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SPATIO-TEMPORAL CHANGES IN THE STRUCTURE OF THE ANT, BEE, AND TREE COMMUNITIES IN THE BRAZILIAN CERRADO

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Abstract: In this study, we described the changes in land cover and land use, in climate, and in the incidence of fires that have occurred over the last decades within the region of the "Triângulo Mineiro and Southeastern Goiás" site (TMSG) of the Long-term Ecological Program (PELD-CNPq). We also evaluated to what extent some stressors, such as habitat fragmentation, fire events and the creation of artificial dams, are related to temporal changes in the communities of euglossine bees, ants and trees. We detected abrupt changes in climate, fire frequency and land use in the TMSG region. Since 2000, the area occupied by native vegetation has declined from 34.5 to 25.5 % while the incidence of fires increased exponentially. Moreover, the annual maximum temperature is 2.5 °C higher than it was about 30 years ago. Temporal changes in the composition of the euglossine community in forest fragments (varying in size from 16 to 200 ha) were gradual and non-directional, suggesting that the community is at equilibrium. For arboreal ants associated with savannas, our data also indicate an absence of directionality in the community trajectory. However, there is evidence that changes are no longer gradual in the presence of recurrent fire events. In contrast, the tree communities showed gradual and directional changes, indicating the existence of a successional process in these communities. These changes started, in one case, by the construction of a reservoir along the margin of the forest fragment and, in the other, by the suppression of anthropic disturbances when the fragment became part of a protected area.

Keywords: Anthropogenic impacts; Community dynamics; Dry forests; Euglossini; Formicidae.

INTRODUCTION

Natural areas are experiencing increasing disturbance rates caused by anthropogenic activities (e.g., deforestation, selective logging and expansion of agricultural and urban frontiers) (UNFCCC 2015). Thereby, undisputed environmental services (e.g., carbon stocks, pollination, biodiversity refuges and climate control) have been lost or degraded over the last decades (Pyles *et al.* 2018, Marshman *et al.* 2019). Understanding how native species and environmental services are affected by different anthropogenic impacts is critical to define effective public policies that ensure biodiversity conservation (Poorter *et al.* 2017). In this sense, long-term studies (e.g., the Long-Term Ecological Program – PELD – CNPq) are extremely important to understand several ecological processes that require the monitoring of biological communities.

A long-standing question in ecology is to understand how communities change over time (Matthews *et al.* 2013). Temporal changes in species composition can result in at least four different trajectories of the communities. Trajectories can be directional, when dissimilarity in species composition increases over time, or non-directional (idiosyncratic trajectory), when community dynamics lack an overall directional trajectory over time. Furthermore, temporal changes in species composition can be either gradual (i.e., when changes in species composition occur at similar rates through time) or saltatory, when changes are abrupt at some time intervals but not at others (Matthews *et al.* 2013). Long-term datasets on temporal variations in community composition are rare, notably for some invertebrate groups (Sánchez-Bayo & Wyckhuys 2019). Yet, these data are essential for assessing the temporal trajectories of these communities and to better understand how disturbances can affect community structure and composition (Matthews *et al.* 2013, Donoso 2013).

Most studies evaluating the relationships between biodiversity and anthropogenic disturbances were conducted in tropical rainforests (Finegan *et al.* 2015, Rozendaal & Chazdon 2015). However, these relationships are fundamentally different between ecosystems that are constrained by different resources and suffer different impacts (Lohbeck *et al.* 2013 , Poorter *et al.* 2017). For instance, the Cerrado biome of Central Brazil has a strong seasonal climate, and droughts and fire events are frequent and impose environmental filters on local species that are different from those observed in the Amazon and the Atlantic Forest (Prado-Junior *et al.* 2016). Many elements of the regional Cerrado species pool have adaptations to survive and develop well under these filters, including leaf deciduousness, deeper roots, greater bark thickness and underground reserve organs among plants (Coutinho 1990), and changes in activity level and habitat use as well as the use of thermally protected nests or shelters among animals (Redford & Fonseca 1986, Morais & Benson 1988, Costa *et al.* 2013). Despite these adaptations, extreme disturbance events (such as prolonged droughts and catastrophic fires) can lead to large biodiversity and productivity losses in these ecosystems (Pivello 2011).

The study region covered by the PELD Triângulo Mineiro e Sudeste de Goiás (TMSG) represents an ideal study area to test the effects of anthropogenic disturbances on the structure, composition and dynamics of biological communities. The research of the PELD-TMSG involves a variety of biological groups including bees, ants and trees (the groups analyzed in the present study), spiders, galling insects, aquatic invertebrates, birds and non-flying mammals of small, medium and large sizes.

Here, we first evaluated how environmental conditions (annual precipitation, maximum temperature, incidence of fire events and land use) changed over the last decades in the PELD-TMSG study area. We expected that, due to global climate change and fast economic growth of the region, anthropogenic impacts have intensified in the recent years, with a reduction in annual precipitation and native vegetation cover, and an increase in maximum temperatures and in the frequency of fires. Secondly, we evaluated the temporal trajectories of the communities of euglossine bees, ants and trees and related these trajectories to various stressors, such as the occurrence of fires or the construction of dams. Our aim was to determine whether the observed changes in the species composition were directional or not, and whether they were gradual or abrupt (Matthews *et al.* 2013).

