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Original article

Driving factors of small-scale variability in a savanna plant population after a fire

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The severity of fire impacts on fire-prone vegetation is often spatially heterogeneous, and may lead to small-scale patchiness in the structure of plant populations by affecting mortality, topkill, and reproduction. This patchiness, however, is not usually taken into account in fire ecology studies. We show that a dry-season fire may result in small-scale patchiness in the population structure of the common shrub *Miconia albicans*, mostly by differential topkill and resprouting. We related fire severity to population structure parameters of the study species and assessed the effects of fire on its soil seed bank. Basal area of non-woody live stems and of dead stems increased with fire severity, whereas that of woody live stems decreased, indicating topkill and resprouting. However, there was no relationship between fire severity and the total number of live or dead plants, showing that mortality in the fire was low. We found very few seedlings, indicating that resprouting, not germination from the soil seed bank, is the main recovery strategy of this species. The fire also affected the soil seed bank, as there were fewer seedlings emerging from soil collected in burned patches. Although this study was performed with a single species, it is likely that other species, especially those with basal resprouting, will show similar patterns of post-fire patchiness in population structure. This patchiness, in turn, may affect the spatial distribution of future fires, and should be taken into account in studies of fire ecology.

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1. Introduction

In fire-prone environments such as savannas, natural fires resulting from lightning are a common phenomenon (Ramos-Neto and Pivello, 2000). These natural fires burn relatively small patches and occur in the beginning of the wet season, in contrast to human-induced fires, which burn extensive areas and often occur in the dry season (Ramos-Neto and Pivello, 2000). Even so, the severity of dry-season fires may be patchy, or spatially heterogeneous, and leave unburned or lightly burned patches interspersed with severely burned ones (Roman-Cuesta et al., 2009; Werner, 2010). Here, we define heterogeneity, or patchiness, as the complexity and/or variability of a system property in space and/or time (Li and Reynolds, 1995). Fire behavior and therefore the formation of unburned patches depends on factors such as fuel type and quantity, moisture, and wind speed and direction (Hoffmann et al., 2012; Roman-Cuesta et al., 2009). For example, in a mesic Eucalypt savanna, only early dry season fires were spatially heterogeneous, especially in areas with a smaller grass cover (Werner, 2010). Spatially heterogeneous fires may result in patchiness in the structure of plant populations, due to factors such as topkill, resprouting (Hoffmann and Solbrig, 2003), differential mortality (Watts et al., 2012), and germination from the seed bank (Keeley, 1987).

Fires often result in noticeable changes in the size structure of plant populations even when mortality is low, as is often the case in savannas (Hoffmann, 1998; Hoffmann and Solbrig, 2003). Therefore, a patchy fire may result in patchiness in a plant population not only by promoting spatially structured mortality (Watts et al., 2012), but also by causing different degrees of topkill and resprouting (Hoffmann, 1998; Hoffmann and Solbrig, 2003) and thus modifying the population's size structure (Lehmann et al., 2009; Silva et al., 2009). Resprouting is a major part of the "persistence niche" and one of the main adaptations in fire-prone

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ecosystems with more frequent fires (Bond and Midgley, 2001; Hoffmann, 1998; Lamont et al., 2011), as it drastically reduces fire-induced mortality and increases the probability that an established plant will maintain its space in the community. An important distinction is between epicormic resprouting, characterized by the growth of new branches from buds on the main trunk or branches, and basal resprouting, in which resprouts grow from the stem's base after the loss of aerial structures during topkill (Bond and Midgley, 2001). Resprouting intensity depends on bud characteristics, such as their location, number, and protection, and also on fire characteristics such as frequency and intensity (Bellingham and Sparrow, 2000; Vesk and Westoby, 2004; Clarke et al., 2013).

Patchiness in population structure may also be related to changes in the soil seed bank, which is important for the establishment and persistence of many species from fire-prone communities (Gonzalez and Ghermandi, 2008; Måren et al., 2010; Måren and Vandvik, 2009; Wright and Clarke, 2009). Soil seed bank response to fire is more important in systems dominated by obligate seeders, which are more common in areas with longer fire return intervals (Menges and Hawkes, 1998). However, seed bank may also play a role in other ecosystems, as fire stimulates the germination of some species, either directly, by breaking the seeds' outer coat, or indirectly, by increasing the amount of light and releasing stimulatory compounds from charred wood (Keeley, 1987). Fire may also stimulate flowering, with a subsequent production of a large number of seedlings (Menges and Hawkes, 1998). Even though the post-fire environment can offer more suitable conditions for the survival and growth of seedlings (Tyler, 1996), a decrease in the number of seedlings immediately after a fire has also been observed (Romo and Gross, 2011). However, because of the lack of studies about the soil seed bank of species from the Brazilian savanna (Ikeda et al., 2007; Pereira-Diniz and Ranal, 2006), the importance of germination from the soil seed bank for the maintenance of their populations is unknown.

