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Resilience to fire and climate seasonality drive the temporal dynamics of ant-plant interactions in a fire-prone ecosystem

Fernanda V. Costa[a,*], Nico Blüthgen[b], Arleu B. Viana-Junior[a], Tadeu J. Guerra[c], Laura Di Spirito[a], Frederico S. Neves[a]

[a] Insect Ecology Lab, Biological Sciences Institute, Federal University of Minas Gerais, Belo Horizonte, Brazil
[b] Ecological Networks Group, Department of Biology, Technische Universität Darmstadt, Germany
[c] Graduate School in Botany, Federal University of Minas Gerais, Belo Horizonte, Brazil

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ABSTRACT

Animal-plant interactions have a major influence on ecosystem structure and functioning. Understanding to what extent the temporal dynamics of interactions is determined by climate and disturbances is thus relevant to predict ecological and evolutionary outcomes in a changing world. Here, we assessed whether the temporal dynamics of ant-plant interactions in a mountainous fire-prone ecosystem is driven by seasonal variation in abiotic conditions, and to what extent fire disturbance alters this dynamic. We also examined the thermal responses of foliage-dwelling ants in order to predict the effects of seasonal oscillations of temperature on ant activity. To do so, we monitored ant-plant associations in 35 sampling plots for one year before an unmanaged fire has occurred. Then, 26 burned and nine unburned plots were monitored for another year after fire. We found that warmer and wetter conditions let to increases in the diversity and frequency of ant-plant interactions, mainly via upturns in plant resource availability and ant foraging activity. Beyond the positive effects of temperature on interaction networks, however, ant species exhibited a low heterogeneity and a huge overlap in thermal niches. Moreover, fire has led to short-term negative effects on the diversity and frequency of interactions in ant-plant networks. In spite of it, these network metrics in burned plots took up to half a year to return to similar levels from unburned plots, highlighting the resilience of ant-plant interactions after fire disturbances. This study shows that wide thermal niches of ant species and fire resilience likely beget ant-plant networks reliability over seasons. The high overlap and broad thermal niches of ant species interacting with plant resources suggest that ant diversity plays a minor role in the tolerance against climatic changes in this fire-adapted community. These findings open a new pathway to explore thermal responses of species and their ecological interactions in broader gradients of environmental conditions and ecosystem disturbances. We advocate that long-term studies comprising assisted burnings are desirable to forecast the impact of fire regimes and how their synergy with climate would affect the functioning of fire-prone ecosystems. Lastly, this study adds evidence that studied interaction networks can be useful to monitor the impacts of environmental changes such as anthropogenic disturbances, being representative of many even more complex species interactions in ecosystems.

1. Introduction

Animal-plant interactions have a major influence on ecosystem structure and functioning (Valiente-Banuet et al., 2015). Ants act as mutualist and antagonist of a great diversity of plants (Bronstein, 1998; Rico-Gray and Oliveira, 2007), mediating many ecosystem functions and processes whose temporal dynamics depend on environmental filters (Del Toro et al., 2015; Dell et al., 2014). Climatic conditions and anthropogenic disturbances figure among the key drivers of ant species occurrence and their interactions with plants (Gibb et al., 2015; Paolucci et al., 2016). Therefore, to predict the ecological and evolutionary outcomes of ant-plant interactions in a changing world (Parmesan, 2006; Siepielski et al., 2017), we need to understand to what extent their temporal dynamics depend directly on climate variables and associated disturbances such as fire (Lehmann et al., 2014).

The dynamics of ant-plant interactions might result from oscillations in plant resources availability and ant foraging activity upon them. Indeed, the effect of climatic seasonality on plant phenology and food availability for ants is well-known (e.g., Belchior et al., 2016). Besides, it is remarkable that ant foraging activity and ant richness are

* Corresponding author at: Graduate School in Ecology of Tropical Biomes, Federal University of Ouro Preto, Ouro Preto, Brazil.
E-mail address: costa.fvc@gmail.com (F.V. Costa).

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positively influenced by temperature, humidity, and rainfall (Gibb et al., 2015; Kaspari, 1993). Temperature is described as the main abiotic predictor of activity and distribution of thermally constrained groups such as ants, in which species display specific tolerances to temperature oscillation (Diamond et al., 2012; Peters et al., 2016). Ecological communities may differ in their responses to temperature fluctuations according to species thermal niches (Arnan et al., 2015; Kühsel and Blüthgen, 2015). For instance, some communities include species with narrow and non-overlapping thermal breadths, i.e., low complementarity in thermal niches. As result, strong temperature fluctuations may act as environmental filters reducing species diversity. In contrast, other communities encompass species with broader and overlapping thermal breadths, thus species diversity in these communities are less affected by temperature oscillations (Arnan et al., 2015; Kühsel and Blüthgen, 2015). This divergence is most likely to occur in habitats that differ in temperature oscillation, e.g., highly seasonal environments which might comprise communities with high heterogeneity in their thermal breadths, in response to the experienced selection for distinct optimal conditions (Arnan et al., 2015; Kaspari et al., 2015). Hence, it is expected that marked seasonality, i.e., the temporal periodicity in climatic conditions (Tonkin et al., 2017), regulates plant resource availability and patterns of ant foraging with extensive effects on the dynamics of ant-plant interactions.

