



Vegetation composition and structure determine wild bee communities in a tropical dry forest

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Abstract

Understanding the factors that influence the composition and structure of bee communities in natural habitats is critical for conservation and restoration efforts, mainly in disturbed ecosystems that are widely used for agricultural crop production, such as tropical dry forests (TDF). The aim of this study was to evaluate the effects of tree species composition and vegetation structure on the composition, abundance and species richness of eusocial and non-eusocial wild bee assemblages. Bees (19,909 individuals of 96 species) were collected in fifteen plots in different secondary succession stages in a TDF in the state of Minas Gerais, Brazil. We found a positive relationship between tree community similarity and bee community similarity, for both eusocial and non-eusocial bees. Average tree height positively affected the abundance and species richness of eusocial bees, while the abundance of non-eusocial bees was negatively affected by tree species richness. Similar tree species composition and vegetation structure between plots at the same stage of secondary succession probably determined more similar bee communities than dissimilar tree communities. Most eusocial bee species are dependent on cavities in large trees to house their colonies, while most non-eusocial bees probably prefer open habitats because they provide a greater density and diversity of floral resources, and suitable areas for ground-nesting species. Since eusocial bees represented 94% of the individuals sampled, the conservation and restoration of mature forests is of primary importance in order to increase eusocial bee diversity, and the maintenance of these areas in the vicinity of agricultural systems is crucial to increase the ecosystem service of pollination.

Keywords Pollinators · Plant–pollinator interactions · Resource availability · Conservation · Restoration

Introduction

Bees are the most important pollinators of several human food crops (Klein et al. 2007). The recent population decline of managed honey bees (*Apis mellifera* Linnaeus, 1758) in

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many parts of the world has raised great concern worldwide (Ashworth et al. 2009; Ellis et al. 2010; Neumann and Carreck 2010; Potts et al. 2010a, b; Novais et al. 2016). This fact in turn increases the importance of wild pollinating bees providing an insurance against honey bee decline (Winfree et al. 2007). Many species of wild bees have already been demonstrated to be important pollinators of a variety of food crops (Klein et al. 2007; Giannini et al. 2015).

Keeping the quality of the surrounding landscape and local management practices such as diversified and organic fields are proposed as main drivers favoring wild bee assemblages in agroecosystems (Holzschuh et al. 2008; Kennedy et al. 2013; Pires et al. 2014). At the landscape scale, natural areas surrounding farms may provide essential floral resources and nesting sites to sustain wild bee populations (Williams and Kremen 2007). At a local scale, greater bee species richness and abundance in organic fields was mainly attributed to the enhancement of the availability of floral resources (Holzschuh et al. 2008; Tuck et al. 2014; Garibaldi et al. 2014). However, recent studies evaluating the effectiveness of pollinator-friendly practices in crop fields have demonstrated contrasting results (Garibaldi et al. 2016; Hardman et al. 2016; Hipólito et al. 2016), while some diversification methods are not sufficient to promote pollinator populations (Wood et al. 2015; Sardíñas and Kremen 2015). Therefore, understanding how vegetation characteristics in natural ecosystems affect wild bee communities is of primary importance for the development of effective management practices, mainly in disturbed ecosystems that are widely used for agricultural crop production, such as tropical dry forests (TDFs; Quesada et al. 2009).

In the Neotropics, TDFs are highly endangered by deforestation and the development of anthropogenic activities, such as agriculture and cattle breeding (Sánchez-Azofeifa et al. 2005; Miles et al. 2006). After soil depletion, agricultural fields and pasturelands are abandoned, allowing dry forest regeneration, and consequently, TDF landscapes are often a mosaic of remnants in a range of successional stages depending on the duration of the recovery time (Madeira et al. 2009; Quesada et al. 2009). In addition to changes in the plant species composition as the forest regeneration progresses, there is a general tendency to increase vegetation structure as secondary succession advances (e.g., height, stem density, woody species richness and abundance; Guariguata and Ostertag 2001; Kalacska et al. 2004; Madeira et al. 2009; Quesada et al. 2009). Some studies have addressed how these changes in vegetation throughout the secondary succession in TDFs affect the distribution patterns of different insect groups, such as ants, beetles, butterflies and bees (Neves et al. 2010a, b; Neves et al. 2014; Macedo-Reis et al. 2016; Sousa-Souto et al. 2016; Ramos-Fabiel et al. 2019). However, it is difficult to separate the effects of vegetation composition and structure on insect communities

along a successional gradient when both parameters vary in parallel in the compared areas.

Previous studies have found that vegetation composition is a major mechanism affecting wild bee community composition (Schaffers et al. 2008; Sydenham et al. 2016; Wu et al. 2018). Bee communities are expected to be more similar between areas that share a greater number of plant species (Sydenham et al. 2016). Regarding vegetation structure, wild bee responses might differ depending on bee social organization (i.e., eusocial or non-eusocial; Williams et al. 2010; De Palma et al. 2015). Eusocial bees depend on large cavities in living trees and dead logs for nesting, which are more abundant in old forests, whereas non-eusocial bees are considered to be more attracted to grassland-like habitats, mainly due to a greater availability and diversity of floral resources (Eltz et al. 2003; Taki et al. 2013; Sydenham et al. 2014; Ramos-Fabiel et al. 2019). Although eusocial bees should be also positively affected by a greater availability and diversity of floral resources in grassland-like habitats, a greater abundance of eusocial bees is expected to be found in natural forests due to nest site limitations in open areas (Ricketts et al. 2008; Winfree et al. 2009; Williams et al. 2010; Taki et al. 2013).

