

Universidade Federal de Uberlândia
Instituto de Biologia
Programa de Pós-Graduação em Ecologia, Conservação e
Biodiversidade

MUDANÇAS NO USO DA TERRA NO CERRADO E SEUS
EFEITOS SOBRE AS ABELHAS EUGLOSSINI

Brunna Machado Leão Gomes

2022

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**MUDANÇAS NO USO DA TERRA NO CERRADO E SEUS
EFEITOS SOBRE AS ABELHAS EUGLOSSINI**

Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia, Conservação e Biodiversidade.

Orientador

Prof. Dr. Heraldo L Vasconcelos

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Resumo

Leão-Gomes, Brunna Machado 2022. Mudanças no uso da terra no Cerrado e seus efeitos sobre as abelhas Euglossini. Dissertação de Mestrado em Ecologia, Conservação e Biodiversidade. UFU. Uberlândia-MG. 33p

A intensificação da agricultura ameaça diversas espécies, especialmente abelhas nativas, sobretudo no Cerrado, onde grande parte das savanas e florestas nativas foram substituídas pela por áreas destinadas a exploração da agricultura e pecuária. No presente estudo, foram avaliados os efeitos das mudanças no uso da terra sobre a diversidade e morfologia de abelhas euglossinas. Nós avaliamos a comunidade de abelhas presente em pastagens, plantações de soja e eucalipto, verificamos se diferenças de disponibilidade de recursos entre os usos da terra causam diferenças no tamanho e na assimetria corporal. Durante seis meses de coleta com iscas aromáticas e armadilhas, foram coletados 1399 machos pertencentes a onze espécies de abelhas de orquídea, observamos riqueza e abundância maiores nos ambientes naturais como Cerrados e Matas. *Eulaema nigrita* representou 91,4% dos indivíduos, sendo a única espécie que ocorreu em todos os usos da terra, além disso, apresentou diferenças no tamanho corpóreo entre as áreas. Machos coletados em cultivos de eucalipto, pastos ou soja são menores do que os coletados em cerrado e mata, bem como nas plantações de eucalipto o nível de assimetria flutuante foi maior do que nas matas. Os resultados indicam que a conversão de savanas e florestas causa homogeneização da fauna de abelhas Euglossini, gerando um subconjunto empobrecido. A baixa abundância de *El. nigrita* em plantações de eucalipto, somado ao menor tamanho corporal e maior nível de AF em indivíduos nesse habitat indica que alguns usos da terra podem ser adversos até mesmo para uma espécie generalista. Concluímos, que a conversão de ambientes naturais de mata e cerrado causa perda de qualidade ambiental às euglossinas, uma vez que tanto o menor tamanho corporal quanto a assimetria de abelhas são atribuídas à escassez de alimentos, ao estresse térmico e/ou à exposição aos pesticidas. Enfatizamos a importância de legislação para preservação do Cerrado para garantir também a preservação de abelhas nativas como Euglossinas.

Abstract

Leão-Gomes, Brunna Machado 2022. Land-use changes in a Neotropical biodiversity hotspot and its effects on Euglossini bees. Dissertação de Mestrado em Ecologia, Conservação e Biodiversidade. UFU. Uberlândia-MG. 33p

Agricultural expansion threatens multiple species, including native bees, especially on Cerrado, where the major natural savannas and forests were replaced by agricultural exploration. Here we studied the effects of land-use changes on euglossine bees' diversity and morphology. We evaluated bees' communities in pasture, soybean crops, and eucalyptus plantations, and we investigated if availability differences between the land use cause differences in corporeal size and asymmetry. During six sampling months, using aromatic baits and traps we collected 1399 orchid bees' males belonging to 11 species. We observed higher species richness and abundance in natural areas. *Eulaema nigrita* males represented 91,4% of all specimens, being the only species that occurred in all land uses, besides, presenting corporeal size differences between the land uses. Our results indicate that savannas and forest conversion lead to Euglossini bees' fauna homogenization, causing a poor subset community. The lower abundance of *El. nigrita* on eucalyptus plantations indicates that some land uses can be an adverse event for a generalist species as this conversion causes environmental quality loss for Euglossini. Males from eucalyptus, pasture, or soybeans plantations were smaller than those from savannas and natural forests, as on eucalyptus the FA level was higher than it was on natural forests. We emphasized legislation importance to Cerrado preservation, as to guarantee also native bee preservation.

Introduction

The conversion of natural habitats for human use is one of the major causes of increases in extinction rates for several plant and animal species. Thus, understanding how land-use changes affect native bees' species has great relevance to biodiversity conservation. In South America, the Cerrado is one of the most threatened regions by agricultural expansion; this region used to host the largest and most diverse tropical savanna ¹. Cerrado occupies around 20% of Brazilian territory and has lost half of its natural cover from the past 50 years ², even so, deforestation rates in this region tend to grow ³. Most Cerrado species are not able to survive on modified habitats, causing local extinctions ⁴, and consequent loss or lack of ecosystem services ⁵. On the other hand, even generalist's species, who can tolerate new conditions, can suffer impacts, as the environmental stress can alter species development ⁶ and physiology ⁷.

Not just for the diversity maintenance of natural ecosystems ⁵, but also for our society ^{8,9}, bees are important pollinators to several flowering plants and thus they offer a relevant ecological service. For example, is it known that the productivity of many cultures is increased through the bees' pollination, who nest in natural remaining areas near those plantations ^{10,11}. Euglossine bees are pollinators to a great variety of tropical plants, including orchids, and are capable of flying long distances looking for resources ¹². Although primarily associated with forest environments ¹³, these orchid bees can also occur in urban ^{14,15} and agricultural areas ^{16,17}, such as planted forests ¹⁸. In the Cerrado region, at least 15 species of euglossine bees occur in savannas and forests ¹⁹, but little is known about how much of this diversity is lost with Cerrado conversion to other land uses.

On bees, body size is directly related to flight and dispersion capacity, which determines foraging area and spatial scale where bees can promote pollination ²⁰. Despite some orchid bees being capable of living even in large monocultures, a study on Cerrado has shown that specimens in this area are smaller than those collected on adjacent native vegetation, probably because of differences in availability and quality of food resources between both habitats ²¹. On the other hand, contrasting to a Cerrado study, another study on Amazonia has shown that males of two euglossine species have larger wings on palm planted forests than on natural forests ²², showing that it is still early to generalize land uses changes effects over phenotypical variation on euglossine morphological traits.

Similarly, there is evidence that land use changes do not cause fluctuating asymmetry (FA) on euglossine males' wings (i.e., small non-directional deviation on

wings symmetry which can be resultant from individuals' disability of dealing with environmental stresses²³. However, these pieces of evidence are resultant from studies that observed changes due to only one, not multiple land uses^{21,22}. As FA shows the environmental stress level experienced by individuals during their development²³, and as land uses can be more or less suitable for euglossine ontogenetic development, it may have effects in some uses but not in others. In other bee groups, there are observations about larger FA in pesticides exposed populations²⁴, due to hybridization or transport stresses²⁵.

In this study, we evaluated the effects of land uses changes on Cerrado over Euglossini bees. The aim to combine diversity and morphological data was to promote a broader comprehension of how Euglossini has been affected by growing human action on ecosystems. Our main goal was to answer the following questions: 1) Which is the effect of forests and savannas conversion on pasture, soybean and eucalyptus plantations over the Euglossini community? 2) Is there evidence that bees' ontogenetic development is being affected by changes on land use, resulting in differences on body size and wing symmetry on male bees? We test the hypothesis that the bee community on pasture, soybean, and eucalyptus plantations represents a poor subset of the original community. Additionally, we believe that eventual differences on food resources quality and availability between land uses is one of the factors that causes differences in body size and symmetry in generalist species.

Material and methods

Study site

The study was conducted in Uberlândia region (18°56'S, 48°18'O), Minas Gerais state, southeastern Brazil. The region has a tropical climate, characterized by a dry winter and a rainy summer. The average annual precipitation is 1600 mm, and temperature is 22°C²⁶. The predominant vegetation in the region is tropical savanna (Cerrado stricto sensu), with semi-deciduous or gallery forests on humid or richer soils. The vegetation has been gradually replaced by pasture, to cattle grazing, agricultural areas to grain monocultures (principally soybean and maize), also to Pinus and Eucalyptus plantation.

Euglossini bees' community was sampled in five land uses: savanna fragments (Cerrado stricto sensu), semi-deciduous forests fragments, pasture, soybean plantations (vegetative phases), and eucalyptus plantation (≥ 6 years). We selected at least six sites of each land use sampled, totalling 35 sampling sites (Figure 1).

