should result in species more closely related than expected by chance (i.e., phylogenetic clustering). By contrast, species living in communities driven by competition should be less closely related (i.e., phylogenetic overdispersion; Webb et al., 2002; Cavender-Bares et al., 2006; Kraft et al., 2007; Vamosi et al., 2009; but see Mayfield and Levine, 2010). However, if functional

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traits are convergent in species lineages, environmental filtering should assemble communities containing distantly related species, whereas competition should remove any systematic associations resulting in community assemblages indistinguishable from random (Webb et al., 2002). Note that the effects and relative strengths of environmental filtering are likely to change with spatial scale (Gómez et al., 2010; Thuiller et al., 2010), though this is not a focus of our study.

Strongly parallel literatures have developed on the measurement of phylogenetic and functional diversity, and of the respective clustering or over-dispersion of species. The concomitant use of measures of phylogenetic diversity and functional diversity thus seems likely to help in understanding the mechanisms of community assembly (Pavoine and Bonsall, 2011; Diniz Filho et al., 2011). To date, however, there have been rather few such studies (but see Pavoine et al., 2010; Meynard et al., in press; Safi et al., 2011). In an experimental grassland, Cadotte et al. (2009) found more support in using phylogenetic diversity than functional diversity to understand productivity patterns. However, a meta-analysis showed that this is not always the case (Cadotte et al., 2008). Further, there is evidence that species traits may be more important than species relatedness to ecosystem processes (Díaz and Cabido, 2001; Hooper et al., 2002). If important traits were very labile with a low phylogenetic signal or when species exhibit considerable phenotypic plasticity, phylogenetic distances will fail to resemble ecological (functional) distance among species (Losos, 2008).

Although both phylogenetic and functional diversity have most commonly been determined using species as the most finely resolved taxonomic units, inclusion of intra-specific trait variation is also important (Cianciaruso et al., 2009; Albert et al., 2010; de Bello et al., 2011). Competition for resources, niche width expansion and, ultimately, natural selection occur at the individual level (Pachepsky et al., 2007). Plant phenotypic diversity was found to influence ecosystem functioning in several studies (e.g., Madritch and Hunter, 2002, 2003; and references in Schmitz et al., 2003), and there is evidence for a role of phenotypic variability in species coexistence and responses to both biotic and abiotic filters (Jung et al., 2010). Furthermore, environmental variation can cause important trait variation without species turnover (Fajardo and Piper, 2011). Intraspecific variability can generate trait-mediated indirect interactions and thus influence the strength of competition, facilitation, and species-environment relationships (Miner et al., 2005). In flooded meadows Jung et al. (2010) found that plant species were sorted not only according to their mean trait value but also according to their ability to 'fit' their trait values to local abiotic and biotic requirements. This implies that a priori 'unexpected species' (species whose mean trait values do not satisfy the abiotic and biotic requirements) are still able to pass through environmental filters (Jung et al., 2010). This said, empirical analyses of the role of functional diversity at the individual level remain scarce.

Fire-prone communities are very useful to test community assembly theories, because fire may act as a strong environmental filter for particular combinations of functional traits in communities with different fire frequencies (Pausas and Verdú, 2008; Silva and Batalha, 2010). Savannas have experienced fire for millions of years and, as a consequence, savanna plants evolved fire-tolerance mechanisms, and sometimes even require fire to maintain their populations (Hoffmann, 1998). Among woody species, the main adaptations are those that allow thermal isolation of living internal tissues, such as strong suberisation of the trunk and branches, clonal reproduction, and the ability to sprout vigorously from underground organs (Miranda et al., 2002; Pausas and Lavorel, 2003). Moreover, different processes related with recruitment, flowering, dispersal, and germination might be modified by fire (Coutinho, 1990). The role of fire in assembling plant communities

has been widely investigated, especially in the Mediterranean basin (see Verdú and Pausas, 2007 for references), where it produces functionally and phylogenetically clustered communities (Pausas and Verdú, 2008). However, there are few studies focusing on community assembly in savannas and, as far as we know, none including intraspecific trait variation.

Here, we determined the effect of fire on the phylogenetic and functional diversity of woody species in savanna communities under different fire frequencies. We used null models to test whether levels of community phylogenetic and functional structure were different from what we would expect by chance. In summary, we asked the following questions: (i) Are the functional traits more similar among closely related plant species? (ii) Do phylogenetic and functional diversities differ between sites experiencing different fire frequencies from that expected by the random assembly of communities? (iii) Are there any differences between species- and individual-based approaches to community assembly based on functional attributes?

## Methods

### *Study area and data*

The Emas National Park (ENP) is located in the Brazilian Central Plateau, southwestern Goiás State (17°49'–18°28'S and 52°39'–53°10'W), and is one of the largest and most important savanna reserves in South America, covering ca. 133,000 ha. Regional climate is tropical and humid, with a wet summer and dry winter, classified as Aw following Köppen (1931). The dry season is from June to August and the wet season from September to May. Annual rainfall and mean temperature lie around 1,745 mm and 24.6°C, respectively. In the park, we find a gradient from open (68.1% of its area) to closed savannas (25.1%), as well as wet grasslands (4.9%) and riparian and semideciduous forests (1.2%) (Ramos-Neto and Pivello, 2000).

Historically, ENP was exploited by farmers for cattle ranching, and dry season burnings were used to promote forage regrowth every year. In 1984, the park was completely fenced, cattle were no longer allowed inside, and a fire exclusion policy was established (Ramos-Neto and Pivello, 2000). As a consequence, uncontrolled wildfires occurred every 3–4 years, burning on average 80% of its total area (Ramos-Neto and Pivello, 2000; França et al., 2007). Since 1994, when a catastrophic fire burned almost 95% of ENP's area, approximately 10 km<sup>2</sup> of preventive firebreaks are burned annually in the dry season, and a fire brigade is permanently stationed in the park to prevent anthropogenic fires during this period (França et al., 2007). As a result, nowadays there are few occurrences of anthropogenic burnings inside the park (almost all fires are lightning fires), and fire frequency at a given point is around 6–7 years on average.

We used a long time-series of satellite images to map fire scars within ENP from 1973 to 2009, creating a fire map from which we can determine the number of fires in this period for any location in the park. Using this information, we selected sites covered with savanna vegetation that experience high (HiFi), intermediate (MidFi) and low (LowFi) fire frequencies. We randomly placed 64 plots (each a 25 m<sup>2</sup> quadrat) across the study sites: 21 plots in HiFi sites, 21 in MidFi sites, and 22 in LowFi sites. There was no overlap in fire frequency among each classification. On average, the number of fires between 1973 and 2009 (mean ± standard deviation) was 16.00 ± 1.12 in HiFi plots; 10.50 ± 1.15 in MidFi plots; and 7.00 ± 1.03 in LowFi plots. In each plot, from September 2009 to January 2010, we sampled all woody individuals with stem diameter equal to or higher than 3 cm at soil level. We

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