

No Evidence of Habitat Loss Affecting the Orchid Bees *Eulaema nigrita* Lepeletier and *Eufriesea auriceps* Friese (Apidae: Euglossini) in the Brazilian Cerrado Savanna

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Abstract

Habitat loss, landscape fragmentation, and agriculture intensification constitute the main threats to bees. As the organisms responsible for almost one third of the food produced worldwide, there are growing concerns on bees' response to human-related disturbances. Among all bee groups, orchid bees (Apidae: Euglossini) compose an interesting group to test landscape-related hypotheses. In here, we tested the effect of landscape features (amount of anthropic areas and isolation) on the probability of occurrence and the abundances of both *Eulaema nigrita* Lepeletier and *Eufriesea auriceps* Friese in the Cerrado savanna. In general, we did not observe any effect of landscape features on the probability of occurrence and abundances of both species in our sampling sites. Given their potential high dispersal abilities, these bee species may be less sensitive to fragmented landscapes or even positively affected by the increase of anthropic habitats. Since we sampled many *E. nigrita* specimens in highly preserved Cerrado savanna areas, we believe that at least for this biome, this species may not be a good indicator of landscape disturbance.

Introduction

Agriculture intensification is accepted as a severe cause of worldwide biodiversity loss (Brittain *et al* 2010, Robinson & Sutherland 2002), together with habitat loss and fragmentation (Tylianakis *et al* 2008, Dobrovolski *et al* 2011). Unfortunately, future scenarios on global economy suggest that given the increasing demands on food production (Cirera & Masset 2010, Kearney 2010), these problems will continue to affect biodiversity in the twenty-first century (Rockström *et al* 2009, Foley *et al* 2011), along with other human-related processes (Tylianakis *et al* 2008, Rockström *et al* 2009). Since croplands and pastures currently cover more than 38% of the planet's surface (Foley *et al* 2005, 2011), it is reasonable to rank them as the greatest worldwide "biomes" on Earth, and the main causes of conservation conflicts elsewhere (Dobrovolski *et al* 2013), mainly in tropical regions, those with the highest deforestation rates since the 1980s (Foley *et al* 2011, Hansen *et al* 2013).

Depending on the combination of life-history traits they possess, species inhabiting areas affected by habitat loss and changes in landscape structure may either perish or flourish (Davies *et al* 2004, Henle *et al* 2004). From metapopulation perspectives, both habitat amount (expressed by the available habitat patches) and the isolation between them are important determinants of a given species' success or failure to persist within a given landscape (Hanski 1994, Moilanen & Hanski 1998). Therefore, the higher the amount of habitat available for the species and the higher the connectivity, the higher the species' expected abundance and occupancy rates in the available habitat patches and the whole landscape, once species' colonization and extinction rates are directly affected by both variables (Hanski 1994, Fahrig 2013).

Considering a theoretical framework (MacArthur & Levins 1964), generalist species may perceive the landscapes as fine grains, allowing them to easily cope with different landscape features and easily percolating through any given landscape.

Otherwise, specialists may perceive their surroundings as coarser grains, hampering their movements, inhibiting their movements, and persistence in the changing landscapes (MacArthur & Levins 1964). Additionally, such contrasting landscape perception between different species may also vary according to the spatial scale analyzed, and strong and consistent relationships of species features may not hold in other finer- or coarser-spatial scales, given the so-called scale effect (Jackson & Fahrig 2012).

Bees compose one of the insect groups most potentially affected by decreases in habitat quality and habitat loss (Potts *et al* 2010). Depending on the considered species, these organisms show a wide variety of life-history traits, such as different nest locations (above vs. below ground), sociality degree (solitary, parasocial, communal, highly eusocial, and cleptoparasites), the exploration of their food resources (specialists/oligolecy vs. generalists/polylecy), and body sizes (Michener 2007, Williams *et al* 2010). Since they are responsible for the pollination of a great proportion of all the food consumed by humans (Klein *et al* 2007) and given worldwide decrease reports of bee abundance and species richness due to habitat loss and agriculture intensification (Biesmeijer *et al* 2006, Brosi *et al* 2008, Winfree *et al* 2009, Williams *et al* 2010, Brittain *et al* 2010), the effects of habitat loss on these insects are of growing public concern (Biesmeijer *et al* 2006, Bartomeus *et al* 2013, Burkle *et al* 2013).

