




Natural habitat cover and fragmentation per se influence orchid-bee species richness in agricultural landscapes in the Brazilian Cerrado

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Abstract – Habitat loss and fragmentation in the human-modified landscape affect bee assemblages by reducing the available natural resources. The life history features and adaptations of bees to environmental conditions affect how they perceive and interact with landscape structure. Therefore, it is crucial to quantify the magnitude of the effects of the landscape structure on this group at multiscale. We address the relative contribution of landscape structure in explaining the abundance of orchid bees, richness, and diversity in landscapes of Brazilian Cerrado. We mapped the surrounding landscape around 18 focal patches and sampled male orchid bees attracted by chemical baits. We used VIF and generalized linear models (GLM) to evaluate the effects of landscape structure (composition and configuration) at different spatial scales. We sampled 658 euglossine bees from five genera and 12 species. The savanna cover, forest cover, and fragmentation per se (i.e., the number of patches) were the best predictors of the richness of euglossine bees. The abundance of bees was explained by the savanna cover. The increase in natural habitat area and the reduction in landscape fragmentation favoring the assemblages of orchid bees are supported by our results. Savanna cover also modulates the abundance of euglossine bees, confirming that the habitat amount is essential for maintaining the populations of these bees. Our results reinforce the importance of habitat loss and fragmentation effects on the richness, abundance, and composition of euglossine bees, particularly in the naturally heterogeneous landscapes.

bee biodiversity / habitat loss / landscape diversity / multiscale effects / pollinators

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1. INTRODUCTION

Landscape changes caused by natural area conversion for human activities jeopardize biodiversity and severely impact ecosystem structure and stability (Fahrig 2003). The decline of wild populations (Brow and Paxton 2009) and dispersal of individuals and migration rates may be caused by agricultural activities and other human-induced changes in land cover via habitat loss and degradation. In such a scenario, a decrease in genetic diversity, along with a loss of ecosystem services, may also occur (Potts et al. 2016). Pollination is one of the vital ecosystem services affected by habitat loss in the Anthropocene (Dicks et al. 2021). The global decline in bee species richness and abundance has been of significant concern (Brown and Paxton 2009; Goulson et al. 2015) because of food security (Klein et al. 2007; FAO 2019) and the overall decline in plant diversity (Potts et al. 2010, 2016; Lundgren et al. 2016). Insects, especially bees, are the primary pollinators of most crops and native plants and are essential for production in ~75% of all crops used for human food (Klein et al. 2007; Ollerton et al. 2011).

Reciprocally, bees rely entirely on flowering plants for food, and a higher plant species richness is correlated with a higher number of bee pollinator species (Ebeling et al. 2008; Kaluza et al. 2018). Worldwide, agricultural expansion and intensification lead to natural vegetation loss and fragmentation, causing global bee declines. Therefore, the amount of habitat and structure of landscapes have crucial roles in conserving these insects (e.g., Brown and Paxton 2009; Winfree et al. 2009; Goulson et al. 2015; Cameron and Sadd 2020). For instance, while habitat loss and fragmentation decrease bee richness and abundance due to the reduction in floral and nesting resources (Brosi et al. 2008, 2009; Viana et al. 2012; Potts et al. 2010, Coswosk et al. 2018), natural habitats can buffer the harmful effects of pesticides (Park et al. 2015), climate change (Giannini et al. 2017; Papanikolaou et al. 2017), toxic metals (Barbosa et al. 2021), and invasive alien species (Garibaldi et al. 2021) on bee communities. Agricultural landscape

heterogeneity and configuration may also increase the diversity of bees (e.g., Hass et al. 2018; Miljanic et al. 2019), providing different resources (Fahrig et al. 2011). However, in intensive farming, the abundance of bees may be reduced due to land use management and higher crop cover in the landscape (Hass et al. 2018). Additionally, the response of bees to anthropogenic disturbances may be related to life-history traits (Brosi et al. 2008; Williams et al. 2010). For instance, bee species nesting above the ground are more affected by habitat loss, isolation, and intensive farming than those nesting below the ground (Williams et al. 2010; Ferreira et al. 2015). Moreover, the response of bees to landscape features may be scale-dependent (Medeiros et al. 2019b), i.e., local and regional variation in landscape metrics may affect different components of community diversity and different taxonomic groups (Steffan-Dewenter et al. 2002; Ferreira et al. 2015; Montagnana et al. 2021). The importance of the α -diversity of pollinators (i.e., species richness and abundance) as a driver of ecosystem service delivery is well-demonstrated in various settings (e.g., pollination, pest control, water quality, disease control; Duarte et al. 2018). Therefore, a better understanding of how bee communities respond to landscape structure features at different scales is critical for reducing the anthropogenic disturbances' impacts on the diversity and ecosystem services provided by this group (Winfree et al. 2011; Viana et al. 2012; Duarte et al. 2018).