In this study we referred to different secondary succession stages in a Brazilian TDF to investigate the effects of tree species composition and vegetation structure (tree species richness, abundance and height) on eusocial and non-eusocial wild bee communities. We tested two hypotheses: (1) Particular plant communities are pollinated by specific wild bee species. We predicted that tree communities with similar species would have similar eusocial and non-eusocial wild bee communities. (2) Vegetation structure differently determines eusocial and non-eusocial wild bee communities, with eusocial bee populations being favored in old-growth forest areas, while non-eusocial bee populations are favored in open areas. We predicted that an increase of vegetation structure (tree species richness, abundance and height) would positively affect the species richness and abundance of eusocial bees, but negatively affect non-eusocial bees.

Material and methods

Study area and sampling design

The study was conducted in tropical dry forests in two protected areas (PA) in northern Minas Gerais state, Brazil: the Lagoa do Cajueiro State Park (LCSP; 14° 55' 17" S, 43° 56' 07" W) and the Mata Seca State Park (MSSP; 14° 50' 58" S; 44°00' 28" W). LCSP is located in the municipality of Matias Cardoso, with a total area of 20,500 ha, while the MSSP is located in the municipality of Manga, with a total area of 15,466 ha. The main economic activities in the

areas before protection were cattle breeding and bean and corn crop production. Both parks reach the banks of the São Francisco River (Fig. 1). The climate in the region consists of rainy summers and dry winters (Peel et al. 2007). The dry season extends from May to October and 90–95% of the tree species shed their leaves during it. The annual average temperature is 24.4 °C and the annual average precipitation is 818 mm (Pezzini et al. 2014).

We selected five sites at different stages of secondary succession based on the age of abandonment and on vegetation characteristics. Two successional stages (sites) could be distinguished in MSSP: early regeneration (13 years after abandonment), characterized by sparse patches of woody vegetation, shrubs, herbs and grasses with a single stratum of tree crowns composing a very open canopy up to 7 m (Table 1; Fig. 2a); and (2) late

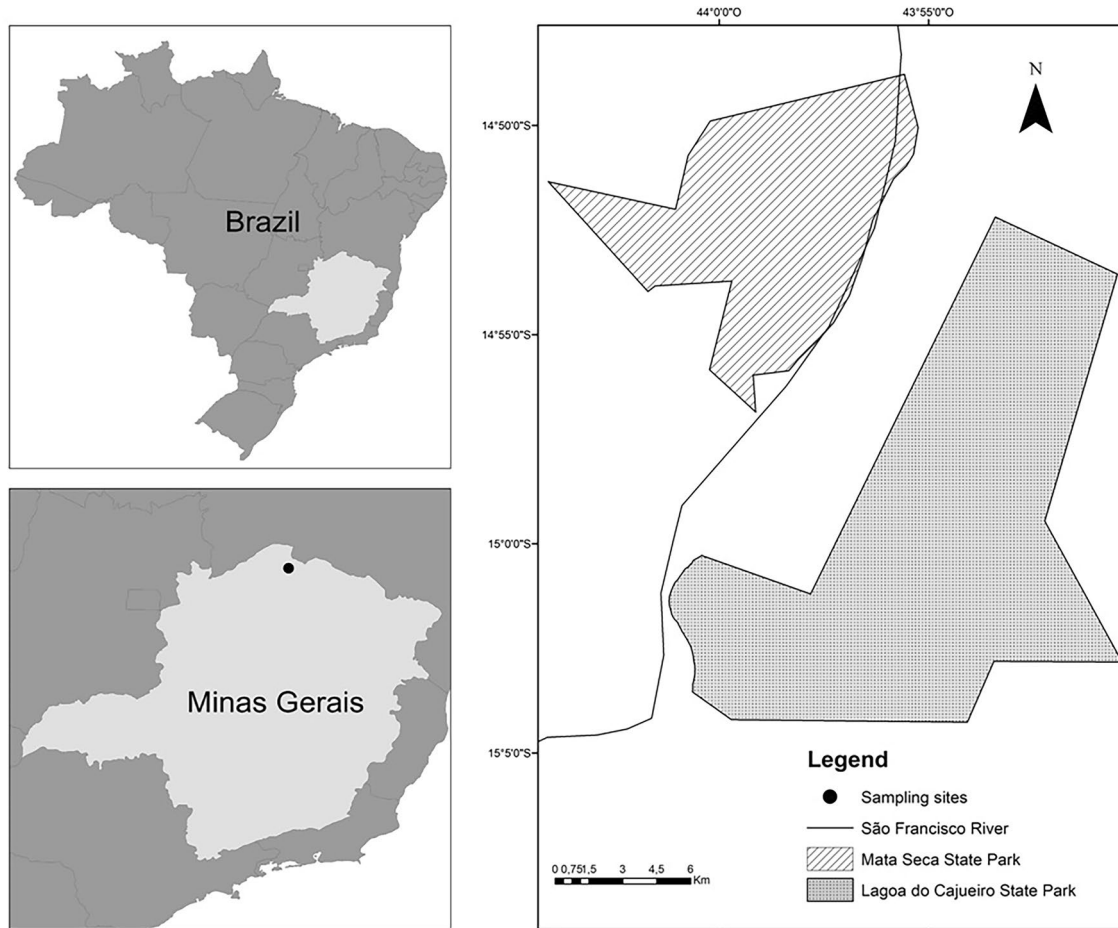


Fig. 1 Mata Seca and Lagoa do Cajueiro State Parks, where the sampling sites were located in northern Minas Gerais state, Brazil

Table 1 Age (at sampling time) and structural characteristics of the five sampling sites (mean of three plots \pm SD) located in the Mata Seca and Lagoa do Cajueiro State Parks, in northern Minas Gerais state, Brazil