Orchid bees (Apidae: Euglossini) are one of the most remarkable bee groups existent, not only because of their day-glow metallic coloration but also because of the visits male orchid bees pay to several orchid species to collect fragrances, supposedly used as precursors of their sexual pheromones (Dressler 1982, Eltz *et al* 2006), in return, for the pollination of the Neotropical orchids and many others botanical families (Dressler 1982, Roubik & Hanson 2004). Such attraction to plant fragrances allowed the development of aromatic artificial fragrances (Dodson *et al* 1969), facilitating their consequent and community studies (Janzen *et al* 1982, Ackerman 1983, Morato 1998). Despite some taxonomic issues (Nemésio 2012), this group of bees is very diverse, currently comprising almost 250 species endemics to the Neotropics (Nemésio & Rasmussen 2011). Additionally, some of these bees have been recorded to have high daily-dispersal abilities (Janzen 1971, Raw 1989, Wikelski *et al* 2010), what make of them unique components while assessing the effects of habitat loss, agriculture intensification, landscape and fragmentation on biodiversity (Brosi 2009, Nemésio & Vasconcelos 2013).

Small habitat patches, even those embedded within urban areas, were proven to maintain minimal viable population of some orchid-bee species (Nemésio & Silveira 2007a, 2010). However, other studies have shown that these bees are negatively affected by habitat

loss, especially by changes in landscape structure and the decreasing sizes of remnant vegetation fragments (Powell & Powell 1987, Becker *et al* 1991, Tonhasca *et al* 2002, Brosi *et al* 2008, Brosi 2009, Aguiar & Gaglianone 2012, Nemésio 2013). Otherwise, some species have also been shown to be positively affected by habitat loss. For instance, *Eulaema nigrata* Lepeletier is a species known to be associated to disturbed and anthropic matrices, which further allows it to increase its abundance (Morato 1998, Nemésio & Silveira 2006, Peruquetti *et al* 1999, Tonhasca *et al* 2002). This species with medium to large body size (~18 mm; Roubik & Hanson 2004) occurs from southern Mexico to southern Brazil and northern Argentina and pollinates several different plant species (Moure 1967, Zucchi *et al* 1969, Dressler 1982). Other orchid bees are usually associated with forest formations and have their peak abundances and diversity in those areas (Dressler 1982, Nemésio & Silveira 2007b), apparently depending on the size of remnant vegetation available to maintain their population sizes (Nemésio & Silveira 2007a). Contrary to *E. nigrata*, the populations of some *Eufriesea* species (e.g., *Eufriesea violacea*) are believed to be negatively affected by reductions in the sizes of original vegetation patches (Sofia & Suzuki 2004) and consequent genetic effects on the individuals inhabiting fragmented landscapes (Sofia *et al* 2005, Freiria *et al* 2012). Nonetheless, some Amazonian *Eufriesea* species seem to prefer small and urban fragments (Morato 1994, Storck-Tonon *et al* 2013). Additionally, *Eufriesea* orchid bees are usually seasonal species (Dressler 1982, Janzen *et al* 1982, Kimsey 1982, Ackerman 1983, Roubik 2001), which may affect general discussions on their indicator status for anthropic areas.

Given this context, the generalist orchid bee, *E. nigrata*, would also be positively affected by the amount of disturbed areas found in the Cerrado. On the other hand, since other *Eufriesea* species seem to be negatively affected by human-related landscape disturbances (Sofia *et al* 2005, Sofia & Suzuki 2004), *Eufriesea auriceps* Friese (body length ranging from 16 to 19 mm), was expected to be negatively affected by habitat loss in Cerrado. Therefore, here we aimed to test the effect of habitat loss and habitat isolation on these two species of orchid bees. Specifically, we addressed the following questions: (1) if these species are affected by the structure of the landscapes we sampled in Cerrado, in which local spatial scale does the amount and isolation of anthropic areas influence the probability of occurrence of both species the most?, and (2) in what local spatial scale of our sampling sites does the amount and isolation of anthropic areas influence their abundances? As general expectations, we believed that *E. nigrata* would be either positively or not affected by the amount and isolation of anthropic areas while *E. auriceps* would be negatively affected by the features of our sampling sites.