In Brazil, at least 144 bee species have been associated with the 23 most important crops, including the critical commodity soybean, and 56% of them are solitary bees (Giannini et al. 2020). Thus, the decline in bee diversity and abundance may have direct economic impacts in Brazil, estimated at ~4.86 to 14.56 billion dollars/year for the 29 major food crops, representing 6.46–19.36% of the Brazilian GDP (Novais et al. 2018). In the last decades, deforestation rates as high as 1% per year have been caused by agriculture and livestock expansion in the Brazilian Cerrado, leading to a loss of 50% of its original area (Sano et al. 2010; Alencar et al. 2020). The Brazilian Cerrado is naturally composed of a

vegetative mosaic of savanna-like formations and forest forms (Ribeiro and Walter 1998). The Brazilian Cerrado is the most biodiverse and threatened savanna globally (Silva and Bates 2002). Because of Cerrado degradation, plant species may be at higher extinction risk (Strassburg et al. 2017; Velazco et al. 2019), and the addition of habitat loss, pesticide use, and farming management may also threaten bee species (Potts et al. 2016).

Orchid bees (Apidae: Euglossini) pollinate hundreds of native and cultivated plant species (e.g., Dressler 1982; Roubik 1992; Giannini et al. 2015; Silveira et al. 2015). Many Euglossini species have a remarkable flying capacity and may travel long distances in continuous forests (Janzen 1971; Pokorny et al. 2015; Wikelski et al. 2010), but small-size species are forest dependent, rarely leaving forest fragments (Milet-Pinheiro and Schindwein 2005). Most studies investigating the influence of landscape structure on orchid bees have been carried out in the rainforest (e.g., Powell and Powell 1987; Tonhasca et al. 2002; Storck-Tonon et al. 2013, Storck-Tonon and Peres 2017; Rosa et al. 2015; Cândido et al. 2018). Only a handful of studies have been carried out in the Brazilian Cerrado (e.g., Silva and De Marco 2014; Moreira et al. 2017; Silva et al. 2017).

Here, we analyze the effects of landscape composition and configuration on the α -diversity of Euglossini communities in the Brazilian Cerrado. Our study comprises landscapes in intensive farming systems and a protected area,

and we assessed the landscape effects using a multiscale approach (Jackson and Fahrig 2015; Gestich et al. 2019). We expect that landscapes with higher habitat cover and heterogeneity to harbor higher α -diversity, i.e., abundance, species richness, and diversity of bees (see our predictions in Fig. 1). On the other hand, landscapes with higher agriculture and pasture cover, with fewer habitat patches and a higher patch shape index (PSI) (more irregular patches), have lower α -diversity.

2. MATERIAL AND METHODS

2.1. Study area and sampling sites

We carried out the study in the long-term ecological research (LTER) project, the COFA LTER project (Functional Connectivity in Agricultural Landscapes) in Central-Western Brazil (Fig. 2A), one of the most important agribusiness regions in the country. The landscape comprises a mosaic of agriculture, mainly soybean, corn, pasture, Cerrado savanna remnants, seasonally dry and riparian forests (Fig. 2B), and a protected area, the National Forest of Silvânia with 487.4 ha (Santos et al. 2021; Fig. 2B).

We mapped the land cover by visual digitalization and manual classification using high-resolution images freely available at the Geographic Information System QGIS (QGIS Development Team 2017) using the Open Layer Plugin at a scale of 1:5000 m. We mapped 11 land cover

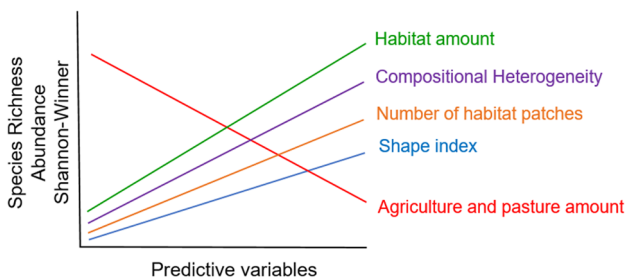


Figure 1. Expected effects of landscape composition and configuration on orchid bees (species richness, abundance, and diversity) in agricultural landscapes in the Brazilian Cerrado. The higher the line slopes, the greater the expected explanatory power of landscape metrics.