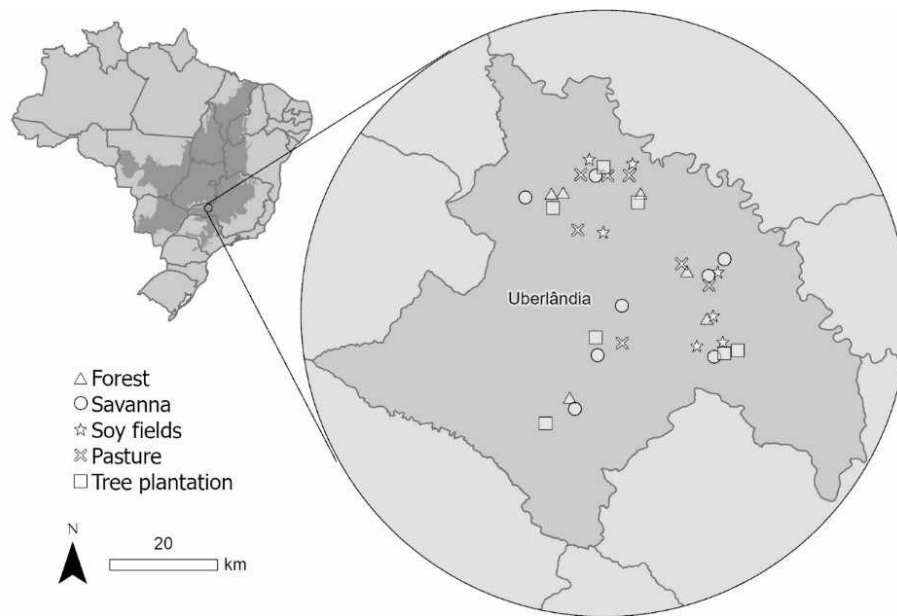


Figure 1: Map of Brazil, with the dark gray area representing the Cerrado, and map of the study region showing the location of the 35 sampling sites

Sampling design

Euglossini males were captured with bait traps once a month between October 2020 and March 2021, during the wet season, the period of greatest activity of bees in tropical ecosystems¹³. The traps consisted of plastic transparent bottles (28 cm), with two lateral holes (2 x 5 cm) turned down like a valve, in a way that allows bee entrance and difficult its escape (Figure 2). Inside the bottle, there was cotton soaked on aromatic and volatile bait. We used 1,8-cineole, vanillin, methyl salicylate, and β -ionone. The baits were chosen based on the most attractive aromatic compounds we have observed in a previous study that was conducted on the same region. We placed two traps baited of each aromatic compound, totaling eight traps in each study site. Traps were collected after 30 hours.

During collection, the individuals that were common species and of easy identification were counted and released, the dead ones and those of difficult identification on the field were taken to the laboratory. The specimens were mounted on entomological pins, drought on an oven, labeled, identified until specie level by a professional using an “Abelhas Brasileiras”²⁷ taxonomic keys, then stored on a zoological collection of the Federal University of Uberlândia.

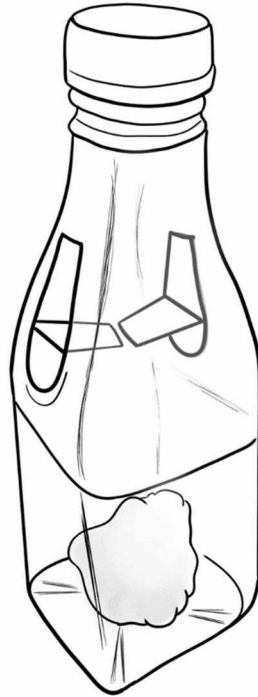


Figure 2: Schematic drawing of the bait trap and the scheme of the entrance and the cotton soaked with aromatic compounds.

Morphometry

We measured head width, thorax width, wing shape, and wing size for a total of 112 *Eulaema nigrita* males collected on all five land uses in order to access morphological traces, these four measures are common as size estimators ²⁸. For that, we selected randomly from three to seven individuals in each land use and in each of the six sampling months. Head and thorax width measures were taken with a digital caliper, for each individual were taken duplicated measures aiming to reduce measurement error. Moreover, for wing morphometry, we removed both right and left forewings from the previously analyzed individuals, then the wings were placed on microscope slides, fixed using an uncolored varnish, and photographed with a camera coupled on 0.85 times increased microscope. We used tpsDig2 (2.32 version) to dig the wing images. Thirteen landmarks were chosen (Figure 3) according to Francoy ²⁹ and dug twice to reduce measurement errors. We used the medium distance from landmarks to the centroid of those landmarks set, as wing size for each individual. The landmarks coordinates were inserted on the MorphoJ (1.07a version) program, which performs Procrustes superimposition in order to remove position, orientation, and size effects and returns shape measures in Procrustes units.

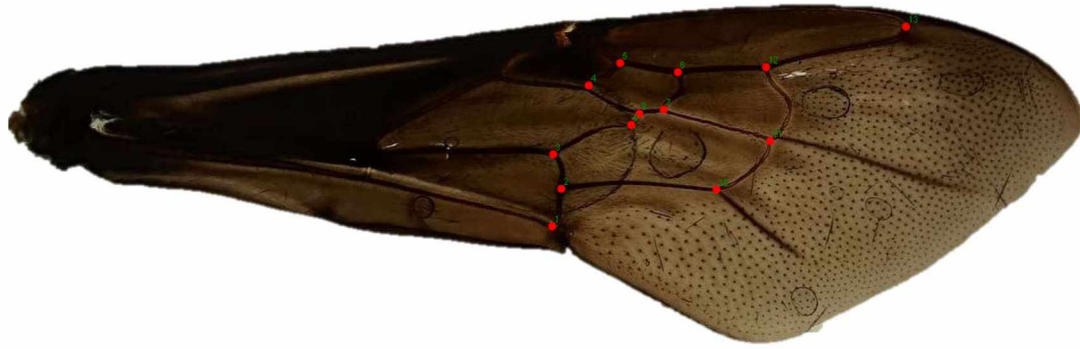


Figure 3: *Eulaema nigrita*'s fore right wing dug. Red dots show the 13 landmarks.

Data analyses

We compared the overall number of species recorded in each land use using individual-based, rarefaction-extrapolation curves built in the “iNext” package³⁰. Differences in mean species richness (number of species recorded per sampling site) and in mean abundance (of all species combined as well for each of the most abundant species) between land uses were evaluated using generalized linear models (GLM), assuming a Poisson error distribution and using a log-linking function. When overdispersion was detected, a quasi-Poisson GLM was used instead. A posteriori, pairwise multiple comparisons were performed using the Tukey method. For the models that evaluated differences in abundance of individual species, we performed planned contrasts comparing data from all three anthropogenic land uses with data from the native habitats (savanna and semideciduous forest).

Differences in the size of *El. nigrita* were assessed using Multivariate Analysis of Variance (MANOVA). In this analysis the explanatory variable was type of land use, while the response variables were head width, thorax width, and the forewing size (centroid size) of the male bees collected in the different land uses. Data from four of the 110 individuals analyzed were regarded as outliers and thus were removed from the analysis. A posteriori, pairwise multiple comparisons were performed using the Hotelling's T-square test.

The occurrence of fluctuant asymmetry (FA) on wing size and shape was assessed using a linear mixed model (data from different land uses were analyzed separately). In this model, “individuals” represented a random factor, while “wing side” a fixed factor that assesses the presence of directional asymmetry. The presence of fluctuating asymmetry is indicated by the interaction between individuals and side, while the model

residuals estimate the measurement error ^{31,32}. As FA was detected in all five land uses, we compared the level of FA between the different land uses using a linear model. To obtain only positive values of FA, we multiplied the negative values by -1.

The MANOVA analysis was done in SYSTAT version 12, whereas the remaining analysis in R version 4.05 ³³, using the packages “car” and “multcomp”.

Results

Euglossini community

A total of 1399 individuals from 11 species were collected (Table 1). *Eulaema nigrita* was the most dominant species, representing 91.4% of all individuals, followed by *Euglossa imperialis* (2.57%), *Eulaema cingulata* (1.93%), *Exaerete smaragdina* (1.50%), and *Euglossa cordata* (1.22%). The other species corresponded singly to less than 1% of the total bees. Of all species, only *Eulaema nigrita* occurred on all five land uses. *Euglossa azurea*, *Eg. pleosticta*, and *Eg. securigera* were exclusive on semi-deciduous forests fragments and *Eg. melanotricha*, *Eg. townsendi* and *Eg. fimbriata* were found only in savanna sites.