Material and Methods

The Cerrado savanna, study areas, and sampling methods

The Cerrado is the second largest Brazilian biome and is considered one of the 25 worldwide biodiversity hotspots (Myers *et al* 2000). Originally, it covered almost a quarter of the country's political territory (IBGE 2004), but according to recent estimates, 39–55% of its range has been converted from its original vegetation types to soya, maize, and sugarcane plantations and pastures for extensive cattle-raising enterprises (Klink & Moreira 2002, Klink & Machado 2005, Carvalho *et al* 2009). This biome is characterized by a marked seasonality throughout the year, with a very humid season from October to April and striking consequences on both flora and fauna (Batalha & Mantovani 2000, Pinheiro *et al* 2002, Batalha & Martins 2004).

We selected our sampling areas considering both a macro- and a micro-regional scale. In the macro-regional scale, we gridded the state of Goiás, a core Cerrado area, with 25×25 km cells considering a land-use classification of the year 2002 for the whole biome (Sano *et al* 2008). Then, we eliminated all grid cells with overlapping boundaries with the state political borders (Fig 1a). Later, we calculated two different metrics, vegetation remnants isolation (log) and the amount of vegetation remnants using FRAGSTATS v3.3 (McGarigal & Marks 1995) and evaluated their correlation within the remaining grid cells (Fig 1b). In the third step, we selected eight grid cells which resembled the overall correlation pattern for all landscapes to be sampled (Fig 1c, d). At the micro-regional scale, within the eight sampled grid cells, we selected areas near either natural vegetation or crop plantation matrices ($n=49$) to sample the orchid bees. An example grid cell is shown in Fig 1e.

Since these bees are generally associated with humid habitats, streamlets and rivers generally serve as dispersal corridors, especially in drier areas such as the Cerrado and the Caatinga (Moura & Schlindwein 2009), all samplings occurred near streamlets we found within each grid cell. We sampled the specimens of both *E. nigrita* and *E. auriceps* from late February–April/2011 and March–April/2012 (late wet season) in 49 sites from the Cerrado savanna from the state of Goiás. We were only able to sample four grid cells each year. The grid cells sampled in 2011 and 2012 were respectively numbered and indicated with either “1” or “2” in Fig 1d.

In each sampling area, we delimited a 250-m transect, where at every 50-m interval, we set up a sampling station. Each sampling station was composed of five scent traps made of 2 L PET bottles, similar to the usual scent traps used in Euglossini field surveys (Campos *et al* 1989). We used the following five aromatic scents as attractants of orchid bees: vanillin, eucalyptol (cineol), eugenol, methyl salicylate, or

methyl cinnamate. Each scent trap was installed 5 m apart from each other and in tree branches with at least 1.5 m height. Three funnel-shaped entrances in the sides of the scent traps allowed the access of the bee specimens to their interior. We added 200 mL of soap water in the bottom of each scent trap to guarantee that the trapped bees did not escape until they were sampled. Each site had six traps of each aromatic scent, totaling 30 traps per sampling site. The scent traps remained at each sampling site for 48 h. Given logistical constraints, the scent traps were not recharged during this period. Although some criticism may be raised concerning this fact, since all sampling locations suffered from this same issue, we believe the population estimates of both *E. nigrita* and *E. auriceps* we obtained in each sampling area constitute a true representation of their abundances in the wild.

The strict use of scent baits sampling, without additional hand-netting surveys, is criticized elsewhere (Nemésio & Morato 2004, 2006, Storck-Tonon *et al* 2009) for underestimating local species richness toward medium to large body Euglossini bees, which are less prone to escape from the scent traps than are small-bodied species (e.g., *Euglossa* bees, Nemésio & Vasconcelos 2014). However, since we dealt with only medium to large body size species in this study, the use of scent traps without hand netting would still allow us to cover so many sampling sites within the same season, with no critical sampling issue (Mattozo *et al* 2011, Nemésio & Vasconcelos 2014). The sampled bees were deposited at the entomological collection of the Theory, Metapopulation, and Landscape Lab at the Universidade Federal de Goiás.

Sampling sites landscape classification

We obtained Landsat Thematic Mapper (TM hereon) images for the year 2010 from the Website of the Instituto Nacional de Pesquisas Espaciais (INPE; <http://www.inpe.br>) to classify our sampling sites. These images have a 30×30-m resolution and were composed by up to seven different spectral bands. From the final composite images used to classify the soil use of our sampling sites, we georeferenced and registered to landscape mosaics for further soil classification considering the TM3, TM4, and TM5 bands. We classified each image considering the scale 1:25,000. The main classes we used to classify our landscapes were: (1) riparian vegetation, (2) Cerrado vegetation remnants, (3) anthropic areas, and (4) water. Later, the classes (1) and (2) were lumped together, and the final classes we used in our analyses were: original Cerrado vegetation, anthropic areas, and water.

