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Original article

Woody plant species co-occurrence in Brazilian savannas under different fire frequencies

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ABSTRACT

Fire plays an important role in determining the structure of the vegetation of savannas. Consequently, frequent fires are expected to assemble closely related plant species with very similar fire-related functional traits. We assessed the influence of different fire frequencies on patterns of co-occurrence of woody species at a fine spatial scale in Brazilian savannas. We used quantile regressions to test the relationship between co-occurrence indices and both phylogenetic distances and functional differences, calculated for every possible pair of species. Our results indicated that fire changes the pattern of co-occurrence of woody plants. Functionally different species co-occurred predominantly in a site protected from fire, whereas functionally similar species co-occurred predominantly in sites frequently burned. However, we did not find correlations between co-occurrence and phylogenetic distance of species, due probably to the random distribution of some functional traits in the phylogeny of savanna species. Thus, fire acts as an important environmental filter at fine spatial scales in Brazilian savannas, promoting functional – but not phylogenetic – clustering of plants.

1. Introduction

Fire is one of the major forms of environmental disturbance in the world (Bond and Keeley, 2005), playing an important role in determining the occurrence of savannas (Thonicke et al., 2001; Bond et al., 2005). The occurrence of fire over the past 25 million year in savannas has allowed the evolution of fire-tolerant and fire-dependent plant species, which without fire could be potentially replaced by tropical forest species (Thonicke et al., 2001; Bond et al., 2005). In South America, the largest savanna region is the Brazilian cerrado (Gottsberger and Silberbauer-Gottsberger, 2006). Like its overseas savanna counterparts, the cerrado vegetation evolved with fire (Coutinho, 1990; Gottsberger and Silberbauer-Gottsberger, 2006). Cerrado woody species present thick corky bark and subterranean meristems that protect them from high temperatures and allow resprouting after fires (Gottsberger and Silberbauer-Gottsberger, 2006). However, annual fires tend to favour herbaceous plants at the expense of woody ones (Durigan and Ratter 2006; Hoffmann et al., 2009). Consequently, the pattern of co-occurrence of woody species is expected to change along a fire gradient.

Environmental filters, such as fire, are thought to determine the functional similarity and the phylogenetic relatedness of co-occurring plant species (Webb et al., 2002; Cavender-Bares et al., 2006; Slingsby and Verboom, 2006). Environmental filters select those species that can persist within a community on the basis of their tolerance to the abiotic conditions (Weiher and Keddy, 1995). As a consequence, they are expected to assemble co-occurring species with similar niches, that is, species with similar morphological and physiological characteristics (i.e., functional traits, Chase, 2003; Fukami et al., 2005). In relation to phylogenetic relatedness, environmental filters are predicted to assemble closely related co-occurring species (phylogenetic clustering; Webb et al., 2002) if functional traits are conserved in the evolution of species lineages (i.e., traits are more similar among closely related species; Prinzing et al., 2001; Ackerly, 2003). Nevertheless, if functional traits evolved convergently and closely related species are functionally different, environmental filters are predicted to favor co-occurrence of more distantly related species (phylogenetic overdispersion; Webb et al., 2002).

In some cases, the evolution of traits is indistinguishable from random (Silvertown et al., 2006), and a clear pattern of phylogenetic clustering or overdispersion may not emerge (Silva and Batalha, 2009). A widespread phylogenetic signal has been observed in plant traits related to environmental tolerances (i.e., light, soil moisture, and pH, Prinzing et al., 2001). These plant traits are related to habitat requirements and, therefore, they define the 'β niche' of the species, referring to the scale at which β-diversity is determined (Silvertown et al., 2006). However, random distributions in the plant phylogeny

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of traits that determine within-habitat α-diversity (α niche) also seem to be common (Silvertown et al., 2006), because α niches define the species interactions within a community and is expected to be different for species coexistence to be possible (Silvertown et al., 2006).

Studies conducted at fine scales have found patterns of phylogenetic overdispersion (Cavender-Bares et al., 2004, 2006; Slingsby and Verboom, 2006). However, the functional similarity of co-occurring species still remains inconclusive (see Leibold, 1998 for references). Recently, we observed that the environmental filters might determine the co-occurrence of functionally similar tree species in cerrado (Silva and Batalha, 2009). Here, we tested whether annual fire frequencies change the pattern of local co-occurrence of cerrado woody species at a fine spatial scale, taking into account the nearest neighbours. We used quantile regressions to test the relationship between co-occurrence indices and both phylogenetic distances and functional differences, calculated for all pairs of species. We expected that the functional similarity among plants would increase with fire frequencies, whereas the phylogenetic distances among plants would either decrease, if functional traits were conserved, or show no pattern, if functional traits were randomly distributed in the phylogeny of the plants.

