



Where the risk is more intense: riparian forests keep the euglossine bees community most affected by anthropic disturbance in the Caatinga dry forest

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Abstract

Anthropogenic disturbances have drastic negative effects on the biodiversity, thereby also compromising the ecosystem service it provides. Bees are one of the key players since they provide essential pollination services for both natural and agriculture ecosystems. Nevertheless, these insects are facing an increasing threat due to expansion of urban areas and inappropriate land use practices. Therefore, understanding the impact of different anthropogenic disturbances on bee communities is essential to assure the ecosystem functioning and human well-being. In this study, we made use of a well-known bee group, i.e., euglossine bees (Euglossine: Apidae), and of a fast-growing city to investigate the impact of anthropogenic disturbance on bee community. Using scent traps, we monthly collected male euglossine bees in seven sampling areas, differing in terms of the anthropogenic use/disturbance. Land use in each area was characterized through pre-georeferenced images and mapping software and from these data we calculated an Anthropogenic Transformation Index. Our results reveal that anthropogenic disturbance negatively impacts the euglossine bee community, in contrast to the positive effect of the proximity to the river. However, and perhaps the most alarming aspect of our findings, is the interaction effect between these two conditions, demonstrating that as we approach the river, parameters such as abundance, species richness, and diversity of these bee communities become more compromised by disturbance. Our study shows the urgent need to implement effective conservation strategies and sustainable management practices to protect and restore riparian forests in Caatinga urban areas, aiming to safeguard its associated biota and the valuable ecosystem services they provide.

Keywords Euglossini · Orchid bees · Conservation · Scent baits · Pollination

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Introduction

Anthropogenic disturbances affect various aspects of ecosystem functioning with drastic consequences on biodiversity, which can vary greatly across species (Hooper et al. 2012; Hautier et al. 2015). While a small group of species can benefit from the disturbance and proliferate, irrespective of whether they are exotic or native (referred as “winners”), a much larger proportion of native species succumb to the disturbance (“losers”) (Morris and Heidinga 1997; Baskin 1998; McKinney and Lockwood 1999; Tabarelli et al. 2012). As winners replace losers in the local area, a process of biotic homogenization occurs, hindering the ability of native biotas to reorganize in the face of landscape modifications (Lôbo et al. 2011). This scenario can be particularly intense in specific regions, such as in seasonal tropical dry forests, where anthropogenic disturbances strongly impact natural

resources exploited by human populations (Singh 1998; Specht et al. 2015). Another example of areas particularly susceptible to anthropogenic disturbance is those subjected to urban expansion (Mattison and Norris 2005). Therefore, studies investigating the effects of habitat disturbance on specific taxa in tropical dry forests, particularly in regions adjacent to urban contexts, are urgent.

Urban areas generate significant modifications to the landscape and environment, thereby impacting interspecific interactions within insect communities (McKinney 2006). Among insects, bees represent an important research focus since they provide essential pollination services for both agriculture and natural ecosystems but are greatly threatened by inappropriate land use practices (Potts et al. 2010, 2016; Kerr et al. 2015; Cardoso and Gonçalves 2018). Bees heavily depend on their habitat to acquire vital resources necessary for their survival and reproduction, including nectar, pollen, resins, and scents (Michener 2007). As a result, they exhibit a high sensitivity to land use modifications (Millard et al. 2021), including habitat destruction and fragmentation (Tonhasca et al. 2002). These anthropogenic actions impact the environment, particularly the local bee communities, by reducing food sources and nesting areas while increasing the exposition to pesticide and predation risk (Roulston and Goodell 2011; Potts et al. 2016; Goulson et al. 2018). Consequently, areas with heavily urbanized and extensively agricultural landscapes typically exhibit lower bee abundance and diversity compared to semi-natural areas (Winfrey et al. 2011; Bracken and Low 2012; Kennedy et al. 2013). Conversely, urban areas can support some bee diversity by providing habitats for species with adaptable traits, such as thermal tolerance and nesting site plasticity (Banaszak-Cibicka and Żmihorski 2012; Ribeiro and Taura 2019). This highlights the need for tailored conservation strategies to ensure the proper preservation of different bee groups amidst urbanization.