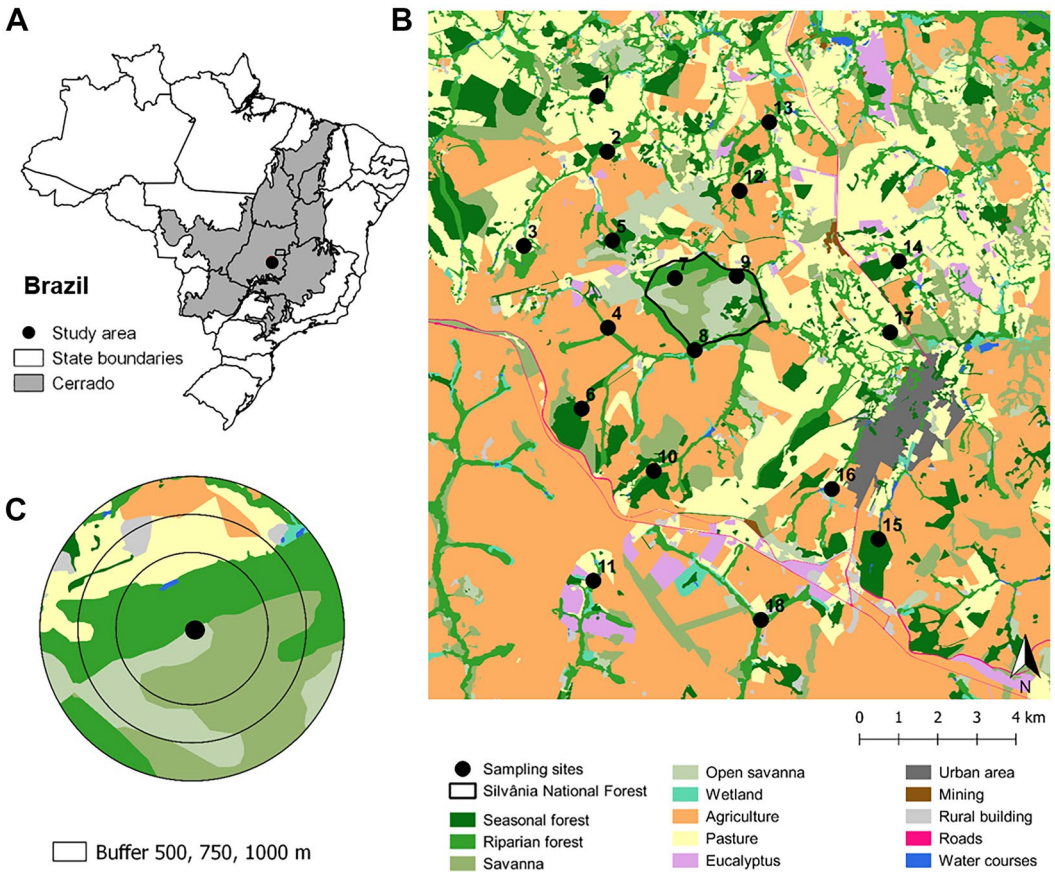


Figure 2. Spatial distribution of the 18 sampling sites of Euglossini bees. (A) The Brazilian Cerrado distribution (gray) depicting the study area (B) the COFA LTER study area with land cover composition and the 18 sampling sites (C) multiscale sampling design used to calculate the landscape metrics. Buffer radii sizes are 500, 750, and 1000 m. Land cover colors correspond to different categories according to the figure legends.

types (Fig. 2B): savanna, seasonally dry forest, riparian forest, wetlands, agriculture (soy/corn), pasture, urban areas, rural buildings, roads, train rails, and water. We performed field inspections to ensure high map accuracy. For landscape analyses, we merged similar land cover types due to their spatial distribution and the low number of some cover types in the landscape, such as riparian and seasonally dry forests (forest, hereafter), savanna and wetlands (savanna, hereafter), and urban areas, rural buildings, roads, and train rails (urban area, hereafter).

We selected 18 landscapes representing landscape composition and configuration gradients using a buffer size of 1000 m around the

sampling sites. Therefore, these landscapes varied their forest and savanna cover, compositional heterogeneity (i.e., Shannon diversity index), number of forest patches, and patch shape (see metric calculations below).