We manually classified the different soil uses of the surrounding landscapes of each sampling sites considering circular buffers from the sampling GPS coordinates with increasing and nested radii of 250, 500, 750, 1000, 1250,

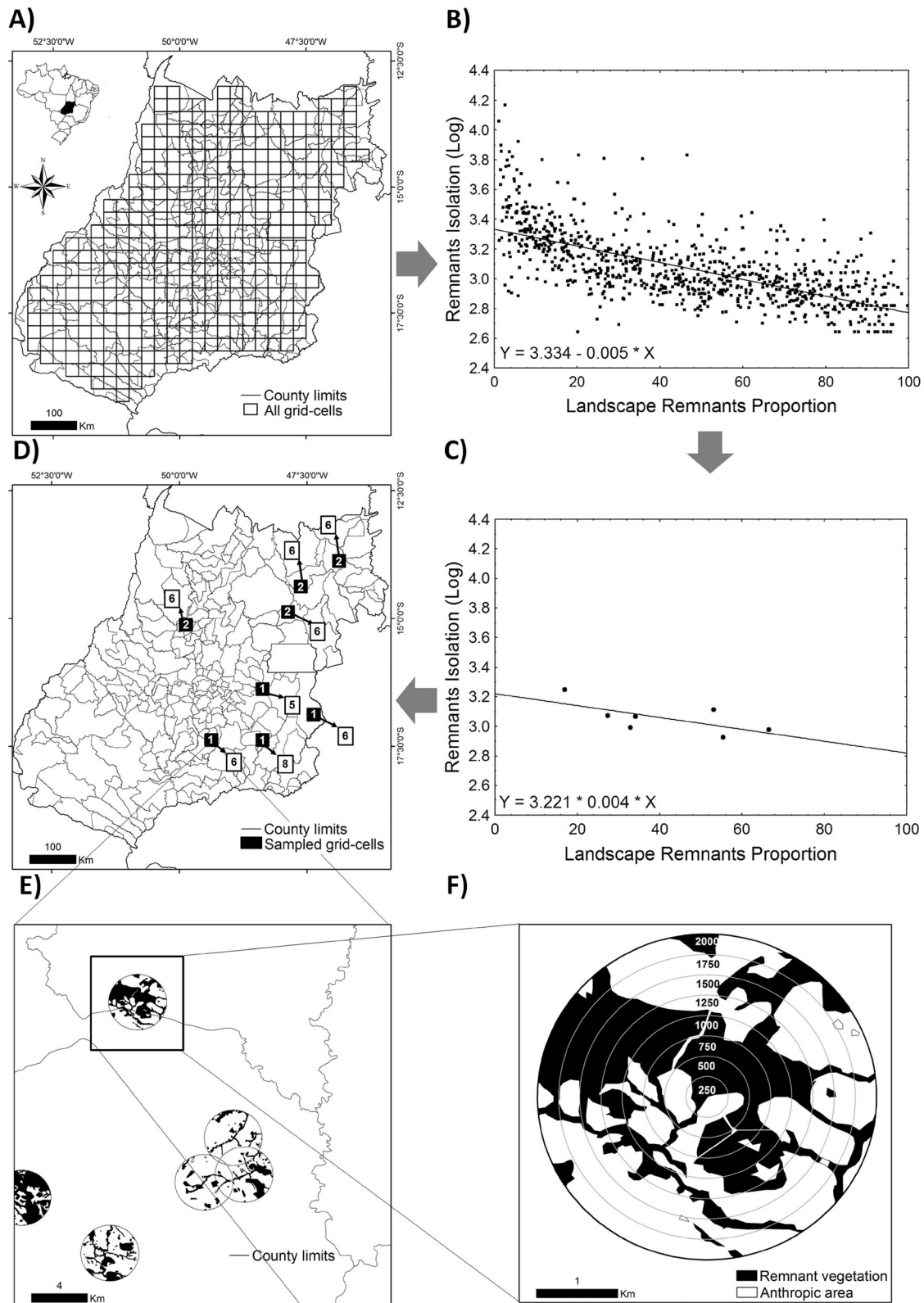


Fig 1 Visual representation of the process involved with the selection of the sampled landscapes. **a** The state of Goiás with all initial 25×25 km grid cells. **b** Gradient between landscape remnants proportion and remnants isolation found for the whole state. **c** Gradient between landscape remnants proportion and landscape remnants isolation found for the sampled grid cells. **d** Spatial distribution of all sampled grid cells within Goiás and the years when the sampling took place (*closed boxes*; 1=2011 and 2=2012) with the amount of sampling points visited within each grid cell (*open boxes*). **e** Visual representation of one 25×25 km grid cell with the 2-km buffers around six sampling sites. **f** All eight buffers surrounding a sampling site. The fitted correlations in (**b**) and (**c**) are expressed by the inset equations in both steps.

1500, 1750, and 2000 m, known to be relevant for bee communities as foraging distances (Fig 1f) (Greenleaf *et al* 2007, Taki *et al* 2007). We considered these different and nested buffers surrounding each sampling site as possible multiple scales affecting both probability of occurrence and abundances of *E. nigrita* and *E. auriceps*.

Statistical analyses

We used logistic regressions to test whether the probabilities of occurrence of *E. nigrita* and *E. auriceps* were determined by the amount of anthropic areas and isolation of the anthropic patches surrounding each of our sampling sites, considering the eight different spatial scales covered by the circular buffers around our sampling sites. We also performed multiple linear regressions in all eight spatial scales to test whether both species abundances were also determined by the isolation and the amount of anthropic areas surrounding our sampling sites. In order to assess the multi-scale landscape effect on the abundances of *E. nigrita* and *E. auriceps*, we retained both the R^2 and p values. We also repeated these procedures considering the amount of remnant Cerrado vegetation and their isolation, considering Fahrig's (2013) Habitat Amount Hypothesis, which states that only the amount of suitable habitats within the landscapes would be the determinants of the responses of species to landscape changes. Consequently, our expectations regarding both *E. nigrita* and *E. auriceps* probabilities of occurrence and abundance would be inverted, in relation to those predicted to the amount of anthropic areas and their isolation rates: with *E. nigrita* showing either no effects or being negatively affected by the amount of remaining Cerrado vegetation and *E. auriceps* being positively affected by increasing amounts of remnant Cerrado vegetation. The data was tested for both normality and homogeneity of variances, and it was transformed whenever necessary (Zar 2010). All analyses were done in Statistica 7.0 (StatSoft 2004).

Results

We sampled a total 506 specimens of *E. nigrita* (281 in 2011 and 225 in 2012), ~83.6% ($n=423$) using vanillin, ~15.8% ($n=80$) with eucalyptol, and the remainder ~0.6% ($n=3$) individuals were captured with eugenol and methyl cinnamate. No bees were captured with methyl salicylate. Regarding *E. auriceps*, we sampled a total of 91 specimens (39 in 2011 and 52 in 2012), ~90% ($n=81$) of which using vanillin. The remainder ten individuals were also attracted either by eugenol, methyl cinnamate, and methyl salicylate. During our samplings, ten other species of orchid bees were sampled. Nonetheless, given the fact that many of them were only

singleton individuals in our sampling sites, they were not considered in our analyses. The list of other species we sampled with the amount of sites where they were observed is shown in Table 1.

Both of our predictor variables, amount of anthropic areas and isolation of the anthropic patches, were negatively correlated in all local spatial scales but the one, at 250 m (2000 m, $r=-0.62$; 1750 m, $r=-0.57$; 1500 m, $r=-0.52$; 1250 m, $r=-0.56$; 1000 m, $r=-0.59$; 750 m, $r=-0.48$; and 500 m, $r=-0.30$). Therefore, we only used the amount of anthropic areas as our predictor variable. Our sampling sites showed varying quantities of the amount of anthropic areas within the buffers with 2000 m radius, with highly disturbed (more than 200 ha within the buffer) and highly preserve sites (less than 70 ha of anthropic areas within the buffer; Fig 2).