Among the various groups of bees, those belonging to the tribe Euglossini (Hymenoptera: Apidae) stand out as an interesting system for studying the impacts of anthropogenic disturbances. This is because of their crucial role as pollinators of hundreds of plant species from no less than 70 families and their sensitivity to habitat alterations (Dressler 1982; Milet-Pinheiro and Schlindwein 2005; Darrault et al. 2006; Grandolfo et al. 2013; Rodrigues et al. 2018). These bees have specific ecological requirements to survive, including a variety of resources and suitable environmental conditions. Females visit flowers in search of: 1) pollen to feed their larvae (Dressler 1982; Ramírez 2009) and 2) resins to construct their nests (Armbruster 1996; Lopes and Machado 1998). On the other hand, males collect and store chemicals from natural sources (mainly flowers), which play an important role in sexual signalling and species recognition, acting as a honest signal of male fitness (Zimmermann et al. 2009;

Weber et al. 2016, Henske et al. 2023). Finally, both males and females rely on nectar obtained from hundreds of plants species as energy source (Dressler 1982; Ackerman 1985; Roubik and Hanson 2004). Therefore, it is reasonable to expect that the depletion of plant sources providing these essential resources can have negative impacts on bees.

Regarding environmental conditions, euglossine bees are predominantly found in areas of tropical rainforests, on which they strongly depend (Dressler 1982; Darrault et al. 2006). In tropical rainforests, euglossine bees exhibit higher species richness and abundance, with records of 62 species in the Atlantic Forest and 127 species in the Amazon Rainforest, while few species are recorded in dry forest environments (Dressler 1982; Peruquetti et al. 1999; Zanella 2000; Nemésio and Silveira 2007). In the Caatinga, the largest seasonally dry tropical forest in the Neotropics, the studies performed so far have reported only five euglossine species (Zanella 2000; Martins et al. 2003; Lopes et al. 2007). However, small areas with vegetation resembling moist forests embedded within the Caatinga, such as mountainous regions and riparian forests, are capable of maintaining a higher diversity of euglossine bees in this environment (Rebêlo 2001; Moura and Schlindwein 2009). Riparian forests represent a special case as they are vegetative formations occurring along the banks of rivers, streams, and springs, playing a crucial role in the protection and conservation of water resources. In these areas, it is even possible to find euglossine species that are typical of the Atlantic Forest, highlighting the important role of this vegetation as biocorridors for these bees (Moura and Schlindwein 2009).

In face of the close relationship between euglossine bees and the environmental conditions of humid forests, only few species are tolerant to open areas or resilient to disturbances. Actually, in most cases, the habitat loss due to the fragmentation of humid forests results in population declines of these bees (Powell and Powell 1987; Tonhasca et al. 2002; Carneiro et al. 2022). This scenario is even more concerning in the Caatinga, where moist habitats are naturally limited. The Caatinga, a peculiar Seasonally Dry Tropical Forests from Brazil, presents at least 13 different physiognomies but is one of the most degraded forests due to excessive exploitation and human occupation (Myers et al. 2000; Pennington et al. 2009). In this context, riparian forests in the Caatinga face serious risks and challenges. These areas are subject to degradation and destruction due to intense anthropogenic pressure. Deforestation for agricultural purposes, removal of native vegetation for infrastructure development, such as roads and dams, and water contamination by pollutants are among the main impacts in the Caatinga, which affect strongly riparian forests (Silva et al. 2020a; Silva-Araújo et al. 2020).

Given the aforementioned scenario, understanding how euglossine bees respond to anthropogenic disturbances and

depend on riparian forests can provide crucial information for proposing effective conservation strategies and management practices to preserve the biodiversity and ecological integrity of the Caatinga dry forest. Therefore, in this study we investigated the impact of anthropogenic transformation on the euglossine bee community in the Caatinga region, as well as the potential influence of different river distances as a proxy for riparian forest occurrence. We used as model a set of locations in Petrolina, a Brazilian Northeast city located in the midst of the Caatinga domain along the banks of the São Francisco River. By examining the effects of human-induced changes on the composition and structure of euglossine bee communities, this research contributes to our understanding of the ecological consequences resulting from land use transformation in the Caatinga ecosystem. Additionally, evaluating the relationship between bee communities and river distance can provide valuable insights into the role of riparian habitats as potential refuges or corridors for these bees.