Table 1: *Euglossine bees sampled between October 2020 and March 2021 in Uberlândia, Brazil's savanna in five different land uses. SAV: Savannas; FOR: Forests, EUC: Eucalyptus plantation, PAS: Pasture, SOY: Soybean plantation.*

	SAV	FOR	EUC	PAS	SOY	Total
<i>Eulaema nigrita</i> Lepeletier	482	281	34	189	293	1279
<i>Eulaema cingulata</i> (Fabricius)	12	10	2	0	3	27
<i>Exaerete smaragdina</i> (Guérin-Méneville)	3	14	2	2	0	21
<i>Euglossa imperialis</i> Cockerell	23	11	2	0	0	36
<i>Euglossa cordata</i> (Linnaeus)	5	11	0	1	0	17
<i>Euglossa azurea</i> Ducke	0	8	0	0	0	8
<i>Euglossa melanotricha</i> Moure	7	0	0	0	0	7
<i>Euglossa pleosticta</i> Dressler	0	1	0	0	0	1
<i>Euglossa securigera</i> Dressler	0	1	0	0	0	1
<i>Euglossa townsendi</i> Cockerell	1	0	0	0	0	1
<i>Euglossa fimbriata</i> Moure	1	0	0	0	0	1
Abundance	534	337	40	192	296	1399
Richness	8	8	4	3	2	11

The species richness observed was different between the five land uses, ($\chi^2= 29.03$, DF = 4, P < 0,001). On forests and in savannas more species were sampled comparing to agricultural land uses such as pasture and eucalyptus and soybean plantations (Figure

4A). Similarly, the bees' abundance also varied significantly between the five land uses ($\chi^2 = 29.97$, $DF = 4$, $p < 0.001$). For the five more abundant species we found significant differences in abundance among habitats (*El. nigrita*: $\chi^2 = 27.8$, $P < 0.001$; *Eg. imperialis*: $\chi^2 = 11.3$, $P = 0.023$; *El. cingulata*: $\chi^2 = 23.87$, $P < 0.001$; *Ex. smaragdina*: $\chi^2 = 14.73$, $P = 0.005$; *Eg. cordata*: $\chi^2 = 29.3$, $P < 0.001$). For *Eulaema nigrita*, the number of males was lower in eucalyptus than in other land use types (Figure 4B).

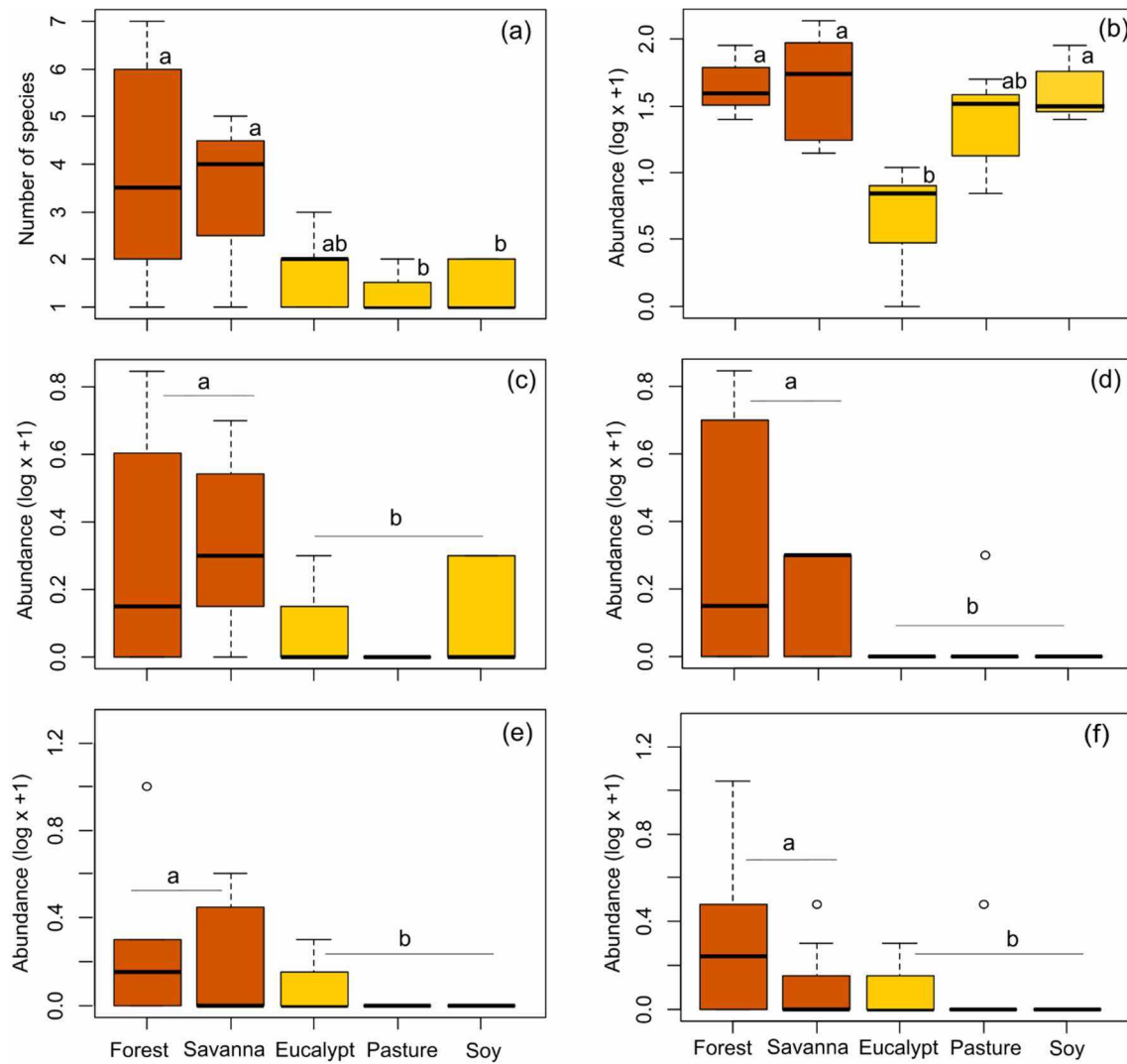


Figure 4: Land use differences in the species richness of Euglossini bees (A) and in the abundance of the five most common species: (B) *El. nigrita*, (C) *El. cingulata*, (D) *Eg. cordata*, (E) *Eg. imperialis*, (F) *Ex. smaragdina*. Different letters above boxplots indicate significant differences in mean values. In panels C to F, comparisons were based on planned contrasts (native habitats x anthropogenic land uses) given small sample size.

Morphometry

Eulaema nigrita exhibited significant differences on body size, which observed as three separate measures in a set (MANOVA; Pillai Trace, $F_{12,303} = 2.32$, $p = 0.007$), as separately (ANOVA; head width: $F_{4,101} = 3.76$, $p = 0.007$; thorax width: $F_{4,101} = 5.02$, p

= 0.001, centroid size: $F_{4,101} = 3.24$, $p = 0.015$). In general, males collected on savannas and forests were bigger than those collected on eucalyptus, pasture, or soybean (Hotelling's T-square, $p = 0.048$ on each paired comparison, Figure 5).

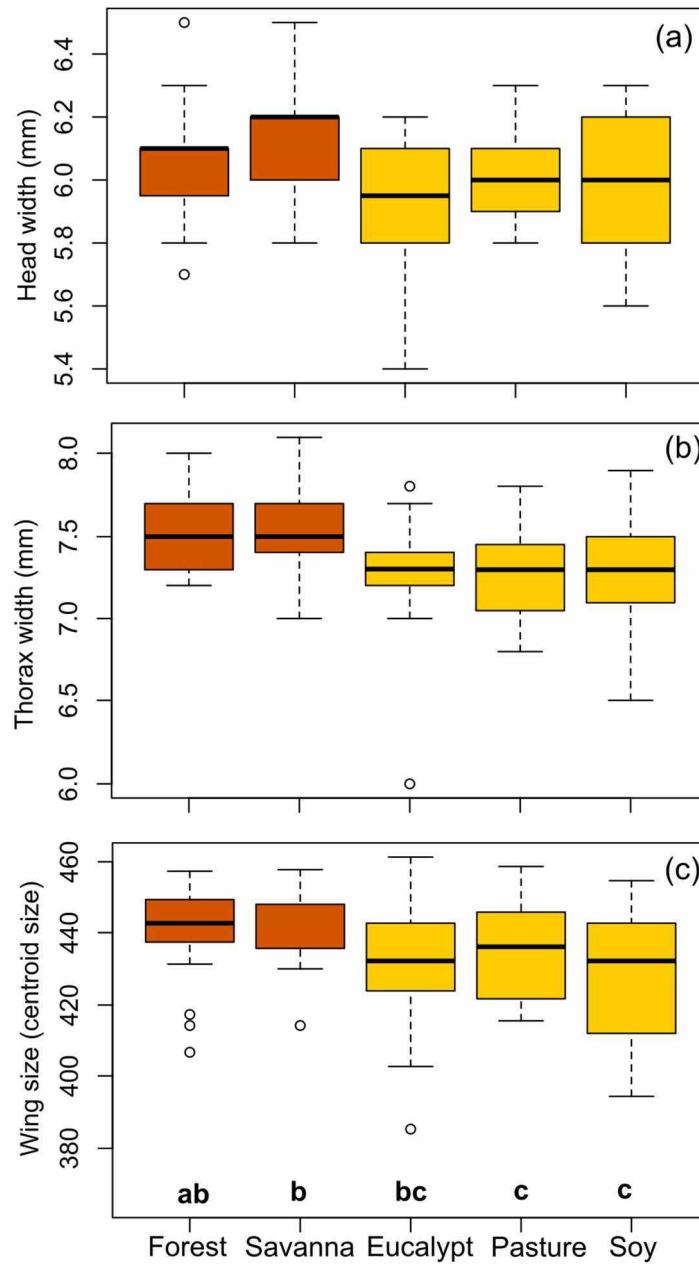


Figure 5: Land use differences in the body size of *Eulaema nigrita* males. (A) Head width, (B) thorax width and (C) size of the forewing (centroid size). Different letters in the bottom of panel C indicate significant differences in mean body size (considering all three morphological traits) between land uses as revealed by multivariate analysis of variance.