Our data did not corroborate any of our previous expectations for *E. nigrita*, since it was present in 48 of our 49 sampling sites in the Cerrado savanna; what implies is that the amount of anthropic areas did not affect its probability of occurrence in those areas at all. On the other hand, *E. auriceps* occurred in only 29 of our 49 sampling sites. Still, its probability of occurrence was not affected by the amount of anthropic areas within each different local multiple spatial scales of our sampling sites (Table 2). In general, our predictor variable also did not show any effect on the abundances of *E. nigrita* in any of our local spatial scales (Table 3). Nonetheless, the abundances of *E. auriceps* were positively affected by the amount of anthropic areas found at the 500-m scale ($R^2=0.115$; $p=0.04$), contrasting our initial predictions that this species would be negatively affected by the amount of anthropic areas in our sample sites. This indicates that this species may be positively affected by anthropic changes in Cerrado, despite the weak relationship. Although we expected broader scales showing the higher explanation of both species abundances, in general, we did not observe any effect for any of the buffers, either the smaller or the

Table 1 List of other euglossine bees sampled in our study in the state of Goiás not included in our analysis given their low abundances.

Sampled species	Number of sites observed
<i>Euglossa townsendi</i> Cockerell	6
<i>Euglossa cordata</i> (Linnaeus)	6
<i>Euglossa securigera</i> Dressler	8
<i>Euglossa imperialis</i> Cockerell	4
<i>Aglae caerulea</i> Lepeletier & Serville	3
<i>Eulaema meriana</i> Olivier	3
<i>Euglossa iopoeila</i> Dressler	3
<i>Eulaema cingulata</i> Fabricius	3
<i>Exaerete smaragdina</i> Guérin	2
<i>Eulaema helvola</i> Moure	1

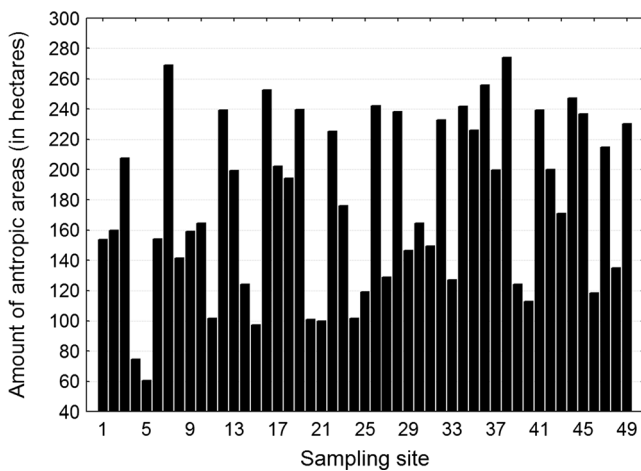


Fig 2 Amount of anthropic areas within all the 49 sampling sites where we sampled both *Eulaema nigrita* and *Eufriesea auriceps* in the state of Goiás, considering the broader buffer we used in our analyses (2000 m).

broader ones. When we considered the amount of remnant vegetation affecting both species, our results were practically the same, with both species not responding to the amount of remnants in any of the local spatial scales we considered (Online Resource Tables S1 and S2).

Discussion

Some studies have already shown the overall effects of habitat loss on orchid bees (Powell & Powell 1987, Becker *et al* 1991, Tonhasca *et al* 2002, 2003, Brosi 2009, Nemésio 2013). Despite our previous expectations, we did not observe any effect of landscape features on the abundances and probability of occurrence in the sampled sites for *E. nigrita*. *Eufriesea auriceps* behaved similarly to *E. nigrita*, once its probability of occurrence was neither negatively (our initial expectation) or positively affected by the amount of anthropic areas. Nonetheless, this species was positively affected at the scale of the 500 m, in contradiction to our prior

Table 2 Logistic regression analysis of the effects of amount of anthropic matrix on the probability of occurrence of *Eufriesea auriceps*.

Spatial scale (m)	Chi-square	<i>p</i> value
2000	1.864	0.172
1750	1.735	0.187
1500	1.736	0.187
1250	2.407	0.120
1000	2.340	0.126
750	1.953	0.162
500	1.831	0.176
250	0.314	0.575

In all regressions, degrees of freedom were equal to 1.

expectations that it would be negatively affected by the amount of available anthropic areas.