Material and methods

Study site and sampling areas

The study was conducted in the city of Petrolina, Pernambuco, in the Northeast region of Brazil (Fig. 1). Petrolina is characterized by a semi-arid climate with an annual precipitation of 435 mm, classified as BShw according to the Köppen classification system, featuring concentrated summer rainfall and an average air temperature of approximately 24.8 °C (Heriberto and Teixeira 2010; Jatobá et al. 2017). It is situated within the sub-middle course of the São Francisco River (the second-largest river in Brazil and the largest entirely within Brazilian territory) and falls within the domain of the Seasonally Dry Tropical Forest known as Caatinga. Petrolina is a prominent center for irrigated fruit production, ranking as the second-largest producer of grapes and one of the leading exporters of mangoes in Brazil (Prefeitura de Petrolina 2022). The original vegetation in the region is

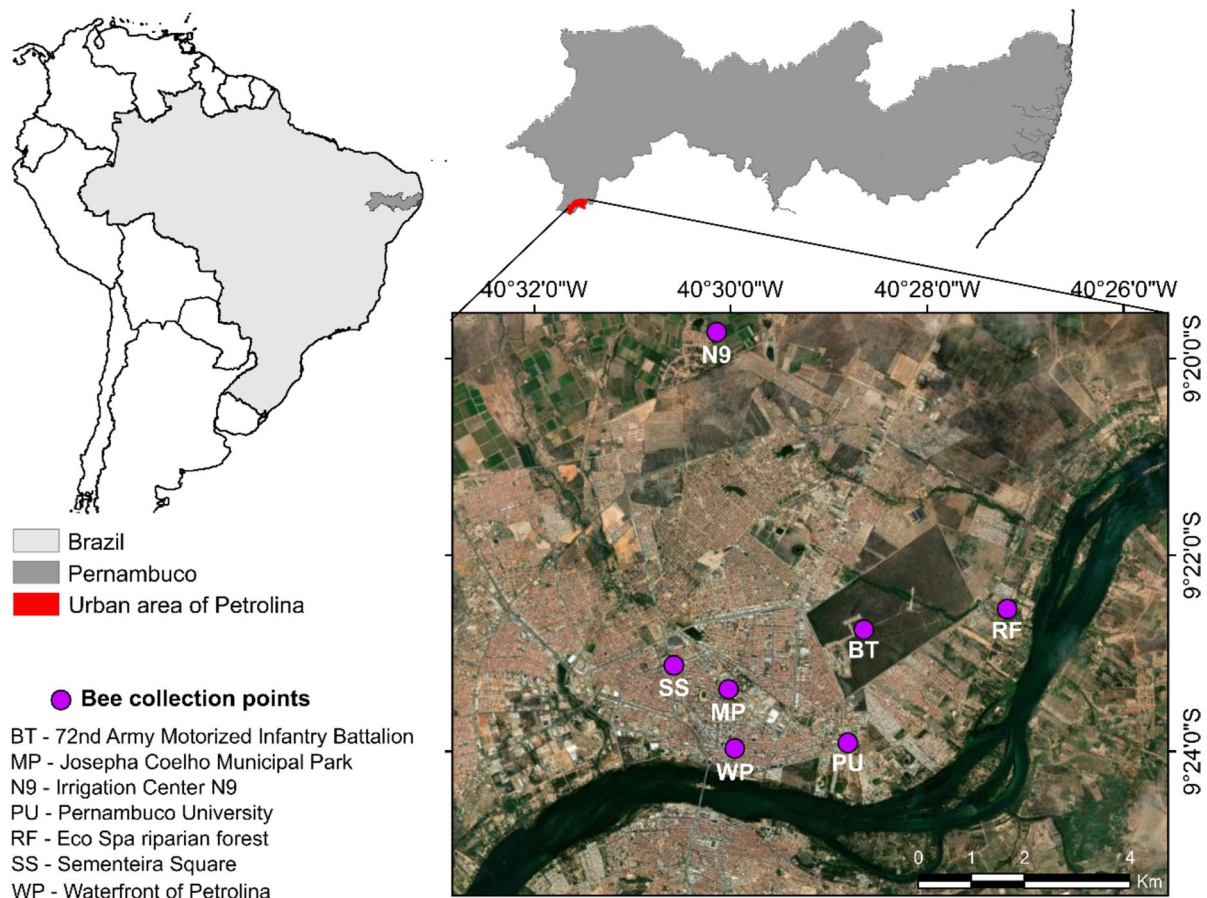


Fig. 1 Sampling sites of male euglossine bees within the urban area of Petrolina municipality, located along the São Francisco River in the State of Pernambuco, Northeast Brazil

progressively being replaced by urban areas and irrigated plantations, resulting in a landscape where the city features extensively transformed vegetation, with only a few remnants of native vegetation and small, heavily impacted strips of riparian forests.