For fluctuating asymmetry on wing centroid, both variations between sides and individuals were significantly different. The interaction side x individual was also significantly different for euglossine bees in all five land uses, the same happened for

wing shape variation. We observed differences in FA between land uses and that was evident for wing size ($F_{4,105} = 2.99$, $p = 0.022$) and wing shape ($F_{4,105} = 3.15$, $p = 0.017$). Generally, FA tended to be higher among males found on Eucalyptus compared to males found on forests (Tukey test, Shape: $p = 0.024$, Size $p = 0.1204$).

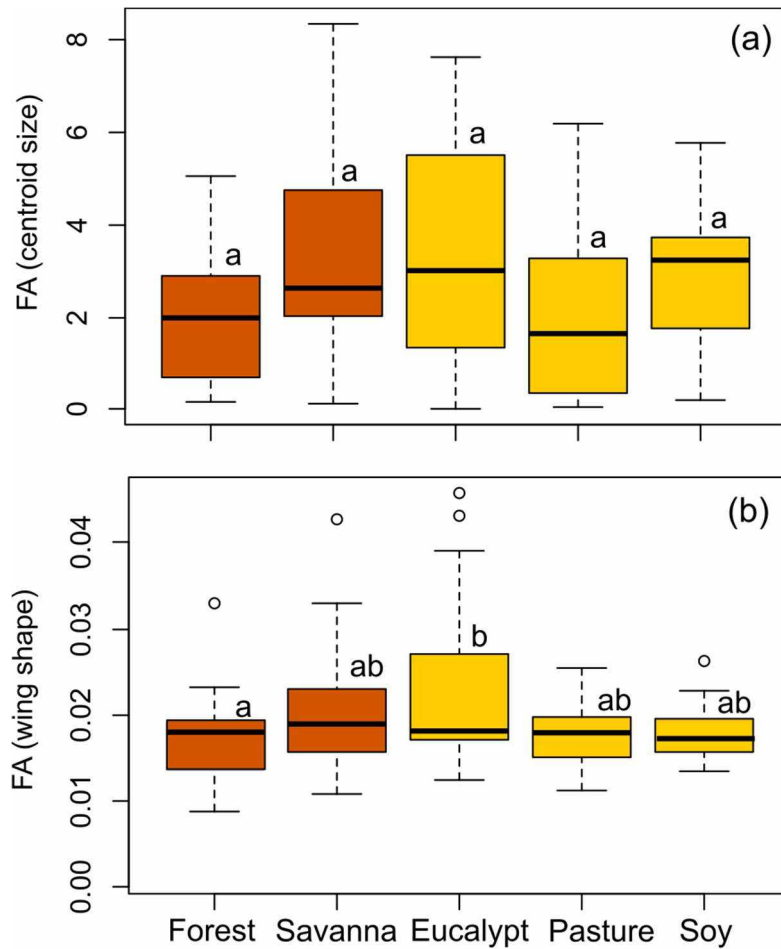


Figure 6: Fluctuating asymmetry in the size and shape of the forewings of *El. nigrita* males collected in different land uses. Different letters above boxplots indicate significant differences in mean values.

Discussion

Changes in land use and Euglossini community

Our results indicate that Cerrado savannas and forests conversion to pasture, soybean crops, and eucalyptus plantations have effects on Euglossini bees' community. Although in some cases, the abundance of bees has not differed between natural and modified areas, there was a decrease in species richness, hence few species seem to be capable of surviving in modified areas. Previous studies also showed that changes in land

use have negative effects on Euglossini diversity ^{18,34,35}, but this study is the first to demonstrate that these impacts are not only on forested areas but also in savannas and that some land uses tend to have relatively minor impacts on Euglossini community rather than others.

Eleven species were recorded on natural areas (forest and savanna), of which only five were also sampled on modified areas, pointing out that in these last Euglossini bees' community is composed of a poor subset from natural areas. Although on average, the number of Euglossini species has not differed between the three modified areas (figure 1a), a larger number of species were found on planted forests (4 species), than on soybean plantations or pasture (2 and 3 species respectively). The magnitude of difference in bees' richness between natural and modified areas is probably even higher than presented here, since the method we used to sample bees is selective. Indeed, previous studies on the same municipal region indicated at least 15 species ³⁶, being *Eg. decorata* Smith and *Eg. amazonica* Dressler regionally known but not recorded in the present study, once both are typical of forest areas and with affinity to Amazonia domain ¹⁹.

Four of five recorded species on modified areas (*El. cingulata*, *Ex. smaragdina*, *Eg. imperialis* and *Eg. cordata*) have occurred in higher abundance in forests or savannas rather than in each one of those converted environments, suggesting that these bees are typical from natural areas, but can eventually forage or nest on altered areas. On the other hand, *El. nigrita* was as abundant in pasture and soybean plantations as in native forests and savannas. Contrasting to other Euglossini, *El. nigrita* has tolerance to open areas ¹⁹, which can explain its high abundance in those two modified areas. Indeed, studies on Amazônia have shown that *El. nigrita* can be 9 times more abundant in pasture and soybean plantations than in adjacent forests ³⁴. Yet, on planted forests, likely to what was observed in other studies ¹⁸, *El. nigrita* abundance was way less than in natural areas, which can be indicative of a lack of resources for this species in this type of environment.

Changes in land use and El. nigrita morphology

In this study, we had evidence that changes in land use cause impacts not only on diversity but also on ontogenetic development, given the observed differences in *El. nigrita* body size and FA levels between males from natural and modified areas. The Cerrado conversion has caused smaller body sizes and greater asymmetry on Euglossine males, and the effects observed were more expressive in planted forests. Factors like food availability, climatic conditions, parasitism, contamination by pesticides, and genetic

factors, such as inbreeding, hybridization, and mutations, can influence the ontogenetic development of an organism³⁶⁷. These morphological changes have the potential to affect the fitness of individuals, as body size has a positive effect on the dispersal ability and reproductive success of bees³⁹. On eucalyptus planted forests, which house the smaller populations, the lack of resources and deficit feeding can be an environmental stress factor³⁸ that implies on smaller bees. Whilst pasture and soybean, as are quite open and preferable to *El. nigrita*¹⁹, they favor the bee occurrence with less variation in size and body asymmetry.

The high fluctuating asymmetry was observed on bees collected on eucalyptus plantations, indicating the occurrence of environmental stressors, as food resources, nest availability, that impact individual expected symmetry. In this study, although FA had been observed in all the habitats, the five land-use comparisons have more contrast possibilities, hence fluctuating asymmetry must be used as a comparative measure³¹. For Euglossini in another biome, Brito and colleagues²² have not found asymmetry on wings from oil palm plantations, as Pinto et al⁴⁰ in agricultural areas in Cerrado, nevertheless, both studies compared only two distinct habitats. Here, we understand the eucalyptus planted forest like the one that causes the most environmental stress to the Euglossini populations, with morphological impacts on individuals that forage or live there.

Conclusions

To sum up, we have that changes in land uses on Cerrado have been affecting Euglossini species, both their diversity and some of their morphological aspects. The Cerrado conversion to explore grains, wood or cattle has reduced the bees' richness, favoring a high abundance of only one plastic, resilient species to altered and open areas. In this case, for a generalist Euglossini, pasture and soybean plantations can act as refuges for individuals, guaranteeing high abundance and keeping populations with minor body size reduction, although under less environmental stress ensured by low asymmetry. Whereas planted forests, such as eucalyptus, are not able to sustain abundant populations and yet impact on smaller body size and higher FA. The Cerrado deforestation to agricultural areas is a fact¹ and it is necessary to head to the less harmful areas. So, the definition of priority areas to conserve Euglossine bees depends on studies that investigate communities such as their populational responses to impacts caused by the conversion.

