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Fire-induced forest transition to derived savannas: Cascading effects on ant communities

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A B S T R A C T

Changes in land-use and climate increase the flammability of forests across southeast Amazonia, potentially driving abrupt fire-mediated transitions to derived savannas – grass-dominated degraded forests with scattered trees. However, the extent to which the forest fauna undergoes a parallel process remains poorly understood. Here we test the hypothesis that the process of fire-driven forest shifts towards derived savannas has congruent cascading effects on ant communities by causing declines in forest specialists and an influx of open-habitat taxa. In 2013 we collected ants using subterranean, epigaeic and arboreal pitfall traps in three adjacent 50-ha plots: an unburnt control and two treatment plots that were burnt either triennially or annually from 2004 to 2010. Frequent fire was associated with a marked decline of specialist forest species (almost 50%), and an influx of open-habitat taxa that were absent from the unburnt plot. The effects were particularly pronounced for epigaeic ants: their abundance, biomass, species richness and species composition were impacted by fires, and this was the main stratum occupied by the open-habitat species. Previous studies have shown that a similar conversion is not triggered by single fires, and they therefore require recurrent fires. Our results provide experimental evidence that the process of tropical forest conversion towards derived savannas caused by repeated burning is a broad one that affects not only plants, but involves parallel compositional shifts of animal communities. The prevention of recurrent fires is a priority challenge for avoiding widespread biotic conversion of tropical forests to derived savannas.

1. Introduction

Land-use and climate change act synergistically to increase the flammability of tropical forests, with the potential of driving abrupt fire-mediated transitions from forests to derived savannas. These habitats are characterized by a low-diversity, grass-dominated vegetation with scattered trees resulted from human-caused disturbances (Veldman, 2016). Such transitions are most likely to occur in areas where forests are fragmented, disturbances are frequent, and dry seasons are prolonged (Brando et al., 2014). These factors can increase fire risk because of the higher flammability of forest edges, due to reduced canopy cover, a warmer and drier microclimate, and invasion by grasses (Alencar et al., 2015; Nepstad et al., 1999). Once burned, a positive fire feedback may be established due to increased canopy openness, and higher and drier fuel loads (Cochrane et al., 1999; Nepstad et al., 2001). This can drastically alter fire return intervals in tropical forests, from an historical 500–1000 years (Pivello, 2011) to as little as 5–10 years (Cochrane, 2001).

Recurrent fires in tropical forests influence both fire intensity and ecological responses. Compared to a single fire, recurrent fires are usually more intense due to higher flame heights and faster spread rates (Balch et al., 2008; Brando et al., 2014), thereby increasing the vulnerability of resprouting stems, reducing tree cover and leading to dominance by short-lived pioneer species and invasion by grasses (Barlow and Peres, 2008; Silvério et al., 2013). Positive fire feedback resultant from these conditions coupled with climate change can ultimately result in a biome shift from forest to a derived savanna (Malhi et al., 2009; Nepstad et al., 2008; Ratnam et al., 2011). Recurrent fires also appear to have a greater impact than single fires on faunal communities (Barlow and Peres, 2006; Silveira et al., 2015), but the extent

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to which faunal change matches that of vegetation during process of savanna derivation remains little studied.

The rainforest-savanna transitional region of the southern Amazon is undergoing extreme land-use change, and is highly threatened by the risk of recurrent fires in remaining forests (Morton et al., 2013). Fire risk in these forests is higher than further north in the Amazon, not only due to human disturbances, but also because southern forests experience more frequent and intense droughts (Coe et al., 2013). In addition, these forests are often adjacent to fire-prone Cerrado (Neotropical savannas), with their boundaries largely determined by fire (Bowman, 2000; Hoffmann et al., 2009). Forests of the southern Amazon are relatively resistant to single fires (Brando et al., 2016), but can be dramatically impacted by repeated burning, especially under extreme climatic conditions (Balch et al., 2015; Brando et al., 2014). Such extreme conditions are expected to become more common in this region under climate change (Marengo and Espinoza, 2015), and these factors combined may trigger the conversion of large areas of these forests to derived savannas (Silvério et al., 2013).

Ants are a globally dominant faunal group that are widely used as indicators of the effects of habitat disturbance (Andersen and Majer, 2004), and changes in their communities usually reflect impacts on other faunal groups (Majer et al., 2007). They are especially abundant and ecologically important in tropical forests (Agosti et al., 2000; Hölldobler and Wilson, 1990). Single fires in southern Amazonian forests have been shown to decrease ant species richness, alter functional group composition, and reduce the effectiveness of seed removal, a key regulating ecosystem service provided by ants (Paolucci et al., 2016; Silveira et al., 2012). Fire can have important direct effects on rainforest ants through the removal of the litter layer (Paolucci et al., 2016), where many species nest. However, fire has particularly important indirect effects on ants through changes in habitat structure (Andersen et al., 2012). Therefore, the marked change to forest structure caused by repeated burning can be expected to have parallel cascading effects on ant communities.