MATERIAL AND METHODS

Study site

The studies of the PELD Triângulo Mineiro and Southeast of Goiás (TMSG) site are being conducted in reserves of various sizes, including the Parque Estadual da Serra de Caldas Novas with 12,500 ha, the Parque Estadual do Pau Furado with 2,200 ha, the Estação Ecológica de Galheiros with 2,847 ha and the Reserva Ecológica do Panga with 409 ha. In addition, studies are also being conducted in 10 remnants of semideciduous seasonal forests (SSF), with sizes ranging from 16 to 200 ha (Figure 1). The PELD-TMSG is located in a politically strategic region, connecting the producing centers of the Southeast and Midwest region of Brazil. This site covers an area of 136,784 km^2, where almost three million people live. It is one of the largest agricultural areas in the country, and has a well-developed industrial center, being considered one of the regions with highest economic growth (Ribeiro & Oliveira 2015). It harbors some parts of the Paraná river basin and is close to the limit of the São Francisco basin, both extremely important in the socioeconomic context of Brazil. The PELD-TMSG site is predominantly in the Cerrado domain, but it also includes some enclaves of Atlantic Forest. Both the Cerrado and the Atlantic Forest are considered as global biodiversity hotspots (Mittermeier *et al.* 2011). Its native vegetation is composed by a mosaic of vegetation types, ranging from grasslands and *veredas*, savanna formations and forest formations such as woodlands (cerradão), riparian forests and seasonal forests (Terra *et al.* 2017).

Despite its great environmental importance, much of the native vegetation of the PELD-TMSG study region has been replaced by pastures, croplands and urban areas (Strassburg *et al.* 2017). In this region, the conservation units at municipal, state or federal levels are few and relatively small in size. Much of the remaining native vegetation is within private properties (such as legal reserves or as areas of permanent preservation). Thus, unlike many other PELD sites, the TMSG site does not concentrate its activities in a single large biological reserve, but rather in several reserves of medium to small sizes (Figure 1).

Temporal changes in climate, land use and fire events at the PELD-TMSG

To evaluate how environmental conditions (annual precipitation, maximum temperature, incidence of fire events and land use) changed over the last decades, we used remote sensing techniques to create a polygon that includes 10 microregions of the Minas Gerais and Goiás states that encompass the PELD-TMSG study region (Figure 1). We used this polygon as a reference for data extraction. To assess the degree of conversion of native vegetation in our study region, we accessed IBGE´s land cover use monitoring maps for the years 2000 and 2016 (IBGE 2018). We evaluated changes in the percentage of coverage of the following classes: water courses, croplands, urban areas, managed pastures, and native vegetation areas (forests, savannas and grasslands).

We evaluated the variation in annual rainfall and maximum annual temperature between 1988 and 2018, using meteorological data for Araxá, Catalão,