The habitat matrix formed after habitat loss occurs may imply in different permeability and resistances for the species that inhabit the newly affected areas. Consequently, the responses of different biological groups vary after a given landscape disturbance (Metzger & Décamps 1997, Baum *et al* 2004, Kupfer *et al* 2006, Fahrig *et al* 2011). Such species' responses to environmental disturbances are generally deeply related to their life-history and ecological traits (body sizes, diet breadth, dispersal abilities, and others), which directly affect their perception of the surrounding habitats, (Davies *et al* 2004, Henle *et al* 2004). Therefore, while some orchid bees are associated with forest interiors, protected from edge effects (e.g., *Euglossa sapphirina* Moure or *Euglossa annalis* Westwood (Nemésio & Silveira 2006, Tonhasca *et al* 2002)), others may either benefit or not be affected at all by habitat loss (e.g., *E. nigrita* and *E. auriceps*).

From the perspective of MacArthur & Levins (1964), the overall lack of responses of *E. nigrita* and the contradicting response of *E. auriceps*, may be related to the way they perceive their surrounding habitats. As medium to large body size species, they may perceive their surrounding habitats as fine grained in contrast to small-bodied ones, for which landscape features may seem coarser. From this stand point, although we did not observe any apparent effect of landscape features on both *E. nigrita* and *E. auriceps*, given their high dispersal abilities, landscape features found in broader spatial scales (bigger than 2 km radii; Jackson & Fahrig 2012) may eventually prove to be important for both of these and other Euglossini bees and should be tested in future studies. According to Jackson & Fahrig's (2012) suggestions, landscapes should correspond from four to nine times of the median dispersal distance of the species of interest or 0.3–0.5 of its maximum dispersal distance. Since medium to large body size orchid bees may cover daily ranges of 10–20 km (Janzen 1971, Raw 1989, Wikelski *et al* 2010), distances from the focal landscape ranging from 3 to 6 km may represent good radial distances from focal areas for the habitat-type classification that may be used by orchid bees.

Additionally, the occurrence of *E. nigrita* in almost all of our sampling sites may be explained by the inherent features of the Cerrado savanna, where even in pristine areas the vegetation is naturally opened when compared with pristine areas of Atlantic and Amazonian rainforests. Such a higher natural amount of open habitats has already been reported to allow increased abundances of *E. nigrita*, especially in the Atlantic forest (Morato 1998, Nemésio & Silveira 2006, Peruquetti *et al* 1999, Tonhasca *et al* 2002). Although *E. auriceps* had considerable smaller abundances in our sampling sites, when compared with *E. nigrita*, it also was not affected by the amount of anthropic areas available. *Eufriesea* species are rarer and seasonal (Dressler 1982,

Table 3 Regression analyses results of the effects of amount of anthropic matrix on the abundances of both *Eulaema nigrita* and *Eufriesea auriceps* in multiple spatial scales.

Spatial scale (m)	<i>Eulaema nigrita</i>					<i>Eufriesea auriceps</i>				
	B	SE of B	t value	p value	R ²	B	SE of B	t value	p value	R ²
2000	-0.018	0.068	-0.273	0.785	<0.001	0.026	0.026	1.006	0.323	<0.001
1750	-0.004	0.067	-0.065	0.948	<0.001	0.028	0.026	1.064	0.296	<0.001
1500	0.012	0.066	0.193	0.847	<0.001	0.028	0.025	1.089	0.285	<0.001
1250	0.031	0.063	0.501	0.618	<0.001	0.029	0.024	1.219	0.233	<0.001
1000	0.043	0.061	0.703	0.485	<0.001	0.032	0.022	1.448	0.158	<0.001
750	0.036	0.058	0.624	0.535	<0.001	0.036	0.020	1.786	0.085	0.072
500	0.059	0.055	1.078	0.286	<0.001	0.038	0.018	2.154	0.040*	0.115
250	0.078	0.053	1.471	0.147	<0.001	-0.015	0.021	-0.714	0.481	<0.001

* $\alpha=0.05$, level of significance.

SE standard error.

Kimsey 1982, Janzen *et al* 1982, Ackerman 1983, Roubik 2001), with abundance peaks occurring during the wet seasons of the year. Therefore, the end of the wet season may explain the abundance differences we observed between *E. auriceps* and *E. nigrita*. Some properties and behaviors of the nesting behavior of both species has been described by Zucchi *et al* (1969) and both use crevices or pre-existent ground cavities from abandoned termite or ant nests, naturally common in Cerrado (Carrizo *et al* 2008), to build their brood cells and nests, what allows these species to maintain the high abundances and higher presence probability.