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Land-use changes in a neotropical biodiversity hotspot and its effects on Euglossini bees

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Abstract

Natural landscapes are facing rapid transformation in many parts of the world, but the consequences of such changes for insects are poorly known. We evaluated how the conversion of the savannas and forests from Brazil's *Cerrado* into lands devoted to intensive agriculture, livestock, or plantation forestry affects euglossine bees. We determined the effects of land-use change on the species richness of euglossines, and functional traits related to the body size and wing fluctuating asymmetry (FA) of a habitat generalist species. Few species were recorded in the anthropogenic land uses and most presented lower abundances in the converted than in the native habitats. The exception was *Eulaema nigrita*, whose average abundance in cattle pastures and in soy fields did not differ from that observed in the native habitats. However, *El. nigrita* males collected in pastures or in soy fields were significantly smaller than those from savannas and forests, whereas those from eucalypt tree plantations were smaller than those from savanna. Furthermore, *El. nigrita* males from the tree plantations had higher levels of FA in wing shape than those from native forests.

Implications for conservation Our results showed that land-use change in the Cerrado biodiversity hotspot causes the impoverishment and homogenization of the Euglossini fauna. Furthermore, we found evidence that the converted habitats present more stressful conditions for the larval development of some species. This indicates that the conservation of euglossine populations in human-modified Cerrado landscapes depends largely on the presence of protected areas, including those within rural private land as required by Brazil's Native Vegetation Protection Law.

Keywords Brazilian savanna · Orchid bees · Species richness · Body size · Fluctuating asymmetry

Introduction

Describing and understanding the biodiversity consequences of land-use change is of great relevance for biological conservation, as the conversion of natural habitats for human uses is one of the leading causes of the accelerated species extinction rates (Laurance et al. 2014). Changes in land cover and land use have been particularly dramatic in regions of high diversity and endemism, also known as biodiversity hotspots (Mittermeier et al. 1998). In South America, one such region is the *Cerrado* biome—home of the largest and

most diverse tropical savanna (Oliveira-Filho and Ratter 2002) –, which has lost 50% of its original vegetation over the past 50 years and where rates of deforestation are still rampant (Rausch et al. 2019). Yet, we have limited information on the nature and magnitude of the effects of land-use change on Cerrado's biodiversity, and this is notably the case for insects, even though these organisms play many important and essential ecosystem services (Aizen et al. 2009; Imperatriz-Fonseca and Nunes-Silva 2010; Del Toro et al. 2012).

Bees (Hymenoptera: Anthophila), for instance, are the main pollinators of a wide range of flowering plants and thus provide an ecological service of great importance not only for the maintenance of diversity in natural ecosystems, but also for public appreciation (Klein et al. 2007; Aizen et al. 2009; Imperatriz-Fonseca and Nunes-Silva 2010). In fact, there is ample evidence that the production of various crops is increased through the action of bees that nest in remnants of natural vegetation adjacent to these crops (e.g.,

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Ricketts 2004; De Marco and Coelho 2004). Bees are also used as model organisms in ecological studies on habitat disturbances, and this has been often the case with Euglossini bees (hereafter euglossines) (e.g., Brito et al. 2018), whose males are relatively easy to attract to synthetic compounds used as scent baits (Janzen et al. 1982). At least 20 of the 244 known species of euglossines have been recorded in some regions of the Cerrado (Silveira et al. 2015; Nemésio 2016; Augusto et al. 2020; Ascher and Pickering 2022), but little is known about how much of this diversity is lost with the transformation of the Cerrado vegetation into other land uses. Although primarily associated with natural habitats, notably forests (Dressler 1982), euglossine bees can also occur in sugarcane (Milet-Pinheiro and Schindwein 2005), oil palm (Livingston et al. 2013; Brito et al. 2021), and eucalypt tree plantations (Nascimento et al. 2015). However, the extent to which these human-managed ecosystems provide suitable conditions for the larval development of euglossine bees is still poorly known.

The size of adult bees is one potential indicator of the developmental conditions experienced by these bees (Greenleaf et al. 2007), but studies to date have provided contrasting results about the effects of land-use change on the size of euglossines. Conversion of the Amazon Forest into oil palm plantations seems to favor the occurrence of bees with larger wings (Brito et al. 2021), while the reverse is true in agricultural areas of the Cerrado where euglossines have significantly smaller wings than in the adjacent forest areas (Pinto et al. 2015). There is not a consensus about the mechanisms explaining these differences. Some have argued that the lower availability of pollen (to females provisioning their nests) in the converted habitats has negative effects on larval development thus resulting in small-sized adults (Pinto et al. 2015), while others believe that pollen scarcity may force the development of individuals with larger wings to allow them a greater flight capability (Brito et al. 2021).

Another potential indicator of larval developmental conditions is the level of fluctuating asymmetry (FA) in the wings of adult bees (i.e., small non-directional deviations in wing symmetry that may be a result of the inability of individuals to cope with the environmental stress; Palmer and Strobeck 1986). For some groups of bees, there are reports of higher wing FA in populations exposed to nutritional stress, insecticides, as well as due to hybridization or physical stress (e.g., Abaga et al. 2011; Gerard et al. 2018). However, even though pesticides are commonly used in agricultural lands—where biotic and abiotic conditions can also be particularly harsh—there is evidence that land-use change does not cause higher wing FA in euglossines (Pinto et al. 2015; Brito et al. 2021). Nevertheless, such evidence comes from studies that evaluated a single type of land-use change (Pinto et al. 2015; Brito et al. 2021). As the occurrence of FA reflects the

level of environmental stress experienced by individuals during their development, and as certain anthropogenic land uses may present harsher conditions for the larval development of euglossines than others, it is premature to generalize about the effects of land use change on wing FA in euglossines.

In this study, we evaluated the effects of land-use change in the Cerrado on euglossine bees, from both a population and community levels. The study was developed within a region where, during the past few decades, most of the original savanna or forest vegetation has been replaced by cattle pastures, agricultural lands (soy or maize plantations mostly), or plantations of exotic trees (eucalypt or pine) (Prado-Júnior et al. 2020). We addressed the following questions: (a) Does the conversion of natural Cerrado habitats into anthropogenic land uses significantly affect the diversity and abundance of euglossine bees? (b) What is the effect of land-use change on the body size and wing FA of a habitat generalist, euglossine species? (c) Does the magnitude of these effects vary between different types of anthropogenic land uses?

Given the dependence of most euglossine species on natural habitats (Dressler 1982; Rocha-Filho et al. 2020), we would expect that the fauna recorded in the converted habitats would represent a nested subset of the original fauna. In addition, we would expect to find differences in the size and FA of male euglossine bees between the natural and converted habitats, since the latter may present more stressful conditions for the larval development of the bees (Pinto et al. 2015; Brito et al. 2021). However, we would also expect that the magnitude of the effects of land-use change on euglossines would vary between the different types of anthropogenic land uses. Given its greater structural similarity to forests, tree plantations would be expected to support a greater diversity of euglossines than areas devoted to intensive agriculture or livestock. Similarly, one might expect that the magnitude of the effects of land-use change on the size and FA of euglossines would depend on how different the conditions for the development of bees between the converted and natural habitats are, and the greater the similarity the smaller the effect. Finally, differences between land-use types may also be related to the spatial configuration of the landscape in which they are embedded. Cerrado landscapes dominated by intensive agriculture, for instance, have fewer and smaller patches of natural habitats than landscapes used primarily for livestock (Carvalho et al. 2009). Since these patches of natural habitat may represent a source of individuals for the euglossine populations inhabiting the converted habitats one might expect fewer euglossine species and/or larger individuals (greater dispersal ability) in areas devoted to intensive agriculture than in other land uses.

Material and methods

Study site

The study was conducted in Uberlândia, in southeastern Brazil (Fig. 1). The region has a tropical climate, characterized by a dry winter and a rainy summer. The average annual precipitation is 1600 mm, and the mean temperature is 22 °C. The original, dominant vegetation in this region is tropical savanna (*cerrado stricto sensu*), with semi-deciduous or gallery forests occurring on the wetter or richer soils (Oliveira-Filho and Ratter 2002). Over the past few decades most (about three-quarters) of this original vegetation was cleared and replaced by cattle pastures, annual crops, or to a lesser extent by plantations of pines or eucalypts (Prado-Júnior et al. 2020).

Euglossini bees were sampled in public or private savanna reserves, in semi-deciduous forests, and in cattle pastures, soy fields, and eucalypt tree plantations (ca. 6 yrs old). At least six sites of each type of land use were sampled, totaling 35 sampling sites (Fig. 1).