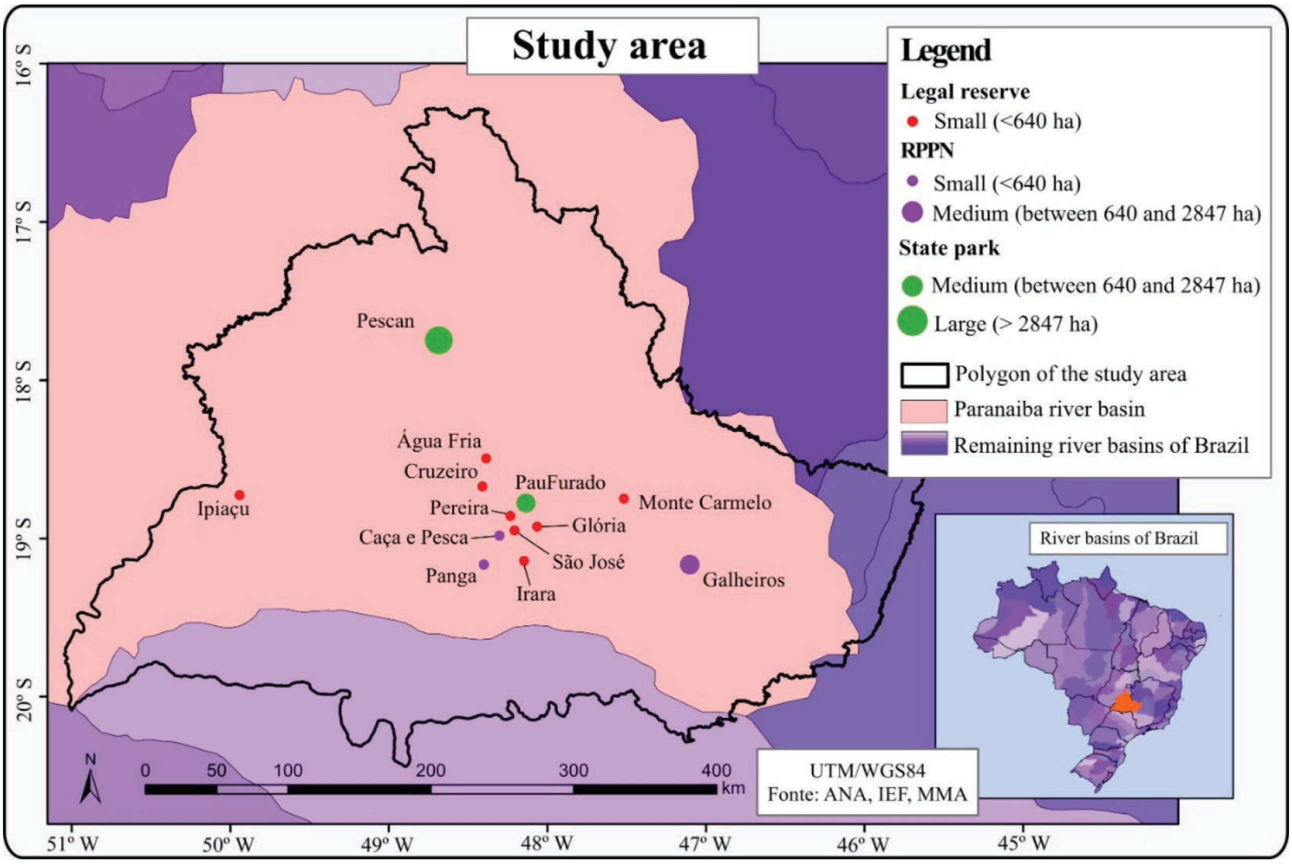

Figure 1. Study area of the site "Triângulo Mineiro and Southeastern Goiás" (TMSG) of the Long Term Ecological Program (PELD-CNPq).

Ipameri, Ituiutaba, Itumbiara, Patos de Minas and Uberaba weather stations (INMET 2019). Moreover, we assessed the yearly variation in the total number of fire events detected by satellite imagery within the region between 2003 and 2018 based on the BD Queimadas database (INPE 2018).

Sampling of the bee, ant and tree communities

Euglossine males were sampled in different years in five semideciduous seasonal forests (SSFs) between the years 2007 and 2015 (Table 1), in a total of 15 sampling events. The surveyed SSFs have different areas and land-use histories (see Lopes *et al.* 2013 for a greater detail on the different disturbance histories). AGU and PAN represent the largest and smallest fragments (200 and 16 ha), respectively, and are the SSFs under lower disturbance intensities (Lopes *et al.* 2013). Each sampling event was performed over five to six days during the rainy season, from October to March. The males were collected using aromatic baits. Seven fragrances were used to attract the males: eucalyptol, eugenol, vanillin, methyl salicylate, benzyl acetate, β-ionone and methyl cinnamate. The baited traps with different fragrances were placed in the shade, hung on branches about 1.5 m above ground, and approximately 5 m apart from each other. All aromatic compounds were replenished every 2 hours to maintain their attractiveness. Sampling occurred from 09:00 h to 13:00 h, totaling 64 hours of sampling in each of the five areas. The bees sampled between 2007 and 2010 were captured with an entomological net and placed in mortiferous chambers containing ethyl acetate. The bees collected between 2012 and 2015 were placed in a cooler containing ice, identified in loco and had their pre-tarsal segment and one tarsomere removed to further genetic analyses. Specimens of rare or unidentified species were collected and deposited in the UFU Entomological Collection. Further details of the methodology can be found in Silveira et al. (2015) and Tosta et al. (2017).

For ants, we used data from several studies performed at two of the PELD-TSMG sites (PANsav and PESCAN, Table 1) in a total of ten sampling events. These involved the sampling of the arboreal savanna ant fauna using arboreal pitfall traps baited with sardine, honey or human urine (Campos *et al.* 2011, Frizzo *et al.* 2012, Vasconcelos *et al.* 2018, Rosa 2020). The management plan of these reserves includes fire suppression whenever possible. Nevertheless, at PESCAN, fires occurred in 2006 and 2008, which affected only part of the reserve (Frizzo *et al.* 2012). Ant sampling at the PESCAN savanna (cerrado *stricto sensu*) took place in 2005, in 2006 (three months after the fire), in 2007, 2011 and 2018 (Table 1). At PANsav there were three fires: one in 2006, which hit only 30% of the reserve and two others, one in 2014 and the other in 2017 that burned almost all of the reserve (Rosa 2020). Ant sampling at PANsav took place in 2005, 2010, 2012, 2013, 2015 and 2018 (Table 1). Sampling in each of these two sites was performed in trees > 2.5 m in height (N = 40 to 60 trees, in each sampling year) spaced at least 20 m apart. For the purpose of the analysis presented here, we recorded the proportion of trees in which each ant genus was recorded for each sampling year.