Sites	Age	Tree species richness	Tree abundance (DBH > 5 cm)	Tree abundance (DBH > 10 cm)	Tree abundance (DBH > 20 cm)	Height (m)
MSSP1	13	13.7 \pm 0.6	78.3 \pm 27.0	13 \pm 2.6	0.0 \pm 0.0	7.0 \pm 0.2
MSSP2	Over 55	17.7 \pm 2.1	92 \pm 18.7	62 \pm 13.2	17.7 \pm 1.5	10.6 \pm 0.9
LCSP1	15	9 \pm 5.6	35.7 \pm 8.7	4.3 \pm 4.0	1 \pm 1.7	5 \pm 2.3
LCSP2	30	27.7 \pm 3.2	107.3 \pm 27.4	27.7 \pm 10.0	5 \pm 5.2	7.2 \pm 1.7
LCSP3	Over 60	22.3 \pm 2.5	110.7 \pm 7.6	47.7 \pm 10.2	11 \pm 3.0	7.9 \pm 3.5

Tree species richness is given as the average number of tree species with diameter at breast height (DBH) greater than 5 cm; tree abundance as the average number of tree individuals with DBH greater than 5, 10 and 20 cm, and height is the average tree height

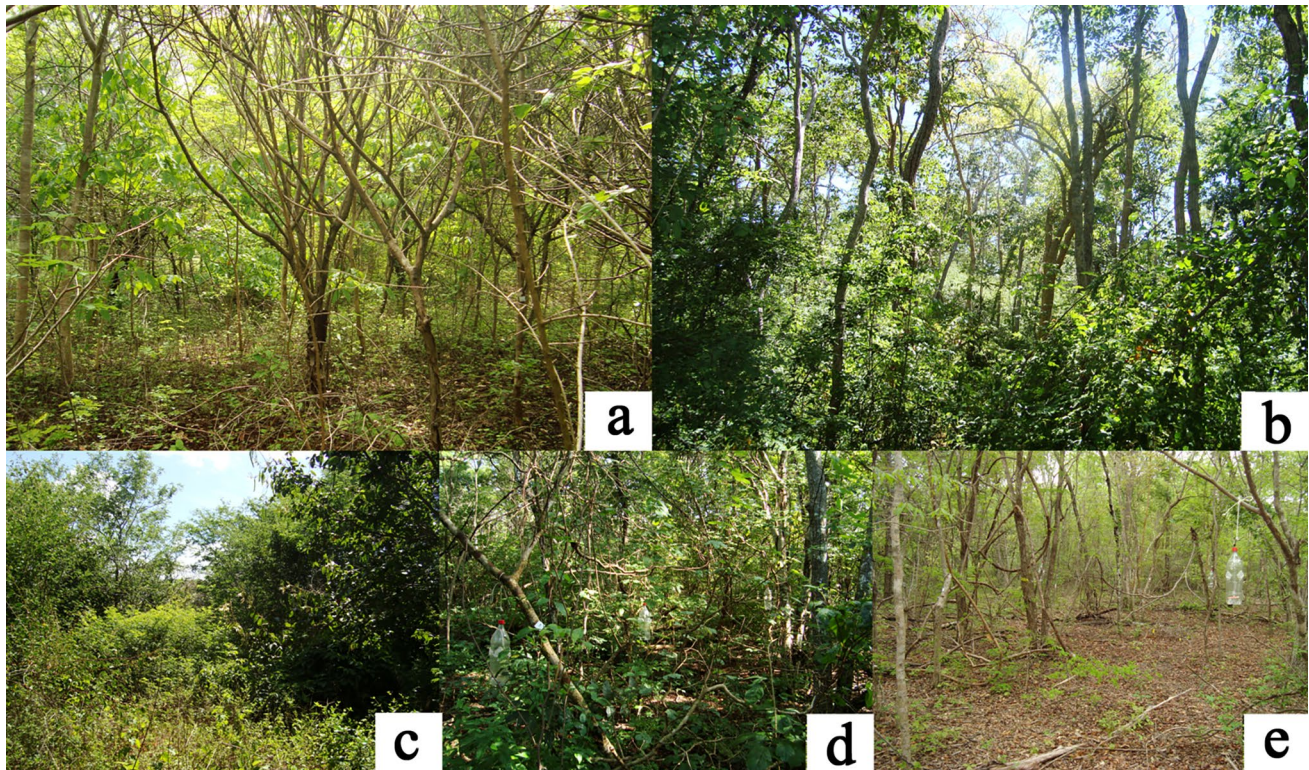


Fig. 2 Five sampling sites in tropical dry forests with different successional ages and structural characteristics in the Mata Seca (a, b) and Lagoa do Cajueiro State Parks (c–e), located in northern Minas Gerais, Brazil. Photos by A. S. Alvarenga

regeneration (over 55 years), characterized by two strata, the first stratum composed by taller trees which form a closed canopy 14–16 m high, and the second stratum formed by a sparse understory with a low density of understory trees (Table 1; Fig. 2b). Three successional stages could be distinguished in LCSP: early regeneration (15 years), with high dominance of shrub-like species and scattered trees approximately 5 m high with a discontinuous canopy (Table 1; Fig. 2c); intermediate (30 years), with two vertical strata, one composed of trees 7–8 m high and a second with a dense understory with many young trees and abundant lianas (Table 1; Fig. 2d); and late (over 60 years), also composed of two vertical strata, being the first with large trees forming a continuous canopy 11–12 m high and some emergent trees up to 15 m high, and the second with reduced light penetration and low density of understory species (Table 1; Fig. 2e). Three plots (0.1 ha, 20 × 50 m) were determined per site, totaling six in the MSSP and nine sampling plots in the LCSP. Plots in the same regeneration stage were placed at least 0.1 km apart. Sampling was carried out at different stages of regeneration in order to cover a broad amplitude of the variables employed to characterize vegetation structure (Yang et al. 2015).