Medium to large body size orchid bees, such as *E. nigrita* and *E. auriceps*, have remarkable dispersal abilities, being capable of covering great distances on a daily basis (Janzen 1971, Raw 1989, Milet-Pinheiro & Schindwein 2005, Wikelski *et al* 2010). Consequently, this trait is expected to protect them from negative effects of habitat loss (Cane 1987, Greenleaf *et al* 2007). On the other hand, some smaller orchid bees demand habitats with higher quality (e.g., less light, low temperature, higher humidity, and high food resources) to maintain viable populations (Morato 1994), which impede them from crossing small opened areas distances (Powell & Powell 1987, Becker *et al* 1991). Large forested patches are very important to maintain viable populations, high abundances of these bees, and orchid bees species richness (Nemésio & Silveira 2007a, 2010). Nevertheless, since the riparian areas found in Cerrado are naturally narrower than those found in the Amazon or the Atlantic forests, rarely reaching more than 100 m wide (Ribeiro & Walter 1998), border effects acting upon them may impede the survival of orchid bees intolerant to either open areas or border effects (Faria & Silveira 2011). Therefore, we suggest that future studies in Cerrado should invest efforts in testing the same hypotheses with small-bodied orchid bees found in this biome (e.g., species of the genus *Euglossa*), which are

expected to show a clearer response to habitat loss in the Cerrado biome than both *E. nigrita* and *E. auriceps*.

Finally, another possibility for the apparent no effect of landscape structure on the abundances of both euglossine bees from Cerrado savanna we analyzed here is related to their thermoregulatory capability. When compared with small-bodied Euglossini, medium to large body species, such as *E. auriceps* and *E. nigrita*, may be more suited to thermoregulate better in hotter and drier areas than small-bodied species, such as the *Euglossa* bees (May & Casey 1983, Casey *et al* 1985, Martins & Souza 2005). In general, basic entomological data on biological and ecological data of the species is far from completeness elsewhere in the world, nonetheless, such shortfall is even greater in tropical regions (Diniz-Filho *et al* 2010, Cardoso *et al* 2011), hindering direct predictions on the responses of bees to landscape changes. For instance, for *E. auriceps* (and *Eufriesea* species in general), which was not negatively affected by Cerrado's landscape features as previously imagined, there is big lack specific biological and ecological data (Nemésio *et al* 2013). Therefore, we believe (and encourage) that these assumptions and hypotheses relating the different orchid bees thermoregulatory abilities and their responses to landscape features need further and direct tests in field studies to better describe all possible responses of orchid bees to landscape changes in the Cerrado savanna, as well as in other biomes.

Considering the results related to *E. nigrita*, its status as indicator species of highly disturbed areas (Morato 1998, Nemésio & Silveira 2006, Peruquetti *et al* 1999, Tonhasca *et al* 2002) needs to be revised for the Cerrado savanna, despite its effective indicator use for disturbance in Atlantic and Amazonian forests (Morato 1998, Peruquetti *et al* 1999, Tonhasca *et al* 2002). Especially in the northern region of the Goiás, one of the more preserved Cerrado regions in the state (Sano *et al* 2008, Silva, personal communication), we

collected several *E. nigrita* specimens. The same also happened in well-preserved Cerrado areas found in the center of the state (e.g., Silvânia municipality), regions, we sampled new occurrences of the cleptoparasitic orchid bees, such as *Aglae caerulea* (Silva *et al* 2013) and *Exaerete* (unpublished data). Given their very specialized traits and dependency on other bees to complete their development, cleptoparasitic bees are usually pointed as good indicators of how preserved an area is, as they occupy the apex of bee communities and are one of the first groups to respond to habitat loss (Sheffield *et al* 2013). Even though the abundances of Euglossini bees may show striking variance from one year to another (Janzen *et al* 1982, Ackerman 1983, Roubik 2001), the predominance of *E. nigrita* and its higher abundances, as also noted in other studies performed within open habitat biomes, such as the Cerrado (Rebêlo & Cabral 1997, Rebêlo & Silva 1999, Nemésio & Faria 2004, Alvarenga *et al* 2007, Nemésio 2008, Faria & Silveira 2011, Knoll & Penatti 2012, Pires *et al* 2013, Viotti *et al* 2013) and the Caatinga (Andrade-Silva *et al* 2012), may not necessarily mean these areas are disturbed.

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