To evaluate the extent to which tree communities changed through time, we used data from PANfor (which has been protected from anthropogenic actions since 1986), and from a deciduous seasonal forest (DSFres) affected by the construction of a hydroelectric reservoir (Amador Aguiar Dam Complex). Before the reservoir was built, the studied sites were located at least 700 m from the riverside, and since the reservoir flooding, they are located close (0 – 60 m) to the water's edge (Raymundo *et al.* 2019). At PANfor, tree samplings were performed in 1997, 2002, 2005 and 2012. At DSFres, tree samplings were performed in 2005 (before dam construction), 2007, 2009 and 2015 (Table 1). In the first sampling (1 ha in each forest), all living trees with a diameter at breast height (DBH, 1.30 m high) ≥ 5 cm were tagged, identified to species level and had its DBH measured and height estimated using a 10 m pole. In the subsequent samplings, all trees were re-measured and classified as survivors, dead or recruits (young trees that were not sampled in the previous survey).

Our dataset included 15 species of euglossine bees (Table S1 in Supplementary Material), 25 genera of ants (Table S2) and 222 tree species (Table S3).

Data analysis

To assess the degree of conversion of native vegetation in our study region, we evaluated the land-use data (water courses, cropland, urban

Table 1. Experimental design for the sampling of the euglossine bee, ant and tree communities. The year of sampling for the three biological groups is indicated. Euglossine bees were sampled at five semideciduous seasonal forests, ants at two savannas and trees at two seasonal forests. Potential stressors (i.e., fire events and the creation of an artificial reservoir) that occurred between samplings are also indicated. In 2006, the fire event at PANsav occurred after the sampling. Site code refers to Figure 1. AGU = Água Fria, GLO = Glória, IRA = Irara, PAN = Reserva Ecológica do Panga (forest or savanna areas), SJO = São José.

Year	Bees					Ants		Trees	
	AGU	GLO	IRA	PANfor	SJO	PANsav	PESCAN	PANfor	Dsres
1997								X	
1998									
1999									
2000									
2001									
2002								X	
2003									
2004									
2005						X	X		X
2006						Fire	X / Fire		Reservoir
2007				X			X	X	X
2008		X			X				
2009									X
2010	X		X			X			
2011							X		
2012		X		X		X		X	
2013	X		X		X	X			
2014		X				Fire			
2015	X		X	X	X	X			X
2016									
2017						Fire			
2018						X	X		

areas, managed pasture, and native vegetation areas) between the years of 2000 and 2016. To evaluate the temporal changes in climate and fire events in the PELD-TMSG study region, we performed linear regressions between the response variables and year. Moreover, we plotted the yearly variation in the response variables using LOWESS smoothing (Locally Weighted Scatterplot Smoothing) as tendency lines.

To analyze the trajectory of the euglossine bee communities (in different sized fragments of semideciduous seasonal forest), the trajectory of the arboreal ant communities in the savannas of PESCAN and PANsav, and the trajectory of the tree community in PANfor and DSFres forests, we initially calculated the relative abundance of each species (or genus in the case of tree-dwelling savanna ants) at each site and sampling period. Next, a multidimensional non-metric ordination (nMDS) was performed, as proposed by Matthews *et al.* (2013). These trajectories of community change can be classified as directional or non-directional. If the trajectory is directional it is expected that community dissimilarity would increase as the time interval between surveys increases (Matthews *et al.* 2013). To test this hypothesis, we used Spearman correlation (r_s) between similarity in community composition between surveys (using the Bray-Curtis index) and the time interval between surveys. When there is a disturbance (e.g. by fire, severe drought or flooding), community trajectories can also be classified as saltatory or gradual. If the trajectory is saltatory, it is expected that disturbance events will promote a drastic change in species composition (Matthews *et* *al.* 2013). To test this hypothesis, we used Spearman correlation (r_s) between the similarity in species composition (Bray Curtis index) between the surveys and the number of disturbance events between these same surveys. Statistical analyses were performed in R 3.5.3 (R Core Team 2019) using the packages "vegan" (Oksanen *et al.* 2019) and "lme4" (Bates *et al.* 2014).

RESULTS

Temporal changes in climate, land use and fire events

Over the whole area covered by the PELD-TMSG site (136,784 km^2), the area occupied by pastures (*ca.* 37 %) remained relatively stable between 2000 and 2016 (Figures 2a and 3a). The area devoted to agricultural activities increased from 24.5 to 34 % over the same period. By contrast, the area occupied by native vegetation declined from 34.5 to 25.5 % (Figures 2a and 3a), indicating a net loss of 25 % of the native vegetation in just over a decade.

Regarding the local climate, there was no significant change in annual rainfall over the last 30 years ($F_{1,246}$ = 0.598, p = 0.44) (Figure 2b). On the other hand, the annual maximum temperature, which was around 30 °C in the late 1980s, is now about 2.5 °C higher ($F_{1,237}$ = 14.76, p < 0.001) (Figure 2c). Fire events have increased exponentially over the past 15 years, from 5,695 events in 2003 to 17,378 in 2018 ($F_{1,14}$ = 17.75, p < 0.001) (Figures 2d and 3b).