2.2. Bee community sampling

Within each of the 18 landscapes, we selected one site in a forest remnant (Fig. 2B, Table S1) to sample the orchid bee community. We installed six sampling stations 50 m apart from each other at each sampling site. Each sampling station comprised six scent traps installed 1.5 m above ground and 3 m apart (see details in Appendix

Figure S1). We built scent traps with 2-L plastic polyethylene terephthalate (PET) bottles, with three funnel inlets on their sides covered with sandpaper to increase friction and facilitate the entrance of the bees. Inside the base of the bottles, we soaked a cotton swab with chemical baits and soapy water. We used six aromatic essences: eucalyptol, methyl salicylate, vanillin, eugenol, methyl cinnamate, and benzyl acetate. At each sampling site, traps remained in the field for 24 h in two field surveys during the rainy season from December 2017 to March 2018. All bees were collected and identified at the species level following the accepted names from the Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region (Bembé 2007; Ferrari and Melo 2014; Hinojosa-Díaz and Engel 2014; Moure et al. 2007; Nemésio 2009; Rebelo and Moure 1995; Roubik 2004). We deposited all specimens in the Zoology Collection of the Universidade Federal de Goiás (Goiânia, Goiás, Brazil).

We estimated α -diversity using abundance, species richness, and diversity for each sampling site. We obtained the number of individuals per species (species abundance), the total number of species, and the individuals sampled. We estimated species richness using the Jackknife method (Heltshel and Forrester, 1983) and the Shannon–Wiener diversity index (H') using the *vegan* package (Oksanen et al. 2017) in R version 3.6.1. (R Core Team 2019).

We tested spatial autocorrelation in our community data using Moran's I test implemented in *ape* package (Paradis and Schliep 2019) in R version 3.6.1. We found no significant spatial autocorrelation (Table S2) for species richness ($r = -0.092$; $p = 0.432$), abundance ($r = -0.014$, $p = 0.282$), nor Shannon–Wiener diversity ($r = -0.091$, $p = 0.447$).

2.3. Multiscale landscape metrics

We calculated the landscape composition and configuration to analyze the effects of habitat loss and fragmentation on orchid-bee communities. We calculated the metrics at three spatial scales, defined by concentric buffers of 500 m, 750 m, and 1000 m radii around each sampling site. We chose these radii buffers considering the

flight range of the orchid bees according to the diversity of the group based on different estimations (e.g., homing, foraging, and communication distance, and range of body size; Borges et al. 2020) and the maximum distance to avoid overlap among landscapes.

We calculated habitat amount as the percentage of two natural vegetation covers (savanna and forest) since different habitats are associated with different floral and nest resource availability (Moreira et al. 2017). We also calculated the proportion of agriculture (mainly soybean and corn crops) and pasture in the landscape. We calculated landscape compositional heterogeneity using the Shannon index (SHDI, McGarigal et al. 2012), considering all land cover categories.

We measured landscape fragmentation or subdivision by calculating the number of forest (NP_forest) and savanna (NP_savanna) patches, as well as PSI (McGarigal et al. 2012; Fahrig 2019). With PSI, the complexity of a patch shape compared to a standard shape (square) of the same size is measured (McGarigal et al. 2012). We calculated the PSI, including savannas and forest patches, and obtained the mean shape index for each landscape spatial scale, ignoring the zero values. Landscapes covered by a single patch had a shape index = 1, assuming the patch as regular. We calculated the landscape metrics using the *landscapemetrics* package (Hesselbarth et al. 2019) implemented in R version 3.6.1. (R Core Team 2019).

2.4. Data analyses

To analyze the effects of landscape composition and configuration in α -diversity in the orchid-bee community, we first selected the scale of effect (Jackson and Fahrig 2015) for each response variable and landscape metrics. We performed a multiscale test of independence for multivariate vectors using the *multifit* function (Huais 2018) implemented in R version 3.6.1. We used R^2 as a measure of the relationship's strength to choose the scale for each response variable (Table S3).

We estimated the variance inflation factor (VIF) to assess collinearity among landscape metrics selected by the effect scale (Tables S4–S6). We used the *jitools* package (Long 2020) available in R

with a stepwise approach, removing models with predictors with high collinearity ($VIF > 5.0$, Zuur et al. 2009).

Finally, to analyze landscape effects on community α -diversity, we used the selected explanatory variables by multicollinearity analysis (Table I) to perform Generalized Linear Models (GLM) using R version 3.6.1. We generated nine univariate models for each response variable: one for each landscape predictor and a null model, including only the intercept, representing the absence of specific landscape processes. We used Gaussian distribution to estimate species richness and diversity models and negative binomial distribution for abundance models. We selected the best predictive model using AIC (Akaike's information criterion; Burnham and Andersen 2002) with the *bbmle* package (Bolker 2009; Bolker and R Development Core team 2020) in R version 3.6.1. We estimated AIC corrected for small sample sizes (AICc), each difference of the model, and the best model ($\Delta AICc$) for model ranking. We also estimated Akaike's weight of evidence (wAICc) as the relative contribution of each model to explain the observed pattern. Models with $\Delta AICc < 4.0$ were considered equally likely (Zuur et al. 2009).