Here we assess the impacts of repeated burning on forest ant communities in the southern Amazon, using a large-scale manipulative experiment where treatment plots were subjected to annual and triennial fires over a six-year period. Experimental fires transformed large portions of the forest edges into a derived savanna (Silvério et al., 2013), and this process has been exacerbated by two recent droughts (Brando et al., 2014). Our hypothesis is that the changes in vegetation structure wrought by frequent fire have led to a parallel conversion of ant communities. We predict that the frequently burnt plots have undergone a marked reduction in the diversity and abundance of specialist rainforest species, and have been colonized by open-habitat taxa that do not occur in unburnt forest. We also hypothesize that the impacts of frequent burning will vary with habitat stratum, according to variation among strata in the extent to which physical structure has been modified by fire. We predict that frequent fire will have greatest impact on epigaeic ants, because their habitat stratum is directly consumed, often entirely so, and because canopy openness caused by fires leads to warmer and drier microclimate conditions in the forest understory. We predict least impact on subterranean ants, because their habitat is the least impacted by fire.

2. Materials and methods

2.1. Study site

The study was conducted at “Fazenda Tanguro”, a privately-owned property located in Querência, Mato Grosso, southern Amazon basin (13°04′S, 52°23′W). The climate is tropical humid, with average annual rainfall of 1770 mm and a marked dry season (< 10 mm/month) between May and September (Rocha et al., 2014). Local vegetation is characterized by tropical evergreen forest, typical of the transitional area between the Cerrado and the Amazon rainforest. Plant species richness and canopy leaf area index are lower compared with central Amazon forests, and there is a high dominance of nine tree species, mainly from Lauraceae and Burseraceae, which represent 50% of the Importance Value Index (Balch et al., 2008). The nearest natural savanna is about 50 km distant, but the study site borders a soybean field that was previously cattle pasture (converted in 2006). The study area has < 2% slope, has never been logged, and had not previously been burnt in historical times.

2.2. Fire experiment

Experimental fires were applied to adjacent 50-ha (0.5 × 1.0 km) forest plots along the soybean field edge (see Fig. 2c in Balch et al., 2015). One plot (B1*yr*) was burnt annually from 2004 to 2010 (except for 2008), and another plot (B3*yr*) was burnt triennially (in 2004, 2007 and 2010). All burning was conducted at the end of the dry season (August or September). Fires were set with kerosene drip torches during 3–4 consecutive days between 9:00 and 16:00 h. The large plot size means that fire behavior approached that of real fires in larger expanses of Amazon forest. A third adjacent plot (Control) was left unburnt. A full description of experimental burns and fire behavior can be found in Balch et al. (2008). Fires were surface fires, with intensities and burned areas greater for triennial compared with annual burnt due to higher accumulation of litter. Balch et al. (2015) provide an overview of fire effects on vegetation at the site. Major changes include shifts in vegetation dominance (from tree species to grass ones along the forest edge) due to elevated fire-induced tree mortality, decreases of plant recruitment and several liana species, along with changes in the composition of plant species (Massad et al., 2015). There was limited effect in the first three years, followed by substantial tree mortality associated with an extreme drought event in the fourth year (2007), and subsequent canopy openness and grass invasion along forest edges after the fifth year. By 2012, grasses (mainly three species, one native C_3 and two African C_4) had invaded up to 250 m from the edges of burnt plots (compared with < 10 m in the unburnt plot, invaded only by the native C_3 species; Silvério et al., 2013). Hence, experimental recurrent burning triggered a process of forest conversion to derived savannas (see Fig. 7 in Balch et al., 2015) – human-caused degraded forests with open canopy, dominated in the edges by a low-diversity grassy vegetation (Veldman, 2016).

Our treatment plots were not replicated due to logistical, legal and financial constraints, and no pre-treatment ant data are available. Therefore, we focus on differences between plots (Davies and Gray, 2015). The plots showed no significant pre-treatment differences in vegetation variables such as species richness, relative abundance of the five most common species, Importance Value Index (IVI), adult composition, woody stem density and composition, and stem regeneration density, nor microclimate variables such as vapor pressure deficit near the soil surface (~10 cm height) and litter moisture content (Balch et al., 2013; Balch et al., 2008).

2.3. Ant sampling

Ant sampling was conducted in June 2013, three years after the last experimental fires. In each plot we established six linear transects of 10 sampling stations with 10 m spacing; the transects were located in a (3 × 2) grid with 250 m spacing, with the first two transects placed 250 m from the plot edge. Each sampling station consisted of three unbaited pitfall traps, one subterranean, one epigaeic and one arboreal. All pitfall traps were 5 cm in diameter, were partly filled with a salt solution and detergent, and left open for 48 h. The subterranean pitfalls were buried 15 cm deep, with lids to avoid filling with soil, and four radial holes – 1 cm diameter – to allow ant entry (Schmidt and Solar, 2010); the epigaeic traps were buried with their rims flush to the soil surface; and arboreal traps were tied at a height of 2 m to the trunk of the nearest tree with dbh ≥ 10 cm. We sorted ant samples to species,