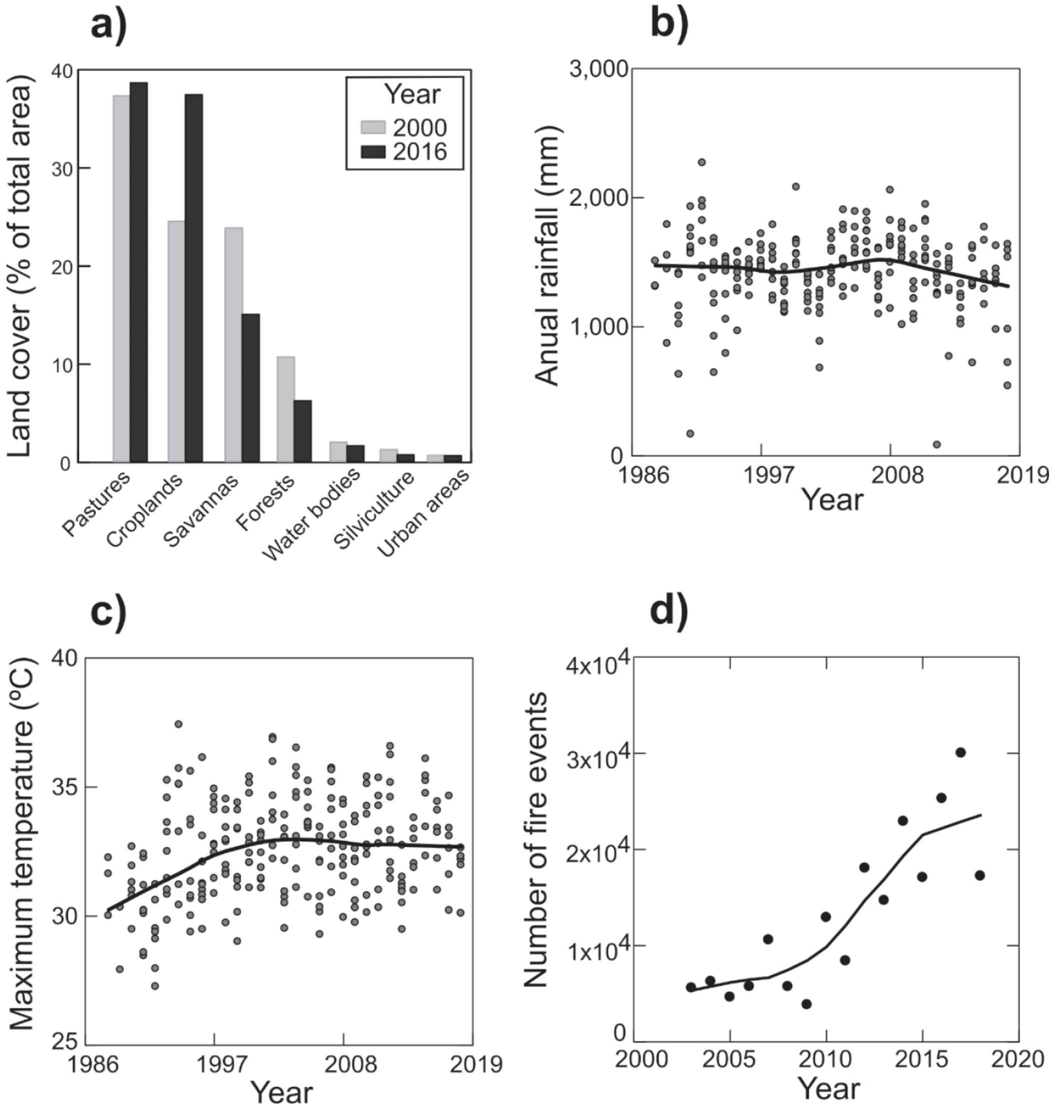

Figure 2. Temporal changes in land use, climate and fires at the PELD TMSG site: a) land cover between 2000 and 2016; b) annual rainfall and c) maximum temperature between 1988 and 2018 (each dot represents a meteorological station); and d) number of fire events between 2003 and 2018. Scatterplot tendency lines were fitted using LOWESS smoothing (Locally Weighted Scatterplot Smoothing).

Temporal trajectories of the communities

For trees, there was a negative correlation between the time interval of sampling events and the similarity in species composition (r_s = -0.85; gl = 11; p < 0.01), indicating that changes in species composition in these fragments were directional (Figure 4). In contrast, for euglossine bees and arboreal ants, temporal changes in community composition were non-directional (bees: r_s = -0.03; gl = 14; p = 0.92; ants: r_s = -0.22; gl = 24; p = 0.29). However, for arboreal savanna ants, there was a negative correlation between the number of fire events between samplings and the similarity in species composition changes (r_s = -0.49; gl = 24; p = 0.01), indicating that the temporal trajectories of these ant communities were saltatory rather than gradual (Figure 4).