2. Material and methods

2.1. Study area

We surveyed three nearby cerrado sites in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49′-18°28′S; 52°39′-53°10′W). The ENP comprises 132,941 ha and is one of the largest and most important reserves in the Cerrado domain (Unesco, 2001). According to Köppen's (1931) system, regional climate is classified as Aw, humid tropical, with wet summers and dry winters. Up to 1984, the ENP was exploited by farmers for cattle ranching, and burning in the dry season was used to promote forage regrowth (França et al., 2007). Afterwards, the ENP was fenced, and a fire exclusion policy was established (Ramos-Neto and Pivello, 2000). As a consequence, catastrophic fires occurred every 3–4 years, burning 80% of the park's area (Ramos-Neto and Pivello, 2000). Since 1995, around 10 km^2 of preventive firebreaks have been burned annually at the end of the wet season, and a fire brigade works in the park during the dry season to prevent anthropogenic fires (França et al., 2007). Thus, there are currently few occurrences of anthropogenic fires inside the ENP (less than 2.2% of the burned area from 1994 to 2003), and the largest wildfires burn less than 30% of the total area. Fire frequency at a given site averages 6–7 years (França et al., 2007).

2.2. Data collection

In the late rainy season of 2006, we sampled the woody species occurring in three cerrado sites with similar physiognomy, similar soil type (Oxisols), and under different fire frequencies: two firebreaks, one burned annually for the last ten years (approximately 18°18′50″S; 52°54′00″W), another burned around every two years (approximately 18°19′01″S; 52°54′10″W), and a site without fires since 1994 (approximately 18°17′28″S; 52°53′41″W). The sites were distant less than 2 km one from each other. In each site, we placed a 2500 m long transect, with 250 points, 10 m apart from each other. In each point, we used the point-quarter method (Mueller-Dombois and Ellenberg, 1974) to sample four woody plants with stem diameters at the soil level ≥ 3 cm (SMA, 1997). We identified the species by comparing collected samples to those of ENP's reference collection (Batalha and Martins, 2002) and to vouchers lodged at the University of Campinas and University of Brasília herbaria.

We measured eight soft functional traits (i.e., traits that are relatively easy and quick to quantify; Hodgson et al., 1999) that may be used as accurate surrogates of plant functional responses, such as growth coefficients and habitat requirements (Cornelissen et al., 2003). These traits were: basal area, bark thickness, canopy height, height, leaf dry matter content, specific leaf area, stem specific density, leaf nitrogen concentration, and leaf phosphorus concentration.

According to Cornelissen et al. (2003): (1) basal area is a trait positively related to space occupation, resource uptake, total biomass, and reproductive capability; (2) bark thickness is a trait related to protection of vital tissues against fire damage and may also decrease mortality by fire or accelerate post-fire recovery; (3) canopy height is related to avoidance of crown fires; (4) height is associated to competitive value, fecundity, interval between two perturbations, tolerance to stress, underground biomass, root depth, lateral ramification, and leaf size; (5) leaf dry matter contents are related to flammability and resistance to physical hazards; (6) specific leaf area is positively related to maximum photosynthetic rates, since low values of it correspond to a high leaf structure investment; (7) stem specific density is related to structural strength and resistance against physical damage; and (8) leaf nitrogen and phosphorus concentrations are related to maximum photosynthetic rate.

We measured and computed most of the traits following the procedures described in Cornelissen et al. (2003). For each species in each site, we measured stem specific density, leaf nitrogen, and leaf phosphorus for five individuals we drew at random. For the specific density, we collected a 10 cm long section of a branch of about 5 cm in diameter for each individual. For the leaf nutrient analysis, we collected 20 g of fully expanded leaves without symptoms of herbivore and pathogen attack for each individual, at the end of rainy season of 2006. We measured the other functional traits for 10 random individuals, except for rare species, for which we measured them in five individuals at least.

2.3. Phylogenetic data

We constructed a phylogenetic tree for all sampled species with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Fig. 1, Webb and Donoghue, 2005). Phylogenetic distances among species from different families were estimated from the dated Angiosperm super-tree of Davies et al. (2004). When a family node presented many polytomies (Fabaceae and Asteraceae, for instance), we distributed the genera into their subfamilies following the last angiosperm classification (Angiosperm Phylogeny Website; Stevens, 2001). We assigned branch lengths of these genera by spacing undated nodes evenly above family node. We drew the phylogenetic tree for the families sampled with the ADE-4 package (Analyses des Données Ecologiques; Thioulouse et al., 1996) for the R environment (R Development Core Team, 2008).

We investigated whether the functional traits tended to be phylogenetically conserved (i.e., phylogenetic signal) or convergent in the phylogeny of the sampled species, using a test based on the variance of phylogenetic independent contrasts (PIC; Blomberg et al., 2003). If related species are similar to each other, the magnitude of independent contrasts will generally be similar across the tree, resulting in a small variance of contrast values (Blomberg et al., 2003). Observed contrast variances are compared to the expectations under a null model of randomly swapping trait values across the tips of the tree. We used the mean trait values normalized by their standard deviations. We did this analysis with the Picante package (Kembel et al., 2008) for the R environment (R Development Core Team, 2008).