The influence that fire patchiness may have on the structure of plant populations is rarely considered in studies of plant population ecology in fire-prone ecosystems, and most studies usually compare either the same population before and after a fire (Silva et al., 2009) or populations located in areas with different fire return intervals (Hoffmann, 1998, 1999; Hoffmann and Solbrig, 2003). In this study, we show that a dry-season fire may indeed result in small-scale spatial heterogeneity in the population structure of a savanna species. We studied the population structure and seed bank of a common Neotropical shrub, *Miconia albicans* (Sw.) Steud. (Melastomataceae), after a spatially heterogeneous fire in a Brazilian savanna. We assessed heterogeneity in fire severity and the relationship between fire severity and *M. albicans*'s population structure as well as the effects of the fire on individual plants and on the seed bank. In this manner, we were able to assess the relative influence of the mechanisms outlined above – mortality, resprouting, and germination from the seed bank on the post-fire heterogeneity in plant population structure.

2. Material and methods

2.1. Study area

The Brazilian savanna is part of the floristic domain known as the Cerrado, which comprises grassland, savanna, and forest vegetation (Coutinho, 1978). A large part of the Cerrado is composed of a savanna vegetation known as cerrado *sensu stricto* (Coutinho, 1978; Oliveira-Filho and Ratter, 2004). We performed this study in a cerrado *sensu stricto* site at the Federal University of São Carlos campus in the municipality of São Carlos, São Paulo State, Southeastern Brazil (21°58′45″S, 47°52′53″W, 880 m above sea level). The climate is seasonal with a dry winter and a wet summer (Cwa according to Köppen, 1931), an annual rainfall of 1339 mm and a mean annual temperature of 22.1 °C (Oliveira and Batalha, 2005). Soil is acidic with low nitrogen and high aluminum and percent sand (Dantas and Batalha, 2011).

The average fire return interval for cerrado *sensu stricto* is approximately 5 years (Ramos-Neto and Pivello, 2000). Part of our study area had been burned in 2004. Previous fire history is unclear but it has been burned at least once every four years (pers. comm. of University staff). The last fire before the study occurred on 26 August 2006, late in the dry season. This fire burned a large part of the herbaceous and tree layer of the study area but left a number of unburned patches interspersed with the burned ones. There have been no prescribed fires in this area and, to our knowledge, all fires were accidental. Occurring in the dry season, these fires tend to be severe in the burned patches and to cause extensive topkill.

2.2. Study species

M. albicans (Sw.) Steud. (Melastomataceae) is a multi-stemmed shrub that grows up to 5 m tall and may have up to 13 stems per individual (P. Dodonov, pers. obs.). The species occurs from Mexico to Paraguay (Martins et al., 1996). In Brazil, it is common in cerrado *sensu stricto* (Assunção and Felfili, 2004; Oliveira and Batalha, 2005) and dystrophic *cerradão* or forested cerrado (Haridasan and Araújo, 1988). It is an evergreen (Damascos et al., 2005), aluminum-accumulating species that is intolerant of calcareous soils (Haridasan, 1988; Haridasan and Araújo, 1988). Its seeds are common in the seed bank and show little to no dormancy and a germination rate around 76% (Miyanishi and Kellman, 1986).

M. albicans is known to suffer complete topkill during fires followed by intense resprouting and resprouts are able to reach reproductive size in the second year after fire (Hoffmann and Solbrig, 2003). It does not produce root suckers, relying solely on sexual reproduction for spreading (Hoffmann, 1998). Seed production is minimal in the first year after burning and only plants older than 3 years are able to survive a fire (Hoffmann, 1998). Therefore, its population is predicted to decline under annual or biennial burning, but may stabilize under less frequent fires (Hoffmann, 1999; Miyanishi and Kellman, 1988; Moreira, 2000).

2.3. Sampling

We sampled the population of *M. albicans* between February and June 2008, approximately 18–22 months after the fire. We placed five parallel 100 m-long belt transects at 20 m intervals. Each transect was divided into 20 5×5 m^2 plots, and all individuals in each plot were sampled. The transects were placed perpendicular to a 6 m-wide firebreak, with the first plot located immediately at the firebreak edge. We are aware that this sampling design has certain pseudoreplication issues, such as the use of one single area and the spatial autocorrelation among the plots. However, the use of contiguous plots enabled us to simultaneously assess the patchiness of fire severity and its relationship with aspects of population structure. Furthermore, the existence of five transects helped to reduce the effects of spatial autocorrelation on the response variables.

As *M. albicans* produces multiple stems but no root suckers (Hoffmann, 1998), we considered a group of stems as a separate individual if it had no connections to another individual at its base. For each individual, we measured the basal diameter and height of all live and dead stems and classified the live stems into adults (all non-topkilled stems, including those with epicormic resprouts) or resprouts (usually growing from the base of topkilled individuals).

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