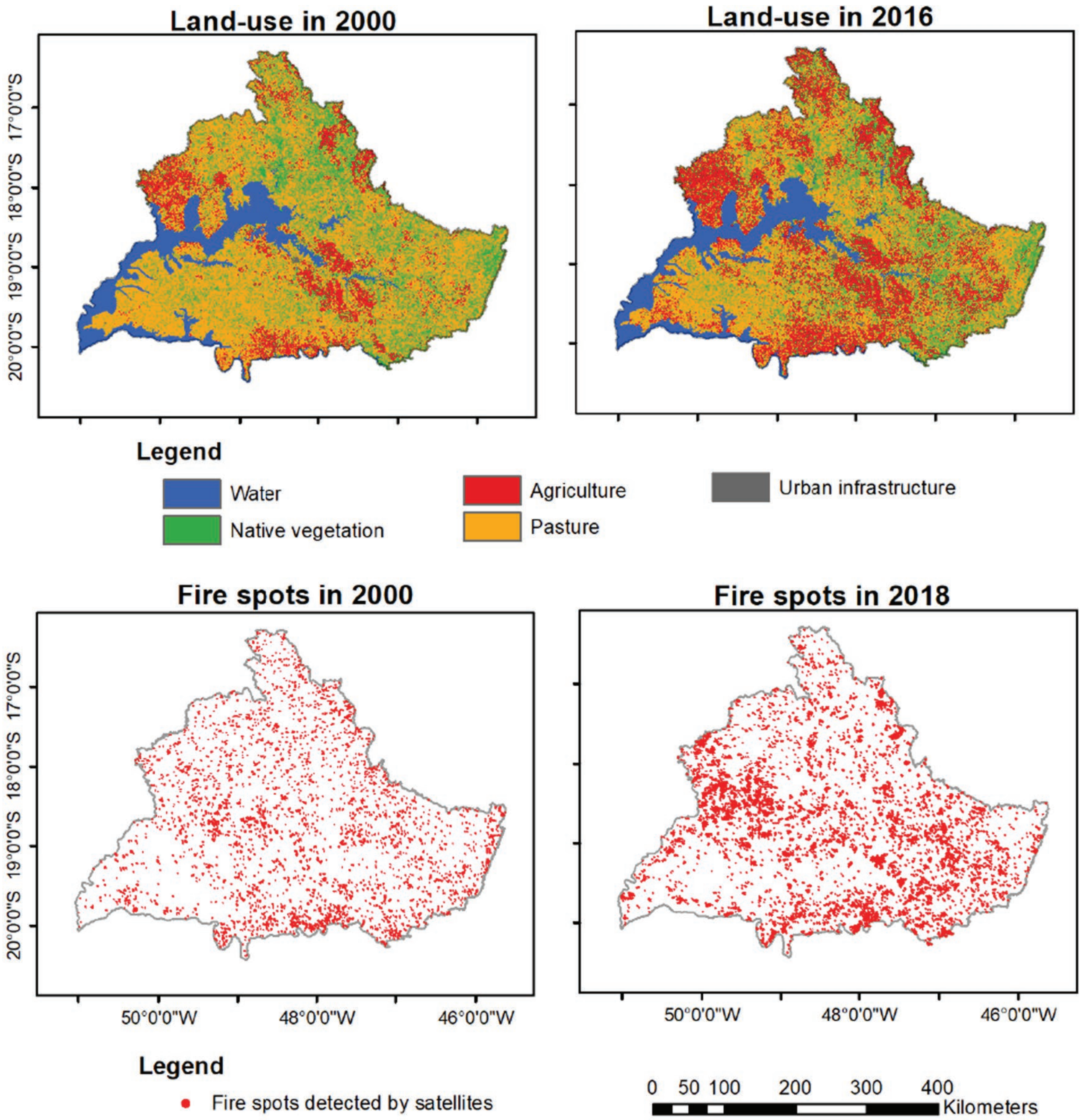

Figure 3. Land use change between 2000 and 2016 (A) and number of fire spots between 2003 and 2018 (B).