Sampling design

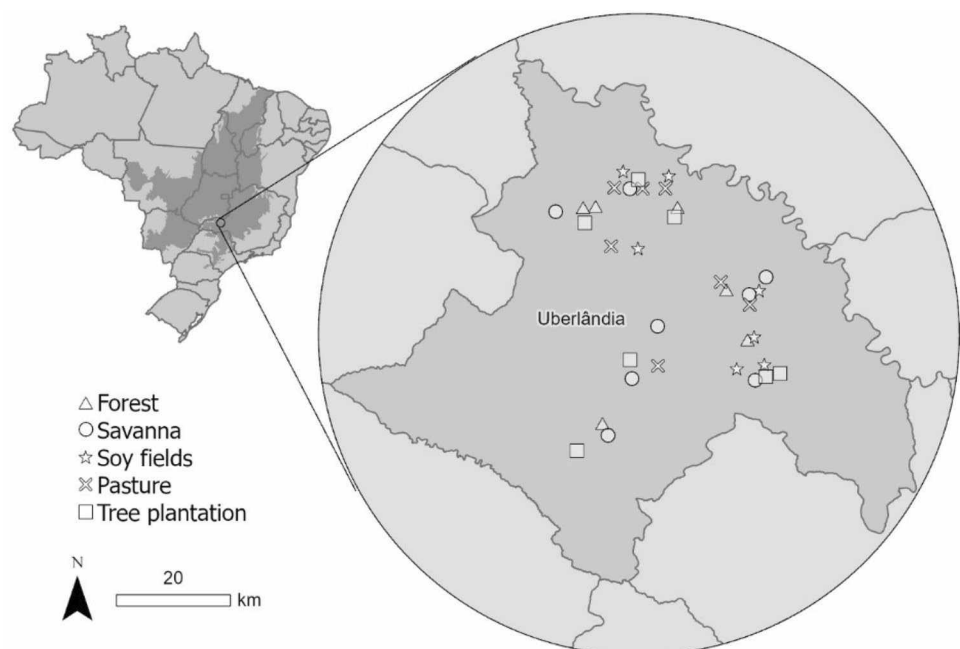
Sampling took place during the wet season (between October 2020 and March 2021), which is the period of greatest activity for euglossines in the Cerrado (Justino and Augusto 2010; Nemésio 2016). Each site was sampled six times (once a month) and male Euglossini bees were captured using traps baited with attractive scents. The traps consisted of plastic

transparent bottles (28 cm in height), in which we cut two lateral openings (each 2 × 5 cm) turned down like a valve (Online Resource 1), so that bees could easily enter the bottle, but once inside was difficult to escape. Inside the bottle, there was a piece of cotton soaked with an aromatic compound used as scent bait (Online Resource 1). We placed a total of eight traps in each site: two with 1.8-cineole, two with vanillin, two with methyl salicylate, and two with β -ionone. These four aromatic compounds have been documented as highly attractive for male euglossines (Alvarenga et al. 2007; Justino and Augusto 2010). The traps remained in the field for 30 h, and after this period we counted the number of individuals from each species present in each trap. All dead individuals were collected, whereas those alive were released except those whose identification in the field was not possible. In January and March 2021, we also performed an active collection of all euglossine males flying around the traps with the aid of an insect collecting net. This procedure took place for a period of two hours, immediately after the traps were set in the field. Species identification was based on Moure et al. (2007). Voucher specimens of all collected species were deposited in the Zoological Collection from the University of Uberlândia (UFU) in Brazil.

Morphometry

Using a digital caliper, we measured the width of the head and thorax from males of *Eulaema nigrata* Lepeletier, 1841 collected in all five land uses. For this, a minimum of three and a maximum of seven individuals collected in each sampling month, and in each land use, were randomly selected

Fig. 1 Map of Brazil, with the dark gray area representing the Cerrado biome, and map of the study region showing the location of the 35 sampling sites



for measurements, totaling 110 individuals in all five land uses. We also measured the size and shape of the wings of these same individuals, and for this procedure the forewings (right and left) from each male bee were removed, placed on microscope slides, fixed using an uncolored varnish, and photographed with a camera coupled on a stereomicroscope (0.85× magnification). The image from each left-wing was mirrored in order to be comparable with the image from the right-wing. The coordinates from 13 anatomical landmarks (Online Resource 2) were extracted using the tpsDig2 program, version 2.32 (Rohlf 2010). Two measures of the coordinates from each landmark were taken, as to obtain an estimate of the measurement error. Measures of wing shape and size were obtained using the MorphoJ program, version 1.07a (Klingenberg 2011). We used the centroid size, which represents the square root of the sum of the squared distances between each anatomical landmark and the centroid, as a measure of wing size. Shape measurements were obtained using the Procrustes method (Klingenberg 2011), which superimposes coordinates in order to remove position (translation), orientation (rotation), and size (proportionality) effects.

Data analysis

We compared the overall number of species recorded in each land use using individual-based, rarefaction-extrapolation curves built in the “iNext” package (Hsieh et al. 2016).

Differences in mean species richness (number of species recorded per sampling site) and in mean abundance (of all species combined as well for each of the most abundant species) between land uses were evaluated using generalized linear models (GLM), assuming a Poisson error distribution and using a log-linking function. When overdispersion was detected, a quasi-Poisson GLM was used instead. A posteriori, pairwise multiple comparisons were performed using the Tukey method. For the models that evaluated differences in abundance of individual species, we performed planned contrasts comparing data from all three anthropogenic land uses with data from the native habitats (savanna and semideciduous forest).

Differences in the size of *El. nigrita* were assessed using Multivariate Analysis of Variance (MANOVA). In this analysis the explanatory variable was type of land use, while the response variables were: head width, thorax width, and the forewing size (centroid size) of the male bees collected in the different land uses. Data from four of the 110 individuals analyzed were regarded as outliers and thus were removed from the analysis. A posteriori, pairwise multiple comparisons were performed using the Hotelling’s T-square test.

The occurrence of fluctuant asymmetry (FA) on wing size and shape was assessed using a linear mixed model (data from different land uses were analyzed separately). In

this model, “individuals” represented a random factor, while “wing side” a fixed factor that assesses the presence of directional asymmetry. The presence of fluctuating asymmetry is indicated by the interaction between individuals and side, while the model residuals estimate the measurement error (Klingenberg and McIntyre 1998; Klingenberg 2011). As FA was detected in all five land uses (Table 1), we compared the level of FA between the different land uses using a linear model. To obtain only positive values of FA, we multiplied the negative values by -1.

The MANOVA analysis was done in SYSTAT version 12, whereas the remaining analysis in R version 4.05 (R Core Team 2021), using the packages “car” and “multcomp”.

Results

Species richness and abundance

A total of 11 species of Euglossini bees were sampled, of which eight in semideciduous forests, eight in savannas, four in the eucalypt tree plantations, three in the cattle pastures and two in the soy fields (Online Resource 3 and 4). Of the 11 species sampled, six were only recorded in the native habitats (forests and savannas), whereas none of them was exclusively found in the anthropogenic land uses (Online Resource 3). There were significant differences in mean species richness between habitats ($\chi^2 = 29.03$, $DF = 4$, $P < 0.001$). On average, we found more species in forests and savannas than in cattle pastures and soy fields (Fig. 2). The mean number of species recorded in the eucalypt tree plantations did not differ significantly from any of the remaining habitats.

There were also significant habitat differences in overall abundance ($\chi^2 = 29.97$, $DF = 4$, $P < 0.001$; Fig. 2), as fewer male euglossine bees (all species combined) were found in the eucalypt tree plantations than in any of the remaining habitats. *Eulaema nigrita* Lepelletier, 1841 was by far the most abundant species in our sampling, representing 91.4% of the 1,399 bees collected, followed by *Euglossa imperialis* Cockerell, 1922 (2.57%), *El. cingulata* (Fabricius, 1804) (1.93%), *Exaerete smaragdina* (Guérin, 1844) (1.50%) and *Eg. cordata* (Linnaeus, 1758) (1.22%). For all these five species we found significant differences in abundance among habitats (*El. nigrita*: $\chi^2 = 27.8$, $P < 0.001$.; *Eg. imperialis*: $\chi^2 = 11.3$, $P = 0.023$; *El. cingulata*: $\chi^2 = 23.87$, $P < 0.001$; *Ex. smaragdina*: $\chi^2 = 14.73$, $P = 0.005$; *Eg. cordata*: $\chi^2 = 29.3$, $P < 0.001$). However, while most species were largely restricted to forests and savannas, *El. nigrita* presented similar levels of abundance in the native and anthropogenic habitats, except for the tree plantations where fewer males of this species were recorded (Fig. 2).