Bee sampling

Bees were collected during two periods in 2012, at the end (February) and beginning (November) of the wet season. In order to collect a wide range of bee species, four different methods were used simultaneously in each plot, between 08:00–14:00: (1) Active collection performed by two collectors with entomological nets in each plot; collectors roamed a single plot per day between the verification intervals of the other methodologies used; (2) Scent traps manufactured with 2-l PET bottles, based on the model presented by Campos et al. (1989). Four sets of six bottles were placed in each plot. Each of the six traps contained one of the following aromatic substances used to attract *Euglossina* males: beta-ionone, methyl cinnamate, eucalyptol, eugenol, methyl salicylate and vanillin. Two sets of traps were installed on opposite sides of each plot, one in the understory and the other in the canopy (with height ranging between 10 and 20 m) in order to cover both forest strata. The traps were checked every hour for bee collection and, when necessary, for essence replenishment; (3) Solution of honey diluted (one part of honey to three parts of water) was used in two points on opposite sides of the plot. At each point, the understory vegetation was sprayed at three sites at least 2 m apart. These points were also inspected every hour. Bees attracted

by the sprayed solution were collected with entomological nets during 1 min. Every two hours the honey solution was again sprayed on each sample point; (4) Eighteen pan traps based on the model presented by Leong and Thorp (1999) were divided into three sets of six traps of the following colors: (yellow, white and blue) and placed in the center of each plot. Pan traps of the same color were grouped together at a distance of 50 cm, and attached to iron rods approximately 1.25 m high. These traps consisted of plastic dishes (volume = 160 ml; diameter = 9.6 cm) painted with luminous Spray Colorgin (UV) paint. All pan traps were filled with 80 ml of water and detergent in the proportion of 2 l of water to 50 ml of detergent. These traps were checked at the end of each sampling day, when bees were collected and stored in 70% alcohol.

All sampled bees were identified to genus and subgenus levels based on identification key by Silveira et al. (2002). Identification to species level was performed with the aid of taxonomic keys, by comparison with identified species in the insect collections from Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais (CCT-UFMG) in Belo Horizonte, Minas Gerais, Brazil, where all specimens were deposited. Some specimens were identified by specialists (see “Acknowledgments” section).

Vegetation composition and structure

All trees with a diameter at breast height (DBH) of the main trunk greater than 5 cm in each plot were counted, identified (see “Acknowledgments” section) and their height was estimated (see Table 1 for the mean of these vegetation structure characteristics by sampling site). Tree species richness, abundance and average height per plot were calculated.

Statistical analyses

Bees were divided into two groups for analyses: eusocial bees (Apina and Meliponina subtribe), which present a high level of social complexity in their colonies, and non-eusocial bees. A species accumulation curve was used to compare cumulative species richness and to evaluate sampling sufficiency for both eusocial and non-eusocial bees. The number of species was plotted as a function of the number of sampled plots, with 1000 randomizations performed—which subsamples the data without replacement to generate a confidence interval. A non-parametric estimator (Chao I) was used to estimate total species richness for eusocial and non-eusocial bees.

Tree and bee (eusocial and non-eusocial) species compositions were compared between plots using cluster analysis (the UPGMA algorithm with Bray–Curtis index). Mantel test was used to evaluate if there was an association between the similarities of tree community composition and bee

community composition among sampling plots. First, we generated independent matrices of similarity for trees and bees (eusocial and non-eusocial) between pairs of plots using the Bray–Curtis index. In this approach, species composition of each plot was compared pairwise with the other plots, giving as output a matrix of similarity with all possible comparisons between plots. Next, the Mantel Test was used to measure the degree of association between the similarity tree matrix and the matrices of similarity of eusocial and non-eusocial bees using Pearson’s correlation coefficient.

Generalized linear models were used to test the effects of vegetation structure on bee species richness and abundance per plot. Tree species richness, abundance and average height were used as explanatory variables, while species richness and abundance of eusocial and non-eusocial bees were used as response variables. We applied a ‘Poisson’ distribution of errors to the models, and overdispersion was adjusted with a ‘Negative Binomial’ distribution of errors when needed. The minimum adequate model (MAM) was obtained by extracting non-significant terms ($p > 0.05$) from the full model (Crawley 2013). The explanation (R^2) of each of these models was divided by the deviance of a null model using the following formula: Explained deviance = deviance H_1 /deviance H_0 . All statistical analyses were conducted with the R software (R Core Team 2018).

Results

We sampled a total of 19,909 bees, belonging to 96 species (some species were morphospecies) of 39 genera. Twenty-two species (18,749 individuals) belonged to eusocial group, while 74 species (1160) belonged to non-eusocial group. *Paratrigona incerta* Camargo & Moure, 1994, *Plebeia flavocincta* (Cockerell, 1912) and *Pl. droryana* (Friese, 1900) were the most abundant species, representing together > 55% of the eusocial specimens (Table S1). *Euglossa* (*Euglossa*) *cordata* (Linnaeus, 1758), *Exomalopsis* (*Exomalopsis*) *analis* Spinola, 1853, *Ceratina* (*Crewella*) sp.3 and *Ceratina* (*Crewella*) sp.1 were the most abundant species of the non-eusocial group, representing together > 47% of the non-eusocial specimens (Table S1). Most eusocial bees were collected attracted by honey solution (83.1%), followed by active collection (10%), pan traps (6.6%) and scent traps (0.3%), while 45% of the non-eusocial bees were collected attracted by pan traps, 30.3% by scent traps, 19.7% by honey solution and 4.4% by active collection (Table S2).