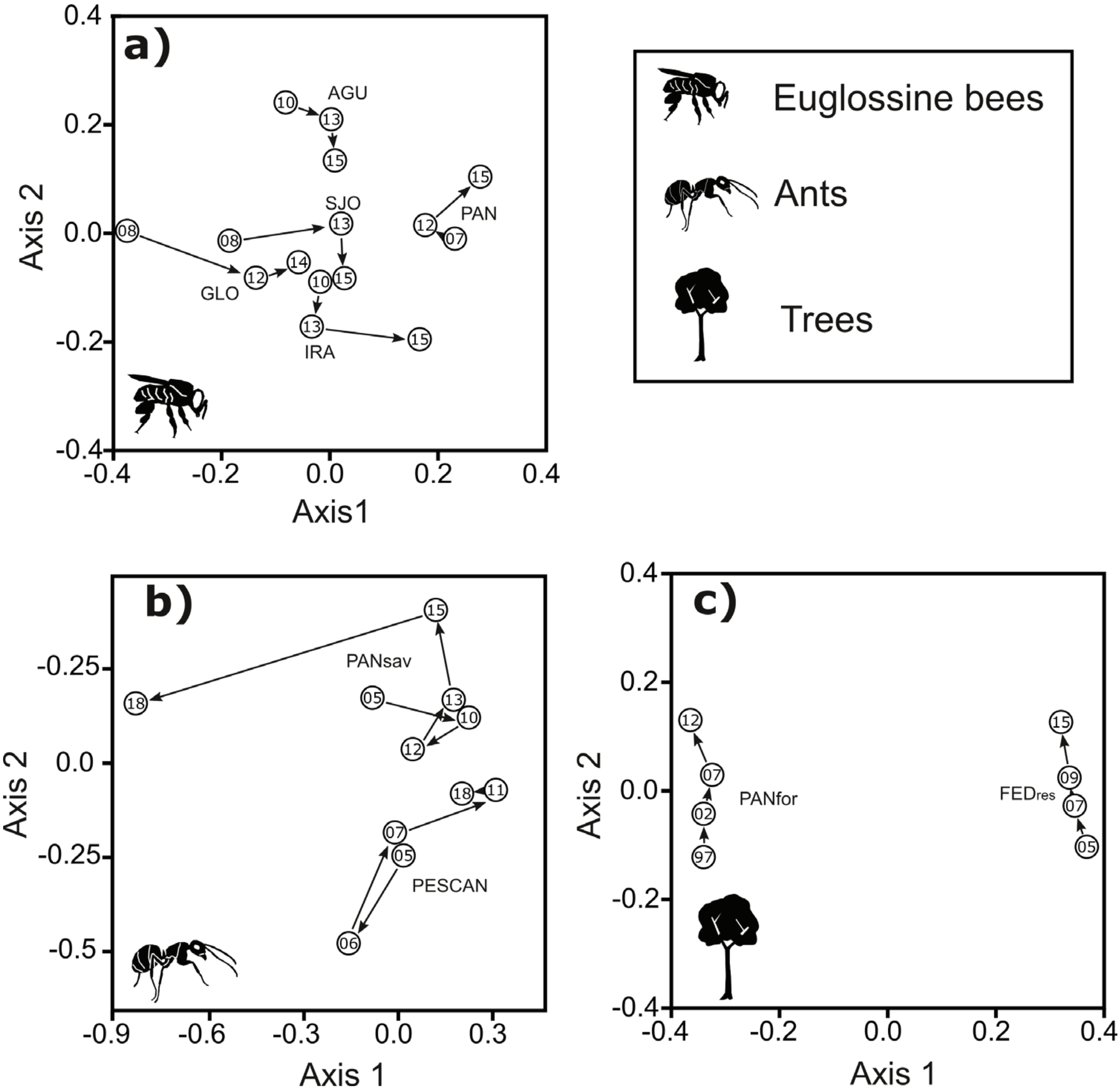

Figure 4. Non-metric dimensional scaling (nMDS) of the communities of a) euglossine bees, b) arboreal ants and c) trees based on the composition of species (or genera, for ants) at different sampling periods. Numbers inside symbols represent the last two digits of the year in which each community was sampled. NMDS stress values for bees, ants and trees were 0.158, 0.104 and 0.042, respectively. AGU = Água Fria, GLO = Glória, IRA = Irara, PAN = Reserva Ecológica do Panga (forest or savanna areas), SJO = São José, PESCAN = Caldas Novas State Park, DSFres = dry seasonally forest affected by the water reservoir belonging to the Amador Aguiar Hydroelectric Complex.

DISCUSSION

Temporal changes in climate, land use and fire events

Our results showed that, between 2000 and 2016, there was a 25 % reduction in the native vegetation cover over the study area encompassed by the PELD-TMSG. These values are higher than those observed for the Cerrado as a whole in the same period, where the loss of native vegetation was approximately 15 % (IBGE 2018). Land conversion for agricultural activities was the main driver of vegetation loss at the PELD-TMSG site. The current area covered by native vegetation at our study site is only 25.5 % of the territory (in the Cerrado it is 58 %, IBGE 2018). Considering that protected areas at the PELD-TMSG site represent less than 1 % of the total region's extent, their conservation will depend on major changes in environmental public policies.

Our results also indicated an increase in maximum temperature and in the frequency of fire events in our study region. We acknowledge that the observed relationships between the changes in land use and climatic changes at the regional scale do not necessarily mean causation. However, several studies show that large-scale losses in native cover are driving worldwide climatic changes (UNFCCC 2015). The role of vegetation in thermal control is related to several processes, such as the sequestration of atmospheric carbon through photosynthesis (which reduces the greenhouse effect), reflection of most of the infrared sunlight back into the atmosphere (preventing it from being absorbed by the soil), and through evapotranspiration, which involves the removal of heat from the air (Berner & Berner 2012). Although we did not observe any reduction in annual precipitation, severe droughts were recorded in our region in both 2014 and 2015. The increase in the number of fire outbreaks observed in the PELD-TMSG study region may be related to both an increase in the frequency of severe drought events and an increase in human activities – and, hence, sources of ignition. Interestingly, recent studies show that the number of fire events around the world has been decreasing, mainly due to the use of more advanced fire control techniques and greater habitat fragmentation (Andela *et al.* 2017). The increasing fire frequency in the PELD-TMSG study area (and notably the occurrence of high-intensity fires) may become a threat to the regional Cerrado's biodiversity, even considering that its endemic flora and fauna have adaptations to cope with fire and thus to a large extent is dependent on fire (Simon *et al.* 2009).