Seasonality as its related disturbances such as fire are most prominent in fire-prone ecosystems (Lehmann et al., 2014), wherein the temporal activity of species (Andersen et al., 2014) and vegetation phenology (Alvarado et al., 2017) are shaped by burning regimes. In fact, the biota in these environments presents adaptations that allow them to survive fire events, as a result of their association over evolutionary time (Bond and Keeley, 2005; Whelan, 1995). Moreover, recent evidence shows that structure and composition of ant communities from flammable environments such as grasslands and savannas are able to recover after burning events (reviewed by Vasconcelos, Maravalhas and Cornelissen 2016). Likewise, plants from fire-prone vegetation usually exhibit a rapid recovery after burning (Maurin et al., 2014), and some species even re-sprout and bloom only in response to fire (Figueira et al., 2016). Alternatively, fire promotes negative impacts on ants by simplifying vegetation structure (Kimuyu et al., 2014), decreasing the availability of nesting sites, and causing direct mortality of colonies, features that together negatively impact ant-plant interactions (Fagundes et al., 2015).

Despite the considerable data on the effects of climate and fire on plants (e.g., Veldman et al., 2015) and animals (e.g., Gibb et al., 2015), little is known about how these environmental filters influence animal-plant interactions. To date, no empirical study has addressed to what extent both drivers may affect the temporal variation of ant-plant interactions. Here, we assessed whether the dynamics of ant-plant interactions in a seasonal fire-prone ecosystem is determined by climate and whether this dynamic is altered by an unmanaged fire event. To do so, we studied ant-plant interactions through ecological networks approach, which has been broadly used to evaluate ecosystem structure and functioning (Okuyama and Holland, 2008). We chose the diversity and frequency of interactions once these network metrics represent a simple and meaningful way to describe quantitative patterns and the complexity of species-rich interacting communities (Blüthgen, 2010; Vázquez et al., 2005), i.e., how many species are actually in association and how frequently they truly interact. Thus, we focused on *campo rupestre*, a tropical megadiverse mountaintop grassland ecosystem (Silveira et al., 2016), wherein plant-related rewards comprising flowers, fruits and extrafloral nectaries are used as food by ants (Costa et al., 2016). This fire-prone environment has been subjected to recurrent anthropogenic fires (Alvarado et al., 2017; Figueira et al., 2016) and climatic filters that regulate species distribution (Fernandes et al., 2016) and vegetation phenology (Rocha et al., 2016). Current findings have shown a short-term negative effect of fire on *campo rupestre* vegetation structure (Le Stradic et al., 2016) and ant assemblages (Anjos et al., 2017; Neves et al., 2016). Likewise, recent studies suggest that climatic conditions in this ecosystem change linearly along the elevational gradient (from 800 to 1400 m a.s.l.) constraining ant occurrence (Fernandes et al., 2016), an abiotic-limiting trend that is consistent in several mountainous ecosystems (Bishop et al., 2016; Peters et al., 2016).

As follows, we have three expectations. First, we expected a positive and linear effect of temperature, rainfall, and humidity on the diversity and frequency of ant-plant interactions. This expectation is based on existing evidence that warmer and wetter conditions linearly increase resource availability and ant activity (see Rocha et al., 2016; Fernandes et al., 2016), when the amplitude of climatic conditions is seasonally-wide, but not extreme as observed for very high mountains (e.g., Dunn et al., 2007). Second, that temperature oscillation over seasons would lead to high heterogeneity in ant species thermal responses, as seasonal habitats might comprise communities with a set of species with high variability in their optimal conditions (Arnan et al., 2015; Kaspari et al., 2015). Finally, we predict that fire would lead to short-term negative effects on interactions' diversity and frequency, as plant and ant communities from flammable ecosystems are supposed to be resilient to fire disturbances (Andersen et al., 2014; Figueira et al., 2016). Here, we adopted the traditional view of resilience as the time required for an ecological system to return to a steady-state following a perturbation (Gunderson, 2000), assuming that unburned plots should reflect a stable state for ant-plant interactions.

2. Material and methods

2.1. Study area

This study was carried out in seven *campo rupestre* sites at *Morro da Pedreira* Environmental Protection Area, a buffer zone of *Serra do Cipó* National Park, in the southern region of the Espinhaço Mountain Range, southeastern Brazil (19°17'49" S, 43°35"28" W, Fig. S1). At higher altitudes (upper to 900 m asl.), the region is featured by *campo rupestre*, a rocky montane savanna composed by a species-rich vegetation, high levels of plant endemism, a large number of threatened plant species (Silveira et al., 2016), and high ant richness (Costa et al., 2015). Fire regimes in this region are moisture-dependent, which means that its occurrence is often related to the dry season length and rainfall distribution along the season. Additionally, there is a strong spatial–temporal variation in fire frequency in the region, wherein in the last 30 y, 51% of all affected areas got burned between one and four times, 22% between five and nine times, and 2% were burned ten times or more (Alvarado et al., 2017). Recent data indicate an interval of two years between two fire events, reflecting the occurrence of large fires in shorter time intervals (Figueira et al., 2016). On the landscape level, the widespread rocky outcrops, associated with rivers and riparian forests, create gaps in the fuel layer that prevent fire spread (Figueira et al., 2016). Generally, most fires are mainly anthropogenic and superficial, consuming fine fuels of herbaceous layer (Figueira et al., 2016). The climatic regime is characterized as tropical altitudinal (Cwb) according to Köppen's classification (Alvares et al., 2013), comprising markedly dry and cold winters and warm and wet summers. Mean Annual temperature is ca. 22 °C, wherein daily minimum and maximum values are 33 °C and 28 °C for the warmest month (February), and 13 °C and 7 °C for the coldest month (July). Mean annual rainfall is ca. 1,500 mm, ranging from 75 to 340 mm during rainy season (October to April, > 60 mm per month), while throughout dry season it ranges from 7 to 32 mm (May to September, < 40 mm per month) (Alvarado et al., 2017).

2.2. Sampling design

In each site, we selected the larger rocky outcrop that also was closer to the weather station to install the sampling transect. On the