3. RESULTS

3.1. The α -diversity of the bees community

We sampled 658 Euglossini bees from 12 species and five genera (Table II). Most specimens were *Eulaema* ($n = 401$; 60.9%), followed by *Euglossa* (30.4%), *Eufriesea* (7.9%), *Exaerete* ($n = 2$; 0.3%), and one specimen of the monospecific genus *Aglae*. *Eulaema nigrita* Lepelletier (1841) was the most abundant, with 349 (53.0%) individuals sampled pooling all sites, followed by *Euglossa townsendi* Cockerell (1922), with 102 (15.5%) specimens sampled, and *Euglossa imperialis* Cockerell (1922) ($n = 68$, 10.3%). The most frequent species were *Eul. nigrita*, found in all 18 sites, and *Eug. townsendi* and *Eulaema cingulata* (Fabricius 1804), which occurred in 16 out of 18 sampling sites.

Table I Landscape metrics used on models to explain the α -diversity of the Euglossini bees in the Brazilian Cerrado landscapes

Response variable	Landscape metric
Species richness	Forest cover (1000 m)
	Savanna cover (500 m)
	Pasture cover (500 m)
	Compositional heterogeneity (500 m)
	Number of forest patches (500 m)
	Number of savanna patches (750 m)
Abundance	Shape index (1000 m)
	Forest cover (1000 m)
	Savanna cover (500 m)
	Pasture cover (500 m)
	Compositional heterogeneity (500 m)
	Number of forest patches (500 m)
Shannon–Wiener	Number of savanna patches (1000 m)
	Shape index (1000 m)
	Forest cover (1000 m)
	Savanna cover (500 m)
	Pasture cover (500 m)
	Compositional heterogeneity (500 m)
	Number of forest patches (500 m)
	Number of savanna patches (500 m)
	Shape index (750 m)

The estimated species richness ranged from 2.0 to 10.5, and the Shannon–Wiener diversity index ranged from 0.517 to 1.804 (Table S1). Sites 7 and 9, within the protected area (Flona Silvânia, Fig. 2B), showed the highest estimated species richness (10.500 and 8.833) and diversity (1.968 and 1.951) (Table S1).

3.2. Landscape effects on bee diversity

Bee species abundance, richness, and diversity had a similar scale of effect (i.e., higher values of R^2), 500 m, for most variables (Tables I and S3). Forest cover (%) affected the bee

Table II Abundance and richness of euglossine bees sampled in 18 landscapes in the Brazilian Cerrado

Species	Landscapes																		Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>Aglae caerulea</i> (Lepeletier and Serville 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Eufriesea auriceps</i> (Friese 1899)	5	0	3	0	0	9	5	0	1	4	1	19	0	1	0	1	1	0	50
<i>Eufriesea</i> sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Euglossa azurea</i> (Ducke 1902)	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	3
<i>Euglossa cordata</i> (Linnaeus, 1758)	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Euglossa imperialis</i> (Cockrell 1922)	0	1	0	1	1	25	6	12	0	0	0	19	1	2	0	0	0	0	68
<i>Euglossa securigera</i> (Dressler 1982)	0	1	0	0	0	2	2	1	0	2	2	1	0	0	0	0	0	0	11
<i>Euglossa tomnsendi</i> (Cockerell, 1922)	1	5	19	6	6	8	3	8	0	11	6	3	4	12	3	3	4	0	102
<i>Euglossa fimbriata</i> (Rebêlo and Moure 1996)	0	0	2	0	0	3	0	3	0	1	1	4	0	0	0	0	0	0	14
<i>Eulaema cingulate</i> (Fabricius 1804)	2	2	3	3	2	4	4	5	2	0	2	4	3	14	0	2	2	1	55
<i>Eulaema nigrita</i> (Lepeletier 1841)	20	11	21	33	18	33	25	40	10	19	17	44	8	11	7	11	9	12	349
<i>Exaerete smaragdina</i> (Guérin 1844)	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Abundance	28	20	49	44	27	85	45	70	13	37	29	96	16	43	10	17	16	13	658
Observed species richness	4	5	6	5	4	8	6	7	3	5	6	8	4	7	2	4	4	2	12
Estimated species richness	4.833	7.5	6.833	6.667	4.833	10.5	6.833	8.667	3.833	5.667	7.667	8.833	4.833	8.667	2	6.5	4.833	4.833	4.833

community at the 1000-m spatial scale for the three variables (Table I, Table S3). The number of savanna patches and PSI had a different scale of effects on the three response variables (Table I, Table S3). We excluded agriculture cover (%) from our models because it had high collinearity ($VIF > 5.0$) with all the other response variables (Tables S4 to S6).

