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Post-fire plant regeneration across a closed forest-savanna vegetation transition

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ABSTRACT

Fire is a major environmental factor influencing vegetation heterogeneity, with closed forest and savanna ecosystems having different management needs due to their different responses to fire disturbance. However, the differences in post-fire vegetation dynamics between these ecosystems have seldom been compared using a uniform set of parameters. Additionally, post-fire dynamics of forest-savanna ecotones is poorly characterized. With the hypothesis that closed forest, savannas and ecotones will exhibit different post-fire responses, we studied the vegetation diversity, structure and dynamics in an upland forest-savanna vegetation mosaic in Minas Gerais, Brazil following a fire that occurred in September 2011. In January 2012, we identified, tagged, and measured the basal diameter of all regenerating juvenile tree stems within forty-six 4 m^2 plots in closed forest, savanna and ecotone vegetation, and conducted recensuses in 2013 and 2014. We modelled the relationship between short-term dynamics parameters (recruitment, mortality, basal area loss and gain, and the turnover and net changes in the number of individual stems and basal areas) and vegetation type. Species diversity was higher in closed forests and ecotones than in savanna. Across all vegetation types, stem density decreased and basal area increased. Parameters such as recruitment, net changes in the number of individuals, and the gain, loss and turnover in basal area did not differ across vegetation types. However, stem mortality was higher in closed forest and ecotones combined than in savannas, and the net change in the number of individuals was the lowest in the savanna. Overall, our results support that within a climatically-similar vegetation mosaic, closed forests exhibit different post-fire regeneration dynamics from savanna as expected. Ecotones exhibited post-fire responses and dynamics more similar to closed forests than to savanna, but more studies will be needed to establish if this pattern is applicable to other areas. Understanding the longer-term vegetation dynamics and plant regeneration patterns is a potential next step that will help inform fire management strategies for forest-savanna mosaics.

1. Introduction

Fire is a key factor driving the distribution of many of the world's vegetation communities (Bond and Keeley, 2005; Bond et al., 2005; Bowman et al., 2009), through interactions with vegetation composition and structure (Bond and Midgley, 1995; Brooks et al., 2004). Given trends in rising concentration of atmospheric CO_2, severe weather events and land use, tropical ecosystems are under a regime of unprecedented change with respects to fire ecology (Dale et al., 2001; Bonan, 2008). Because this impacts on a multitude of socioeconomic, management and ecological issues, understanding vegetation responses to fire is paramount (Cochrane, 2003; Hardy, 2005).

From a macroecological perspective, terrestrial ecosystems are often polarized into fire-adapted or -sensitive systems. Because such systems or vegetation co-occur in landscape mosaics within the same climatic envelope, they can be interpreted as alternative stable states with self-reinforcing dominance, under the control of intrinsic environmental factors and biotic feedbacks (Warman and Moles, 2009; Hoffmann et al., 2009; Staver et al., 2011a; Dantas et al., 2016). Vegetation states will therefore be maintained provided that changes in underlying environmental drivers are not strong or consistent enough to result in a regime shift (Whitlock et al., 2010; Lindenmayer et al., 2011; Knox and Clarke, 2012).

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For instance, closed forests (or rainforests) are characterized by a set of environmental and biotic features that render them fire retardant (Biddulph and Kellman, 1998; Hennenberg et al., 2006; Little et al., 2012). Given the correct environmental conditions however, closed forest can and does burn (Uhl et al., 1988), but can be expected to recover rapidly from a small fire disturbance (Marrinan et al., 2005; Williams et al., 2012). Still, frequently repeating fires or a very large fire may cause a regime shift leading to permanent changes in structure and floristics, or even a vegetation state shift (Kinnaird and O'Brien, 1998; Cochrane et al., 1999; Cochrane, 2003). Conversely, savannas are maintained by a regime of frequent fires (Staver et al., 2011b; Simon and Pennington, 2012), and are characterized by species that are typically resilient to, or even promotive of fire (Bowman, 2000; Hoffmann et al., 2003). Prolonged fire exclusion can therefore lead to an increased tree dominance and canopy closure (Bowman and Fensham, 1991; Durigan and Ratter, 2006; Pinheiro et al., 2010).

Where closed forest and savanna interface, ecotones often arise, and it is much less clear how ecotones will respond to a fire disturbance. Ecotones often exhibit floristic and structural characteristics that are intermediate between their flanking vegetation types (Puyravaud et al., 1994; Durigan and Ratter, 2006; Kark and van Rensburg, 2006). However, some trait-based comparisons between closed forest, savanna and their ecotones suggest a greater ecological convergence between ecotones with their flanking closed forest compared to savanna (Tng et al., 2013). In other words, some closed forest-savanna ecotones may be better interpreted as belonging within the closed forest environmental regime (Tng et al., 2014), and at least some dynamic responses of ecotones to fire disturbance may be hypothesized to be similar to closed forests. Despite the ecological importance of ecotones, they have received little attention (Durigan and Ratter, 2006), and having baseline data on how ecotones respond to fire has important management implications for forest-savanna mosaics as a whole (Tng et al., 2014).