Considering the final slope of the species accumulation curves, the eusocial-bee cumulative species curve tended to stabilize, but not the non-eusocial bee cumulative curve (Fig. 3). However, according to the Chao I estimator, bees sampling sufficiency was 88% for eusocial bees (observed richness: 23; estimated richness: 26.2) and 86%

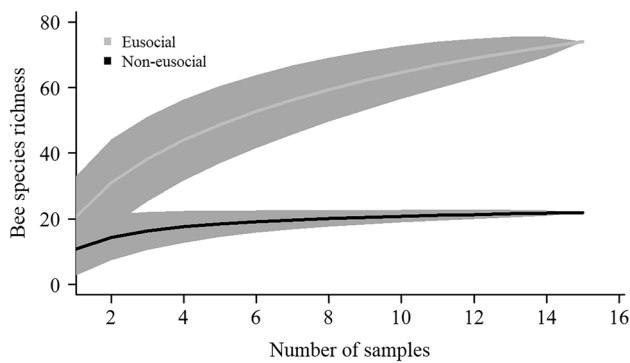


Fig. 3 Sample-based species accumulation curves of the total number of eusocial bees and non-eusocial bees sampled in tropical dry forests in northern Minas Gerais state, Brazil

for non-eusocial bees (observed richness: 77; estimated richness: 89.4), suggesting that a majority of local species were represented in analyses for both groups.

The cluster analysis indicated a greater similarity of tree species between plots at the same park, but within parks the plots at the same successional stage are more similar to each other compared to plots at a different successional stage (Fig. 4a). Eusocial bee species were more similar between plots at the same successional stage regardless of which park, but within a specific successional stage eusocial bee species are more similar in plots belonging to a same park (Fig. 4b). The pattern for non-eusocial bees was not as clear as it was for the eusocial bees; usually they were more similar between plots at the same successional stage regardless of the park, but sometimes more similar between plots within a same park regardless of the successional stage (Fig. 4c). Correlations between tree similarity matrix and similarity matrices for eusocial and non-eusocial bees were positively significant according to the Mantel test (Pearson's product moment correlation, Fig. 5, $p < 0.001$, $r = 0.62$ and $p = 0.02$, $r = 0.37$).

We found no effects of tree species richness and abundance on eusocial bee community, but average tree height positively affected the abundance and species richness of eusocial bees (Table 2, Fig. 6a, b). We detected no effects of vegetation structure on non-eusocial bee species richness, but tree species richness negatively affected the abundance of non-eusocial bees (Table 2, Fig. 7). Comparing the abundance of the fifteen most abundant eusocial and non-eusocial bee species between plots in early and late successional stages (successional stages with 6 replicates each), we found that thirteen eusocial bee species were more abundant in the late successional stage (Fig. 8a), while for non-eusocial bee species eight were more abundant in the early successional stage (Fig. 8b).

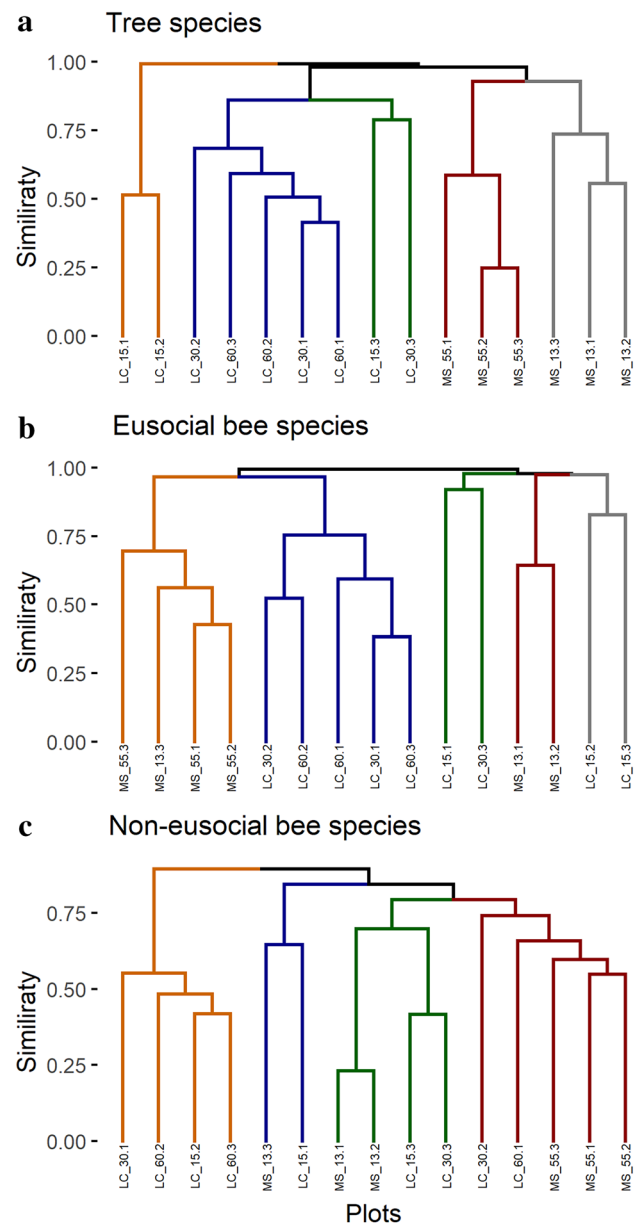


Fig. 4 Cluster analyses of similarity (Bray-Curtis index) by tree species (a), eusocial bee species (b) and non-eusocial bee species (c) sampled in tropical dry forests in Brazil (LC Lagoa do Cajueiro State Park, MS Mata Seca State Park; 13, 15, 30, 55 and 60 represent the age of abandonment of the plot; 1, 2 and 3 represent replicates of plots at a same age of abandonment)