Table 1 Results of the Procrustes analysis of variance (mixed model) used to assess the presence of fluctuating asymmetry in the size and shape of the forewings of males of *Eulaema nigrita* in each land use

Habitat/Land use	Source	Centroid size			Shape		
		MS	DF	F	MS ($\times 10^4$)	DF	F
Forest	Side	117.88	1	19.2**	1.474	22	9.7***
	Individual	683.77	22	111.6***	1.071	484	7.1***
	Side x ind.	6.13	22	3.91***	0.152	484	4.2***
	Error	1.56	46		0.037	1012	
Savanna	Side	1024.52	1	57.2***	1.143	22	5.2***
	Individual	376.47	22	21.0***	1.331	484	6.1***
	Side x ind.	17.92	22	22.2***	0.219	484	4.8***
	Error	0.81	46		0.045	1012	
Eucalypt	Side	825.11	1	64.5***	2.259	22	7.8***
	Individual	1161.87	21	45.8***	1.289	462	4.4***
	Side x ind.	18.00	21	19.6***	0.291	462	6.1***
	Error	0.92	44		0.048	968	
Pasture	Side	511.30	1	65.0***	1.123	22	7.1***
	Individual	761.36	19	96.8***	1.362	418	8.6***
	Side x ind.	7.86	19	7.54***	0.158	418	3.0***
	Error	1.04	40		0.052	880	
Soy field	Side	678.72	1	58.4***	1.150	22	7.3***
	Individual	1200.00	21	103.3***	1.085	462	6.9***
	Side x ind.	11.62	21	16.5***	0.158	462	4.9***
	Error	0.70	44		0.032	968	

In this model, individuals are considered a random factor, while the side is a fixed factor that assesses the presence of directional asymmetry. The interaction between individuals and sides measures the presence of fluctuating asymmetry, while the residuals estimate the measurement error

*** $P < 0.001$, ** $P < 0.01$

Size of *Eulaema nigrita* males

We found significant differences in the size of *El. nigrita* males between land uses (MANOVA; Pillai Trace, $F_{12,303} = 2.32$, $P = 0.007$). The males collected in the savanna sites were, on average, significantly larger than the males collected in tree plantations, pastures or soy fields, whereas the males collected in the semideciduous forest were larger than those collected in pastures and soy fields (Hotelling's T-square, $P \leq 0.048$ in all pairwise comparisons; Fig. 3).

Fluctuant asymmetry

Table 1 presents the results of the models that evaluated the presence of fluctuating asymmetry (FA) in the males of *El. nigrita* collected in each land use. The presence of FA was detected in all land uses for both wing size and shape. There was a significant interaction between the “side” and “individual” predictors in all evaluated models, and in all of them, the mean square of the interaction was much greater than the mean square of the measurement error (Table 1). We also found significant differences in size and shape between the left and right sides of the wings, indicating the presence of

directional asymmetry, as well as differences in wing size and shape between individual bees (Table 1).

When comparing habitats, we found that the level of FA in wing shape was greater in bees from the tree plantations than in those from the semideciduous forest ($F_{4,105} = 3.15$, $P = 0.017$, Fig. 4). Comparable results were obtained for wing size ($F_{4,105} = 2.99$, $P = 0.022$), although here the difference between tree plantations and the semideciduous forest was only marginally significant in the pairwise comparison test ($P = 0.089$, Fig. 4).

Discussion

Land-use change effects on species richness and abundance

We have found that land-use change in the *Cerrado* negatively affects the species richness of euglossine bees. Similarly, a study in the Amazon has shown a sharp decline in the species richness of euglossines following the replacement of the rain forest by oil palm plantations (Brito et al. 2018), indicating that land-use change has pervasive effects on the Euglossini fauna more broadly. The

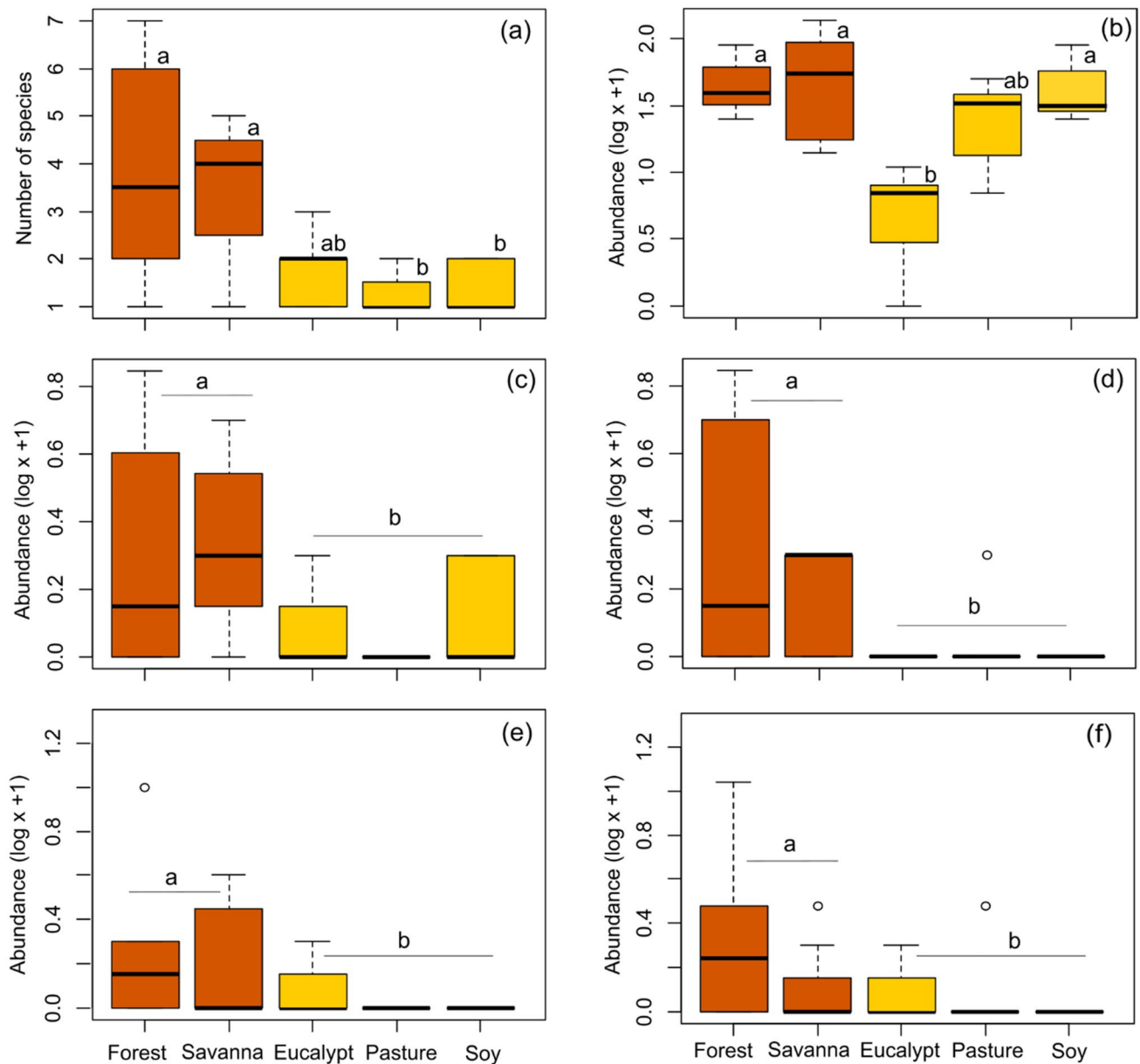


Fig. 2 Land use differences in the species richness of Euglossini bees (**A**) and in the abundance of the five most common species: **B** *Eulaema nigrita*, **C** *Eulaema cingulata*, **D** *Euglossa cordata*, **E** *Euglossa imperialis*, **F** *Exaerete smaragdina*. Different letters above

boxplots indicate significant differences in mean values. In panels C to F, comparisons were based on planned contrasts (native habitats x anthropogenic land uses) given small sample sizes

magnitude of the difference in species richness between the converted and native Cerrado habitats is probably even greater than recorded in here, since the method we used to sample bees is selective and, therefore, our sampling was not able to obtain a complete inventory of the species known to occur in the forests and savannas of our study region. In fact, previous studies in this region indicate the occurrence of at least 20 Euglossini species (Augusto et al. 2020), of which two (*Euglossa decorata* Smith, 1874 and *Eg. amazonica* Dressler, 1982) have strong affinity with

the Amazon Forest (Nemésio 2016). Of the 11 species we found in the native habitats, only five were also recorded in the anthropogenic land uses, indicating that the fauna of the converted habitats is composed of a nested subset of the species from the original fauna. On average we found similar number of species in the three anthropogenic land uses. However, overall, the eucalypt tree plantations tended to support a higher diversity of species than the other anthropogenic land uses as evidenced by our rarefaction-extrapolation curves (Online Resource 4).