Species richness was explained by three models: the percentage of savanna cover at 500-m spatial scale ($wAICc = 0.530$, Table III), the number of forest patches at 500-m spatial scale ($wAICc = 0.185$, Table III), and the proportion of forest cover at 1000-m spatial scale ($wAICc = 0.119$, Table III). Both the proportion of savanna cover in the landscape (Fig. 3A) and forest cover increased bee richness (Fig. 3B), while the number of forest patches decreased

it (Fig. 3C). The savanna cover at 500-m spatial scale positively influenced the variation in Euglossini species abundance among sampling sites ($wAICc = 0.819$, Table III, Figure 3D). Although several landscape metrics explained Shannon diversity variation, the null model was equally likely (Table III). The pasture cover in the landscape, the number of savanna patches, and the PSI of forest and savanna could not explain any response variables (Table S9).

4. DISCUSSION

Our findings show that the α -diversity of the Euglossini communities in the Brazilian Cerrado is affected by landscape composition and configuration. Landscape configuration, measured

Table III Best models for explaining the variation in Euglossini bees α -diversity in 18 landscapes in the Brazilian Cerrado. Bee diversity refers to the Shannon–Wiener index. The $wAICc$, Akaike’s weight of evidence corrected for the sample size, and the model’s number of parameters. $\Delta AICc$, the difference between each model and the best model corrects for small sample size. Models with $\Delta AICc \leq 4.0$ were considered equally plausible

Models	Species richness	
	$\Delta AICc$	$wAICc$
Savanna cover (500 m)	0.0	0.530
Number of forest patches (500 m)	2.1	0.185
Forest cover (1000 m)	3.0	0.119
	Abundance	
	$\Delta AICc$	$wAICc$
Savanna cover (500 m)	0.0	0.819
	Shannon–Wiener	
	$\Delta AICc$	$wAICc$
Savanna cover (500 m)	0.0	0.218
Forest cover (1000 m)	0.1	0.203
Number of forest patches (500 m)	0.8	0.147
Compositional heterogeneity (500 m)	1.0	0.133
Null model	1.1	0.128
Pasture cover (500 m)	2.5	0.063
Number of savanna patches (500 m)	2.7	0.058
Shape index (PSI -750 m)	3.0	0.050

df (degrees of freedom) = 3 for all the models, except null models ($df = 2$). See Table S9 for all models tested