Discussion

Our study demonstrates that tree species composition and vegetation structure are important drivers to wild bee communities in tropical dry forests. Variations in tree community composition were mainly determined by the parks themselves and, secondarily, by the stage of secondary succession. In contrast, the eusocial bee composition was more similar between sites at a same stage of secondary

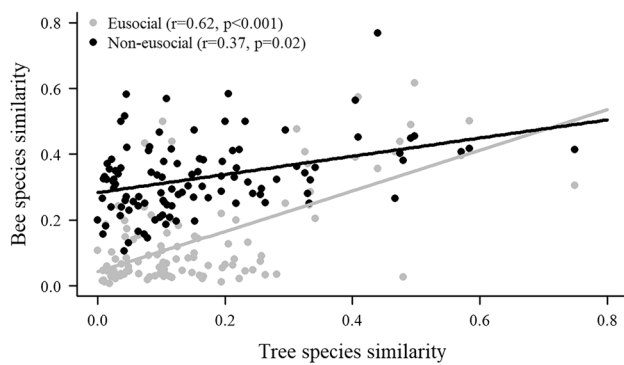


Fig. 5 Relationship between tree-similarity and eusocial bee similarity and non-eusocial bee similarity sampled in tropical dry forests in northern Minas Gerais state, Brazil. Each point represents the similarity of tree species between two sampling plots and the respective similarity of bee species in this pair of plots

succession regardless of the park, suggesting that vegetation structure is a more important factor structuring eusocial bee composition than tree species composition. However, eusocial bee species composition was more similar between plots at a same stage of secondary succession (e.g. late stage of succession) belonging to a same park, which presents a more similar tree composition with each other compared to plots of the other park. Non-eusocial bee species composition also seems to be more affected by vegetation structure than by tree species composition, since plots belonging to a same stage of secondary succession generally presented smaller differences in bee species composition between each other than plots at different stages of secondary succession within a same park.

Considering each park separately, our results corroborated studies that demonstrated that plots at a same stage of secondary succession share more vegetation characteristics (plant species composition and vegetation structure) with each other than to plots at different stages of secondary

succession (Guariguata and Ostertag 2001; Kalacska et al. 2004; Madeira et al. 2009), which probably determined the differences in the species composition of eusocial and non-social bee species between stages within each park. This pattern was more evident for eusocial bee species composition, which presented a stronger positive correlation with tree species composition compared with non-social bee composition. Studies conducted in TDFs for other insects, such as dung beetles and ants, had also demonstrated changes in species composition between early successional plots compared with plots in later succession (Neves et al. 2010a, b; Sousa-Souto et al. 2016). Moreover, a study carried out in a Norwegian boreal forest demonstrated that areas under management practices sharing similar plant-species composition had more similar solitary bee communities compared to native forests (Sydenham et al. 2016).

In our study, eusocial bee species richness and abundance were not affected by variations in tree species richness and abundance but were positively affected by average tree height. In our study sites, tallest plants are present in late successional plots, where a greater number of individuals from most eusocial bee species were collected compared with early successional plots. Among the fifteen most abundant eusocial species recorded, fourteen belonged to the Meliponina tribe, of which thirteen were more abundant in the late successional stage. This result is consistent with reports showing that species of this tribe are more abundant and diverse in old-growth forests (Samejima et al. 2004; Taki et al. 2013; Ramos-Fabiel et al. 2019). The other abundant eusocial species recorded was *A. mellifera*, which was particularly abundant at early successional sites. This result was similar to a study conducted along a successional gradient in a tropical dry forest in Mexico, where differently from the four Meliponina species mostly collected in the late successional stage, *A. mellifera* was more abundant at young and intermediate successional sites (Ramos-Fabiel et al. 2019). Taki et al. (2013) demonstrated that eusocial

Table 2 Results of generalized linear models showing the effects of habitat structure (tree species richness, abundance and height) on the abundance and species richness of wild bees (eusocial and non-eusocial) sampled in tropical dry forests in northern Minas Gerais state, Brazil

Response variable	Explanatory variable	Error distribution	Deviance	p
Eusocial bee abundace	Tree species richness	Negative Binomial	0.52	0.47
	Tree abundance		1.08	0.3
	Tree height		4.86	0.03
Eusocial bee species richness	Tree species richness	Poisson	0.36	0.55
	Tree abundance		2.16	0.14
	Tree height		9.59	<0.01
Non-eusocial bee abundase	Tree species richness	Negative Binomial	6.49	0.01
	Tree abundance		0.87	0.35
	Tree height		0.02	0.88
Non-eusocial bee species richness	Tree species richness	Negative Binomial	1.94	0.16
	Tree abundance		0.40	0.53
	Tree height		1.74	0.19