Temporal trajectories in the composition of bees, ants and trees

The euglossine bee community was monitored for a period of up to eight years in different sized fragments of SSF, and our results show gradual and non-directional changes in species composition. This finding indicates that the euglossine communities at these fragments are in equilibrium (Donoso 2013), a result that is similar to those found in studies at forests of central America and that encompassed an even larger period of time (Roubik & Ackerman 1987, Roubik 2001). However, over the period analyzed here, the variation in community composition tended to be less abrupt (i.e., higher compositional similarity between sampling events) at the two most preserved remnants (AGU and PAN) compared to the remaining ones (Figure 4). Therefore, more long-term studies are necessary to better evaluate the degree of community stability of euglossine bees in forest remnants of different sizes and degree of conservation.

For arboreal ants in savanna environments, our data also indicate an absence of directionality in the trajectory of the community over a period of 13 years. However, different from the bee communities, the compositional changes in ant communities were not gradual – but, rather, saltatory. The reasons for this are not clear but may involve the severe fires that occurred in the Panga Ecological Reserve (PANsav) in 2014 and 2017. Arboreal ants are a numerically and behaviorally dominant arthropod group in Cerrado trees. A meta-analysis indicates that savanna ants are resistant and resilient to fire disturbances (Vasconcelos *et al.* 2017). However, few studies have evaluated the effects of fire on arboreal ants, which are known to be more sensitive to the direct effects of fire compared to ground-nesting ants (Morais & Benson 1988, Vasconcelos *et al.* 2017). Studies at PANsav show that high intensity fires reach the top of the tree canopy, causing high mortality of ants that nest in small branches and twigs, such as species from genera *Cephalotes* and *Pseudomyrmex* (Rosa 2020).

The analysis of the trajectory of the tree community in two forest remnants (PANfor and DSFres) indicates that the changes in species composition were gradual and directional, that is, as time passed each area became floristically more dissimilar than it was some years before. Although both areas had the same trajectory, the processes causing the observed species turnover seems to be different. The directional changes were expected in the community in DSFres, as the construction of the reservoir abruptly increased soil moisture, favoring the establishment of species that are less adapted to water stress (e.g., evergreen species with lower wood density, Raymundo *et al.* 2019).

This continuous disturbance can change the competitive relationships among species (Liu *et al.* 2013), promoting an ongoing species turnover over time. Surprisingly, gradual and directional changes were also noted in the forest at PANfor, where no anthropic disturbances were observed. When the Panga Ecological Reserve was created (in 1986), the entire area was protected and isolated from anthropogenic disturbances, allowing the forest to advance to more mature successional stages (Cardoso *et al.* 2009). Previous studies in the area described the process of "self-thinning" in the forest, related to a decrease in tree density and an increase in basal area (Rodrigues-Souza *et al.* 2015). Successional advancement in seasonal forests alters the microclimatic conditions of the forest (e.g., reduced luminosity and increased humidity) promoting gradual changes in species composition over time, notably the replacement of pioneer by shade tolerant species (Lohbeck *et al.* 2013).

In short, here we described the changes in climate, in land use and land cover, and in the incidence of fire that have occurred in the last decades in the PELD-TMSG study region. We also presented evidence that, in savannas, changes in the composition of the arboreal ant community may be associated with the occurrence of high-intensity fires. The observed changes in the tree community were gradual and directional as result of changes in the disturbance regime of each of the forests analyzed. The detection of these patterns was only possible through a continuous monitoring program of these communities, reinforcing the need of long-term data to better direct conservation efforts.

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Supplementary Material: Table S1. Relative abundance of euglossini bee species sampled at five fragments of semideciduous seasonal forest in the study area of the PELD-TMSG. Relative abundance was calculated as the mean values of abundance among the three samplings periods for each forest.

Supplementary Material: Table S2. Relative abundance of different ant genera sampled in savanna trees in two study areas of the PELD-TMSG. PESCAN = Parque Estadual da Serra de Caldas Novas; PANsav = savana areas within the Reserva Ecológica do Panga. Shown are the mean relative abundance of each genus in each area along the different sampling events (PANsav, N = 6; PESCAN, N = 5).

Supplementary Material: Table S3. Relative abundance of tree species sampled in a semideciduous seasonal forest (PANfor) and a deciduous seasonal forest affected by the construction of an artificial reservoir (DSFres). Relative abundance was calculated as the mean values of abundance among the four different sampling periods for each area.

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