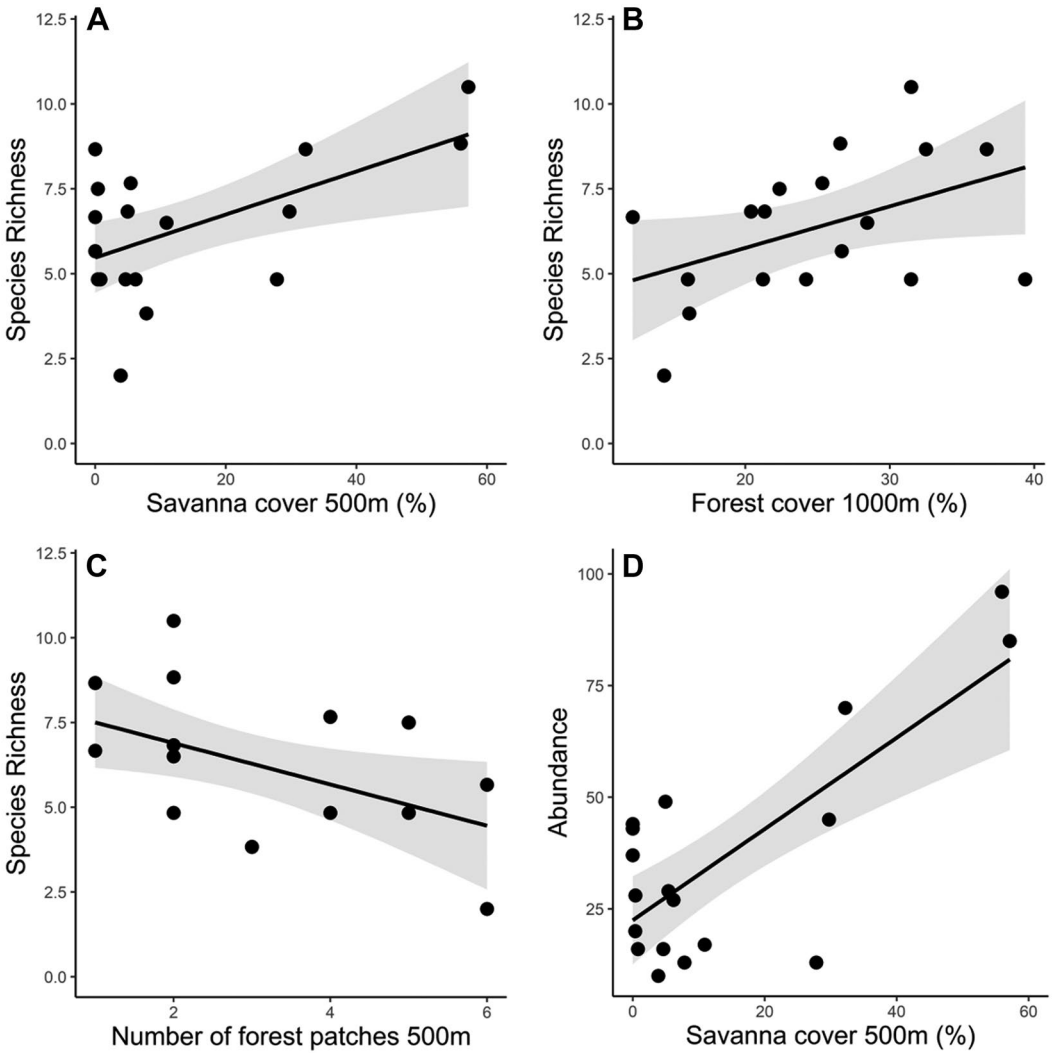


Figure 3. Relationship between Euglossini α -diversity and landscape composition and configuration based on 18 sampling sites in the Brazilian Cerrado. **(A)** Species richness and proportion of savanna cover in the landscape at 500-m spatial scale. **(B)** Species richness and proportion of forest cover in the landscape at a 1000-m spatial scale. **(C)** Species richness and the number of forest patches in the landscape at the 500-m spatial scale. **(D)** Abundance and proportion of savanna cover in the landscape at the 500-m spatial scale. The solid line represents the fitted model, and the shaded area is the 95% confidence interval.

by the number of forest patches, affected species richness on a small spatial scale (500 m), while landscape composition affected both small (500 m) and large (1000 m) spatial scales. The abundance of bees was also influenced by landscape composition on a small spatial scale. However, we analyzed scales up to 1000 m,

suggesting that local landscape features affecting ecological processes may determine the α -diversity in Euglossini bees at the regional scale. Forest cover also explains bee species richness on a small spatial scale (500 m) in coffee plantations in the Atlantic Forest, Brazil (Medeiros et al. 2019a). In these coffee agroecosystems,

wasp richness and abundance were also best explained by forest cover on a small scale (750 m and 500 m, respectively).

Although most of the species we sampled here are habitat and pollen-resource generalists, such as *Eul. nigrita*, *Eug. townsendi*, *Eug. imperialis*, *Eul. cingulata*, and *Eufriesea auriceps*, we found strong evidence of negative effects of either savanna or forest loss in species richness and abundance. Habitat generalists Euglossini, such as some *Eulaema* species (e.g., *Eul. nigrita*), may have a higher abundance in fragmented landscapes in different ecosystems (e.g., Powell and Powell 1987; Otero and Sandino 2003; Brosi 2009; Silva et al. 2014), showing high resilience to habitat loss and fragmentation. Mostly, generalists Euglossini have a large body size and a remarkable flying capability (e.g., Wikelski et al. 2010; Pokorný et al. 2015). Still, small body-sized generalist species may also fly large distances between habitat remnants (e.g., Tonhasca et al. 2003; Milet-Pinheiro and Schindwein 2005), contributing to such fragmentation resilience. However, the negative effects of landscape changes in bee communities have been shown in several studies, as we found here. For instance, visitation rates to flowers and the abundance of Euglossini bees decrease with reduced fragment size in Amazonia (e.g., Powell and Powell 1987). In agricultural landscapes, the abundance of above-ground nesting bees decreases with habitat loss and isolation (Williams et al. 2010), and species composition changes between forest and pasture, with no orchid bees sampled in pastures (Brosi et al. 2008). The abundance of Euglossini bees also has a positive relationship with fragment size (Brosi 2009), percentage of savanna, and compositional heterogeneity in agroecosystems (Briggs et al. 2013; Moreira et al. 2017). Orchid bees show a unique reproductive behavior, where males forage for fragrances in external sources, mainly orchids and flowers from other families, as well as resins and fungi, which are then used to attract mates (Dressler 1982). Despite their high mobility to explore landscapes, the degree of specialization in fragrance sources may also play a role in their response to landscape configuration. Such a specialization