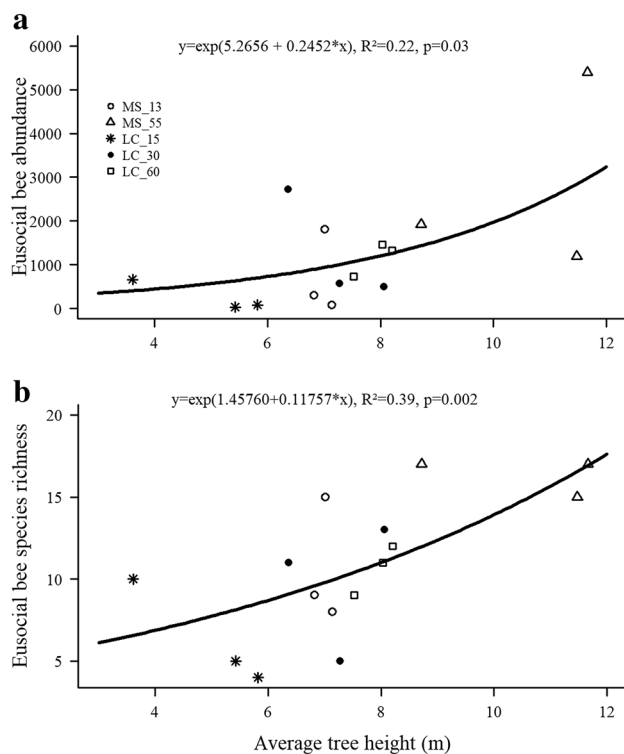


Fig. 6 Relationship between average tree height and abundance (a) and species richness (b) of eusocial bees sampled in tropical dry forests in Brazil (LC Lagoa do Cajueiro State Park, MS Mata Seca State Park; 13, 15, 30, 55 and 60 represent the age of abandonment of the plot)

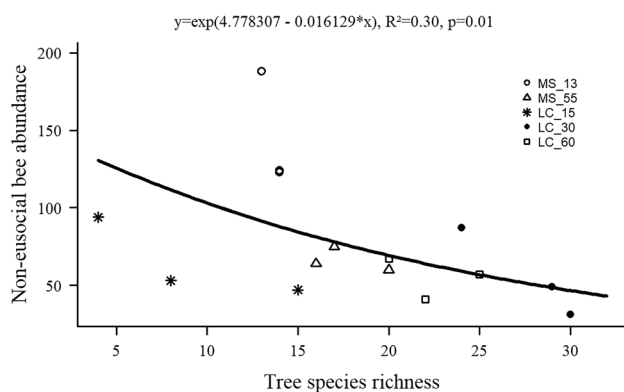


Fig. 7 Relationship between tree species richness and abundance of non-eusocial bees sampled in tropical dry forests in Brazil (LC Lagoa do Cajueiro State Park, MS Mata Seca State Park; 13, 15, 30, 55 and 60 represent the age of abandonment of the plot)

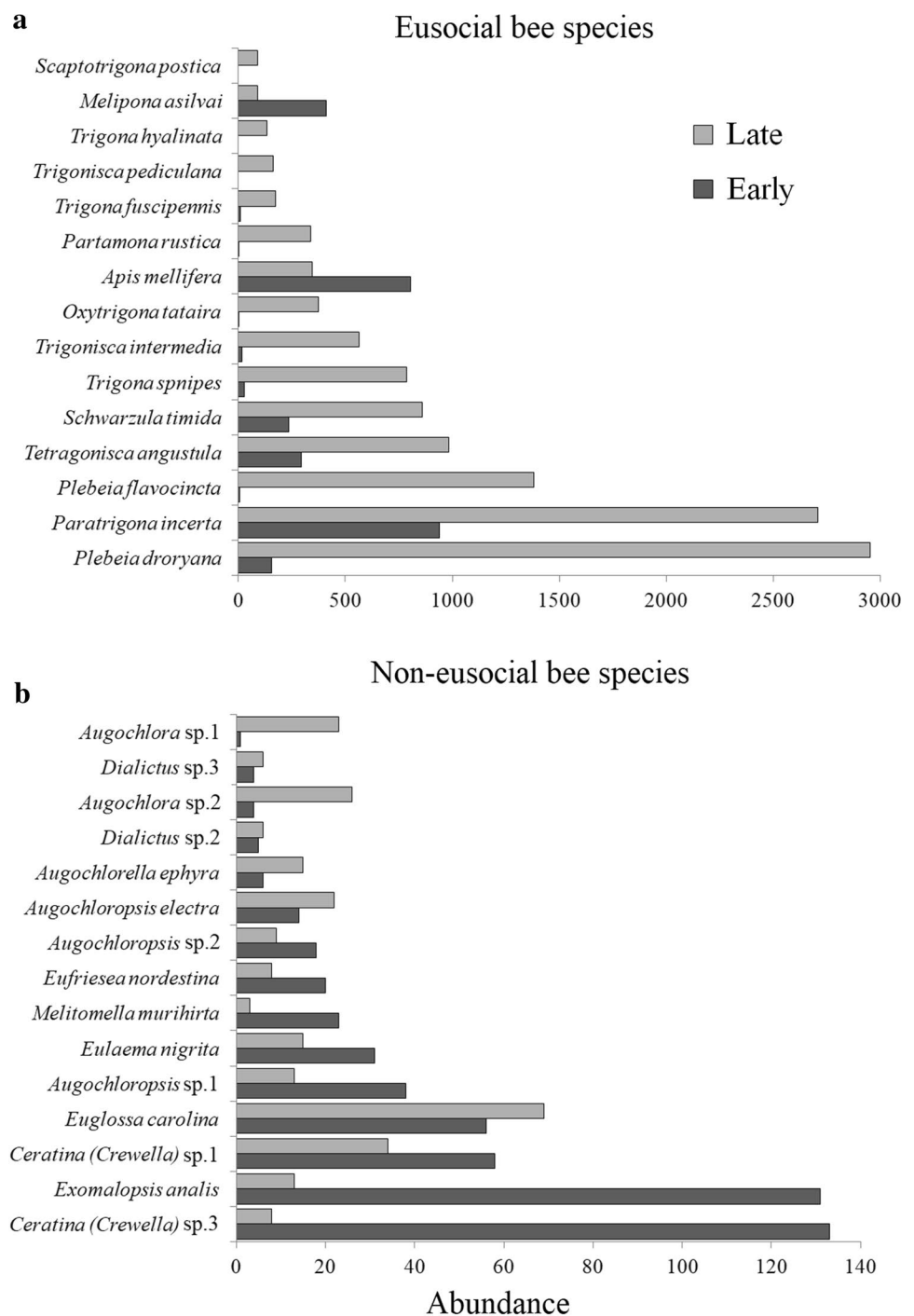
bees were positively affected by forest succession age in a temperate deciduous forest in Japan. They suggested that nesting resources for eusocial bees in naturally regenerated forests might be more widely available at later than at early successional areas. The results above are consistent with nesting tendencies of native eusocial bees, which are more

likely to build nests in large trees that are able to house bee colonies in their cavities (Eltz et al. 2003; Samejima et al. 2004; Michener 2007).