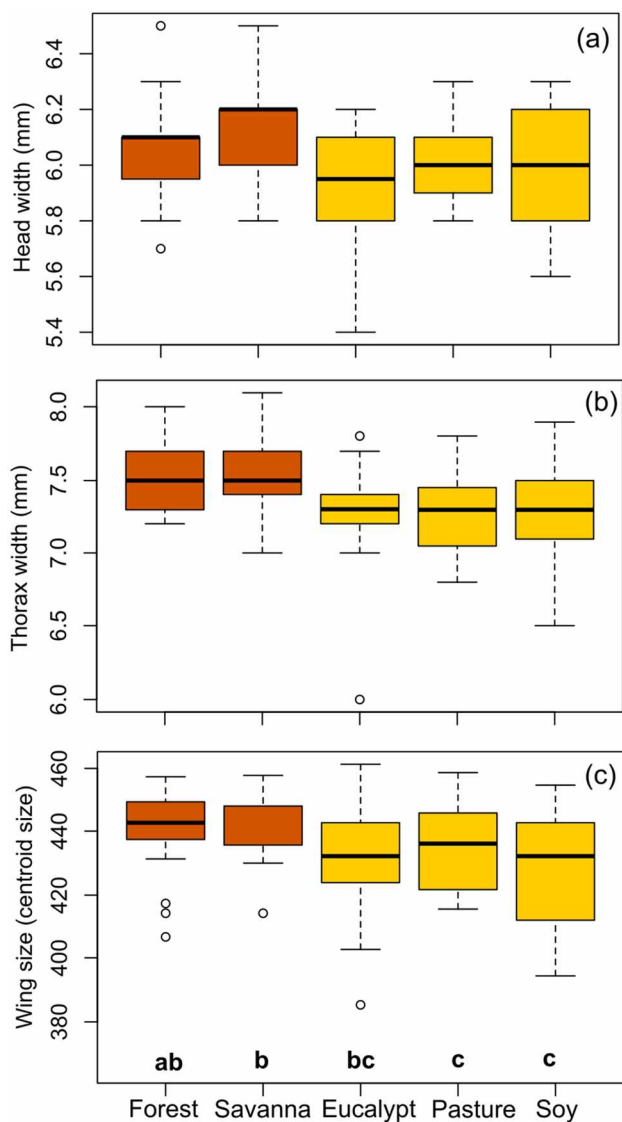


Fig. 3 Land use differences in the body size of *Eulaema nigrita* males. **A** Head width, **B** thorax width and **C** size of the forewing (centroid size). Different letters in the bottom of panel C indicate significant differences in mean body size (considering all the three morphological traits) between land uses as revealed by multivariate analysis of variance

Four of the five species recorded in the anthropogenic land uses (*El. cingulata*, *Ex. smaragdina*, *Eg. imperialis* and *Eg. cordata*) occurred in greater abundance in the forests or savannas than in any of the converted habitats, suggesting that these species only occasionally forage or nest in these habitats. Similarly, comparatively few *El. nigrita* males were recorded in the eucalypt tree plantations (as also detected in previous studies; Nascimento et al. 2015). However, *El. nigrita* was as abundant in pastures and soy fields as it was in the native forests and savannas. *Eulaema nigrita*, in contrast to most Euglossini species, is tolerant to more open and

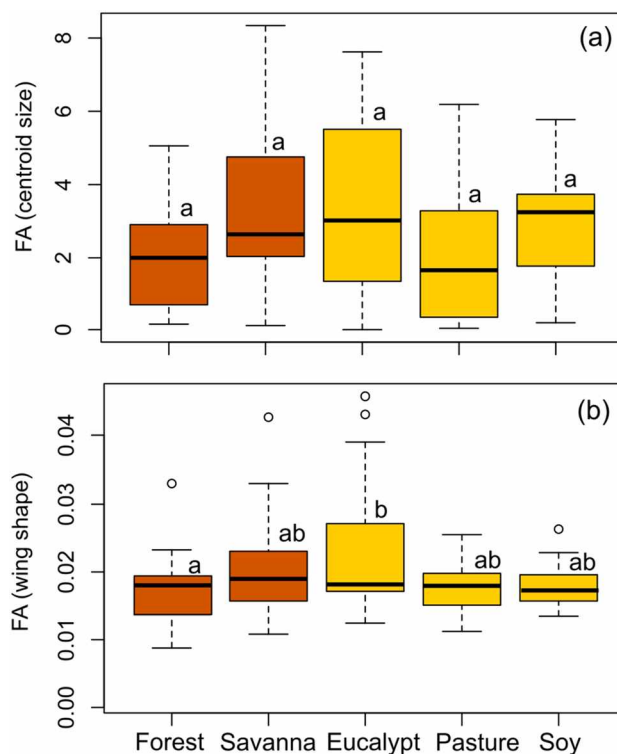


Fig. 4 Fluctuating asymmetry in the size and shape of the forewings of *El. nigrita* males collected in different land uses. Different letters above boxplots indicate significant differences in mean values

xeric habitat conditions (Nemésio 2016), which may help to explain its relatively high abundance in some anthropogenic habitats. In fact, studies in the Amazon show that the abundance of *El. nigrita* is nine times higher in pastures and soy fields than in the adjacent forest (Batista et al. 2020).

Land-use change effects on the size and FA of *Eulaema nigrita*

We found strong evidence that changes in land use in the Cerrado can affect not only the abundance but also the ontogenetic development of *El. nigrita*, given the observed differences in body size between males from the native and converted habitats. In support to our hypothesis, bees from the anthropogenic land uses were smaller than those from the savannas and forests. These morphological changes have the potential to affect the fitness of individuals, as body size has a positive effect on dispersal ability and reproductive success of bees (Araújo et al. 2004), as is also the case for other insects (e.g., Laparie et al. 2013; Saleh et al. 2014). According to Møller (1997), several factors can influence the ontogenetic development of an organism, including food availability, climatic conditions, parasitism, pesticides' contamination, and genetic factors, such as inbreeding, hybridization and mutations. In bumblebees (*Bombus* spp.), several

stress factors, such as the presence of toxins in the pollen, high temperatures, parasitism, and inbreeding, have a negative effect on the body size of individuals (Gerard et al. 2018). In Euglossini, habitat or seasonal differences in the size of males have been attributed to differences in the availability of larval food (Peruquetti 2003; Pinto et al. 2015). Therefore, it is possible that the smaller size of *El. nigrita* in the anthropogenic land uses is related to a lower availability of food resources (namely pollen and nectar) in these habitats than in the native ones. However, the fact that changes in body size were detected in all the three and highly contrasting, anthropogenic land uses, suggests that different stressors may operate in each land use. For example, although soy flowers are frequently visited by bees—notably when pollen from native plants is not available—the pollen from these flowers likely contain high amounts of pesticides and herbicides (Zawislak et al. 2021), indicating that contamination by agrochemicals may be a more important stressor in soy fields than in pastures or tree plantations. Similarly, heat stress – which can also affect the larval development of bees (Gerard et al. 2018) – is potentially much greater in a soy field or pasture than in the understory of a 6-yr old tree plantation.

Contrary to patterns detected for body size, the level of FA in the size and shape of the wings of *El. nigrita* was similar among most of the land uses, except the tree plantations where FA was higher than in semideciduous forest. These results reinforce the view that body size can be a better indicator of environmental stress for bees than FA (Gerard et al. 2018). Why bees from eucalypt tree plantations presented higher FA than those from native forests is not clear, but one possibility is the low availability of floral resources since the tree plantations we sampled presented a very sparse understory vegetation. Studies with *Bombus* indicate that nutritional stress can cause higher FA in wing size (Gerard et al. 2018). Further studies are needed to better understand which factor or factors affect the size and FA of *El. nigrita* males and the relative importance of these factors in different land uses. For this, field studies that evaluate the availability of floral resources for Euglossini in different land uses (as well as their level of contamination) are needed, and eventually tested with laboratory studies that evaluate the impact of different stressors on the development of these bees.

Conclusions

Our results indicate that the conversion of Cerrado native vegetation into other land uses causes the impoverishment and homogenization of the Euglossini fauna. In fact, only one species, *El. nigrita*, was present in all three anthropogenic land uses, but even for this generalist species, soy fields, cattle pastures, and *Eucalyptus* plantations seem to

represent stressful environments as evidenced by the relatively smaller size and/or higher level of wing FA found in bees collected in these land uses. Contrary to our expectations, and despite differences in local environmental conditions and in the configuration of the surrounding landscape (cf. Carvalho et al. 2009) between the land uses we studied, the responses of the Euglossini fauna to land-use change was similar across all land use types for nearly all the population and community metrics measured. The marked differences in species abundances and richness between the native and converted habitats, suggest that the latter represent marginal habitats for most euglossines.

Our study thus reinforces the idea that the maintenance of euglossine diversity in human dominated Cerrado landscapes requires the maintenance of patches of natural vegetation in these landscapes (Sousa et al. 2022). In this sense, where large tracts of natural vegetation still exist, efforts should be directed at creating new protected areas, especially considering that relatively large areas are needed for maintaining viable populations of some species (Nemésio and Silveira 2010). On the other hand, in rural areas, efforts should be made to reinforce the compliance on existing legislation. According to the Brazilian legislation, every rural property in the Cerrado must keep at least 20% of its area with native vegetation as “Legal Reserves” (Sparovek et al. 2010). Nevertheless, attempts to ban this legislation are frequent, despite the mounting evidence of the important role played by the Legal Reserves for biodiversity conservation in regions that have already been largely transformed by human activities (Miura et al. 2019), such as those found in the Cerrado.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-022-00428-w>.

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Author contribution BLG and HLV designed the study, analyzed the data, and wrote the manuscript. BLG collected the data.

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Declarations

Conflict of interest We declare that we have no competing financial or personal interests that could have influenced the work reported in this paper.

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