degree is not well known yet (Mitko et al. 2016; Hetherington-Rauth and Ramírez 2016) and deserves more investigation in future studies. It is important to note that orchid-bee species in the Cerrado are usually more habitat generalist than those from forested areas, composing a completely different species pool compared with rainforests (Silveira et al. 2015). Thus, we expected to sample more generalists than specialist species in Cerrado.

Despite the recent intensive farming in the studied area (~60 years), we found strong evidence of adverse effects of habitat loss and fragmentation in the Euglossini bee communities in Cerrado. These bees are generally open-area generalists. Indeed, the effects of habitat loss and fragmentation on bees are more pronounced in highly disturbed landscapes with very low habitat amount (Winfree et al. 2009). Our landscapes are embedded in a highly intensive farming system with tiny patches of forest and savanna, except by a large savanna area (sites 7 and 9, Fig. 2), which is the protected area Silvânia National Forest (see Santos et al. 2021). Landscapes in the protected area had higher species richness and abundance, higher habitat cover, and fewer forest patches than the other landscapes. Habitat cover may influence resource availability for bees, such as floral, nesting, and fragrance resources, and may strongly limit species richness and abundance.

Intensive agricultural practices may directly and adversely affect bees, such as the impacts of pesticides (Cresswell 2011; Gill et al. 2012). This is especially relevant for those species that use crop plants as nectar and pollen resources, as is the case for several *Euglossa* species (Giannini et al. 2015). The highly intensive farming and habitat loss in our study area and the differences in spatial scale may explain the divergence of our results from other studies that did not find any habitat loss effect upon the abundance of the Euglossini *Eul. nigrita* and *Euf. auriceps*. Silva and De Marco (2014) studied landscapes on a broader geographic scale, where macroecological processes may be more important than ecological processes at the local landscape level (Wiens 1989). Furthermore, in this study, additional metrics of orchid-bee diversity were explored.

In conclusion, we show that despite the recent agriculture expansion (~60 years), agriculture intensification leading to fragmentation and habitat loss affects Euglossini bees at a landscape scale. Due to habitat loss, the decrease in plant species richness and abundance in the studied area (Santos et al., 2022) may have affected the foraging and nesting resources for orchid bees, causing a decline in species richness and abundance. This effect is expected to be even more pronounced for orchid bees than many bee groups, considering that their orchid host plants are especially vulnerable to habitat loss and fragmentation in other regions (Hernández-Pérez and Solano 2015; Hundera et al. 2013). Once many orchid species are highly specialized in their Euglossini pollinators (Ramírez et al. 2011), habitat loss may lead to co-extinctions and other synergistic deleterious effects for this particular system.

Euglossini bees are more diverse in forested environments (Nemésio and Silveira 2007), essential habitats, and ecological corridor elements (Moura and Schlindwein 2009; Silva et al. 2013). In the COFA LTER study area, most riparian and seasonally dry forest patches are linear or irregular. Thus, they have less core area and higher edge effects (Santos et al., 2022). This can impact habitat specialist species, increase population size variability, and decrease the probability of population persistence (Didham 2010). The nesting and foraging behaviors of orchid bees may be negatively affected by environmental stress, such as high temperatures and low humidity (Vilhena et al. 2017). On the other hand, such effects may be softened in fragments with a higher amount of core area and a more negligible edge effect (Nemésio and Silveira 2006, 2010; Cândido et al. 2018). Thus, the maintenance of forest patches in agricultural landscapes is critical to minimize habitat loss and fragmentation in Euglossini bees. Even though Euglossini bees may disperse over long distances and in the agroecosystem matrix, resources for many species may be provided by forest and savannas restoration. Therefore, the richness and abundance of Euglossini bees may be increased, maintaining the ecosystem services provided by them,

which are essential pollinators for both crops and native plants.

SUPPLEMENTARY INFORMATION

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AUTHOR CONTRIBUTION

FGS and DPS conceived designed experiments; all authors participated in the interpretation of the data; FGS, JSS, and FM performed the analysis; all authors wrote the paper.

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AVAILABILITY OF DATA AND MATERIAL

The datasets generated during the field samplings or analyzed during the current study are available from the corresponding author upon reasonable request.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

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Conflict of interest The authors declare no competing interests.

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