The abundance of non-eusocial bees was greater in plots with low tree species richness, specifically in plots at early stage of succession of the Mata Seca State Park. This pattern was mainly determined by two species, *Ceratina* (*Crewella*) sp.3 and *Ex. analis*, which were ten and sixteen times greater in the early stage than in the late. Also in contrast to that found for eusocial bee species, eight of the fifteen most abundant non-eusocial bee species were more abundant in the early successional stage. This result is in agreement with the findings of Taki et al. (2013) for a temperate deciduous forest in Japan (Taki et al. 2013), where the abundance and species richness of non-eusocial bees were higher in the early successional stage. Similarly, a study conducted in another tropical dry forest of Mexico found that non-eusocial bees were mostly associated with young and intermediate fallows (Ramos-Fabiel et al. 2019). The preference of non-eusocial bees for early successional plots may be driven by an increase in floral resources, as direct sunlight enhance the density and number of flowering plant species, thus attracting more bee individuals (Sydenham et al. 2014). Although eusocial bees should be also positively affected by a greater availability and diversity of floral resources in open habitats, reviews that compared the effects of natural habitat isolation and agricultural land use intensification on eusocial vs. non-eusocial bees have demonstrated a stronger negative response of eusocial bees to these anthropogenic disturbances (Ricketts et al. 2008; Winfree et al. 2009; Williams et al. 2010). This pattern has been attributed to limited nesting site availability associated to large trees, which usually are not present when natural habitats are converted to agricultural systems, limiting the forage range of eusocial bee species.

In addition, most non-eusocial bees do not depend on large trees found mainly in late successional forests as nesting sites, such as the two most abundant non-eusocial bee species found in the early successional plots, which belong to *Ceratina* and *Exomalopsis* genera. Bee species of the *Ceratina* genus are known as small carpenter bees because they construct their nest mainly in dead branches or twigs of different plants by chewing out the pith (Rehan et al. 2009; Rehan and Richards 2010; Udayakumar and Shivalingaswamy 2019). Ali et al. (2016) reported the small carpenter bee *Ceratina* (*Pithitis*) *smaragdula* (Fabricius, 1787) preferentially nesting in wooden stalks of Ravenna grass (*Saccharum ravennae* L.; Poales: Poaceae). *Exomalopsis* are ground-nesting species and construct their nests mainly in open areas with sandy soil (Rozen 2011; Aranda and Graciolli 2013; Velez-Ruiz and Smith-Pardo 2013). In addition, other genera of the other most abundant non-social bee species collected have

Fig. 8 Number of individuals of the fifteen most abundant eusocial (a) and non-eusocial (b) bee species sampled in two successional stages (early and late) in tropical dry forests in northern Minas Gerais state, Brazil



been reported preferentially nesting on the ground, such as for *Augochlorella* (Ordway 1966; Mueller 1996) and *Augochloropsis* (Pietsch et al. 2016; Gibbs 2017) genera. Therefore, in addition to having a greater density and diversity of floral resources, open habitats could provide nest requirements for many non-eusocial bee species which nest on the ground in sunny, well-drained, either bare or sparsely vegetated areas (Potts et al. 2005; Williams et al. 2010; Sydenham et al. 2014).

In this study we were able to disentangle the effects of tree species composition and vegetation structure on wild bee communities. Vegetation structure was the major factor determining wild bee community arrangement. The vast majority of the most abundant eusocial bee species was found in sites in advanced stages of secondary succession. In addition, species richness and abundance of eusocial bees were positively affected by the height of the vegetation, probably due to their preference for large trees

as nesting sites. In contrast, most non-eusocial bee species were found associated with early successional plots, probably attracted by a greater availability and diversity of floral resources in open habitats, and better nest requirements for ground-nesting species. These results have important implications for the conservation of wild bee populations and for the development of effective strategies for the improvement of the ecosystem service of pollination in agricultural systems.

In Brazil, TDFs are currently under strong threat by anthropogenic pressures and less than 4% of them are protected (Sevilha et al. 2004; Dupin et al. 2018). In this context, the fauna specialized in resources and conditions provided by old-growth forests (e.g. eusocial bees) can be considered the most vulnerable groups in TDFs. The conservation and restoration of mature forests is of primary importance to enhance eusocial bee diversity, while non-social bee species seem to be more resistant to the simplification of vegetation structure. In our study, eusocial bees represented 94% of the individuals sampled, and therefore, the maintenance of old-growth forests in the vicinity of agricultural systems is needed to increase the ecosystem service of pollination. In addition to benefit crop production, animal pollinators, mainly bees, are responsible for the sexual reproduction of more than 80% of the terrestrial vascular plants (Buchmann and Nabham 1996). Therefore, the conservation of areas capable of supporting large populations of eusocial bees is essential for the maintenance of plant diversity in terms of species number, genetic variation and richness of functional groups (Biesmeijer et al. 2006; Diaz et al. 2006; Fontaine et al. 2006), thus finally contributing to ecosystem services associated to plant diversity (see Mittlelbach et al. 2001; Diaz et al. 2006).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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