An approach to testing if closed forests, savannas and their ecotones have differential dynamic responses would be to use a common set of parameters to characterize community changes during species regeneration after fire (Vesk and Westoby, 2004; Russell-Smith, 2006; Russell-Smith et al., 1998). Plant species in both forest and savanna may survive and persist in an environment after fire through different means: (1) by resisting the direct effects of fire and (2) by tolerating the changed post-fire conditions (Whelan, 1995). Post-fire flushes of seedlings and sprouting are adaptative traits for recovery after fire that can produce community-level changes (Uhl et al., 1981; Hoffman, 1996; Guariguata and Ostertag, 2001; Matt Davies et al., 2010;). While the regenerative capacities of tree species after fire have been intensively researched in some places such as Australia and Africa (Okello et al., 2008; Prior et al., 2009; Ondei et al., 2016), such research is still lacking in some regions in South America (see Balch et al., 2013).

The southeastern region in Brazil encompasses the Atlantic Forest Domain, a topographically and edaphically heterogeneous phytogeographic region comprised of various vegetation types (SOS Mata Atlântica, 2011). The broad geographical vegetation transition of tropical and subtropical closed forests (rainforests) in the Atlantic Forest domain to the open savanna west of the region gives rise to a complex mosaic of closed canopy vegetation grading into open canopy grass-dominated vegetation (Oliveira-Filho and Fontes, 2000). In addition to climatic and soil factors, natural and anthropogenic disturbance are considered the main determinants of vegetation heterogeneity in the region (Oliveira-Filho and Fontes, 2000; González-Pérez et al., 2004). Because the Atlantic Forest region has been subjected to massive land clearing, much of the work on forest regeneration in the region has focused on the effects of forest disturbance by human activity (Oliveira-Filho et al., 1997; Gomes et al., 2003; Guimarães et al., 2008; Carvalho and Felfili, 2011; Fontes and Walter, 2011). Comparatively, the role of fire in shaping vegetation communities in the region has received little attention. Some studies have examined post-fire regeneration of forest vegetation or savanna individually (Hoffman, 1996, 1999; Rodrigues et al., 2005) or focused on responses of target species (Hoffmann et al., 2009) but to the best of our knowledge, there have been no studies comparing the differences in post-fire plant regeneration and vegetation dynamics between vegetation types.

With an aim to answer the question of how post-fire community structure and dynamics will differ across different vegetation types in a forest-savanna mosaic, we made use of an opportunity to study plant regeneration in an upland area in southeast Brazil, after a fire in late 2011. Using the ASS framework as a context for this study, we hypothesize that after a fire, plant communities of closed forests, savannas, and their ecotones will differ in species diversity, community structure, and short-term temporal dynamics. Because closed forests are characterized as species-rich communities with massive regeneration after disturbance (Richards, 1996; Hiratsuka et al., 2006), we predict that this vegetation type will exhibit the highest tree species diversity, density, basal area and abundance of regenerating tree seedlings throughout the census period, followed by ecotones and savanna. Additionally, because ecotones are considered to be zones of rapid change in response to environmental change (Allen and Breshears, 1998; Kark and van Rensburg, 2006), we predict that regenerating ecotones will have the most rapid growth, highest mortality and turnover, followed by closed forests and then savanna.

2. Materials and methods

2.1. Study site and vegetation sampling

Our study site was located in a privately-managed park, the Bonito River Ecological Cascades Park (Parque Ecológico Quedas do Rio Bonito; 21°20′09″ S and 44°58′49″ W, 1100–1300 m a.s.l.), near the city of Lavras, Minas Gerais, Brazil (Fig. 1). The park covers an area of 235 ha, and experiences a subtropical climate with mild summers and winter drought and an average temperature of ~19.3 °C (Oliveira-Filho and Fluminhan-Filho, 1999). The average annual precipitation at the site is ~1490 mm, with 67% of the rainfall concentrated between the months of November to February and peaking in December (Dalanesi et al., 2004).

Geographically, the park is situated in Serra do Carrapato, a part of the Serra da Bocaina complex. The underlying geology of the region consists of granitic gneisses, quartzites and micaschists, giving rise to predominantly Cambisols in the valley areas and Litholic Neosols in plateau areas (Curi et al., 1990). Our study site falls broadly within a biome transition area between closed forest (Atlantic Domain) and savanna (Cerrado Domain) and the vegetation of the park is well-documented and mapped (Oliveira-Filho and Fluminhan-Filho, 1999; Dalanesi et al., 2004). The vegetation consists of a mosaic of closed forests (locally classified as semideciduous Atlantic forests; Oliveira-Filho and Fontes, 2000) and savannas dominated by short trees and grasses (Table 1). The closed forests occupy over deep poorly to moderately drained soils in within valleys and on slopes while the savannas occur over shallow, strongly-drained soils on plateaus and gentler sloping topography. Bands of ecotonal vegetation up to 200 m wide occur in-between the closed forest and savanna vegetation on moderately drained soils of intermediate depth, and these ecotones are characterized by the presence and dominance of *Eremanthus erythropap-*