Within the urban area, seven sampling areas were selected (Fig. 1; Table 1) based on logistical considerations (accessibility, safety, and feasibility of sampling) as well as the specific attributes of interest in this study (different land use levels, anthropogenic disturbances, and varying distances from the riverbank). We ensured a minimum distance of approximately 2 km between each of the sampling points, which is more than twice the average flight distance of the bees (Milet-Pinheiro and Schindwein 2005). This precaution was taken to avoid potential spatial autocorrelation effects.

Characterization of the sampling areas

The areas were characterized based on two aspects. Firstly, the distance from the river, which served as a proxy for the potential occurrence of riparian vegetation in each area. This measure was obtained by determining the minimum linear distance from the focal collection point to the nearest riverbank, using Google Maps. Secondly, we aimed to portray the level of anthropogenic disturbance present in the sampling areas. To achieve this, we employed the Anthropogenic Transformation Index (ATI), a method that assigns weighted scores to different land cover types, resulting in an index of anthropogenic pressure on natural resources (Gouveia et al.

2013; de Almeida et al. 2022). We chose the ATI because it allows us to synthesize the extent of area modification caused by human activities into a single value. The methods used to measure land cover types and calculate the index are described in Supplementary Information.

The selected areas exhibited a wide range of distances from the river and were subjected to varying levels of disturbance. The areas closest to the river were the Riparian Forest (hereafter RF) and the Waterfront of Petrolina (WF), where collections were conducted near the riverbank. The majority of the other areas, i.e. the 72nd Motorized Infantry Battalion (BT), the Experimental Station of the Pernambuco University (PU), the Josepha Coelho Municipal Park (MP) and the Sementeira Square (SS), were situated at intermediate distances from the river, ranging from one to three kilometers away from the riverbank, therefore not under the influence of the river. The Irrigation Center N9 (N9), on the other hand, was situated eight kilometers far from the river.

Regarding land use types, the areas present a diverse range of conditions (Fig. 2A). BT, N9, and RF exhibit the highest vegetation coverage. In BT, there is only two types of land use, i.e. secondary vegetation with small patches of exposed soil. This area presents the highest vegetation coverage of all (89.63%). In contrast, N9 is the only area that has four types of land use, including degraded vegetation, exposed soil, residential areas, and extensive coverage of irrigated fruit orchards. This area has the second-highest vegetation coverage, with 66.28% of the coverage consisting of fruit orchards (mango plantation). RF ranks third in terms of vegetation coverage, primarily characterized by degraded

Table 1 Description of areas in which euglossine bees were sampled in the city of Petrolina, Pernambuco, Northeast Brazil

Area (abbreviation)	Latitude*	Longitude*	Description
Eco Spa riparian forest (RF)	9,37550°	40,44836°	Area under real estate expansion with an advanced degree of degradation yet containing patches of native riparian vegetation
Irrigation Center N9 (N9)	9,32885°	40,50229°	An area of irrigated fruit cultivation situated between two mango (<i>Mangifera indica</i>) plantations
72nd Army Motorized Infantry Battalion (BT)	9,37933°	40,47725°	An area of Caatinga characterized by arboreal and shrub vegetation that has remained unaltered since 1975 when it was a crop field (Tenente Rafael dos Santos Dantas, personal communication)
Pernambuco University (PU)	9,39859°	40,48008°	An experimental field of the university surrounded by a heavily urbanized area, featuring remnants of regenerating native vegetation (arboreal and shrub) within its boundaries
Josepha Coelho Municipal Park (MP)	9,38951°	40,50028°	A tree-covered area consisting of both native and exotic plant species, regularly irrigated and extensively utilized for recreational purposes by the population
Sementeira Square (SS)	9,38536°	40,50955°	An urban area located in close proximity to commercial establishments, residential houses, and schools
Waterfront of Petrolina (WP)	9,40315°	40,50043°	A location on the bank of the São Francisco River where the riparian vegetation has been completely removed to make way for a recreational area

*Geographic coordinates of the sampling areas were obtained using a GPS receiver device from the etrex 20 model by GARMIN, which uses the Global Positioning System via satellite

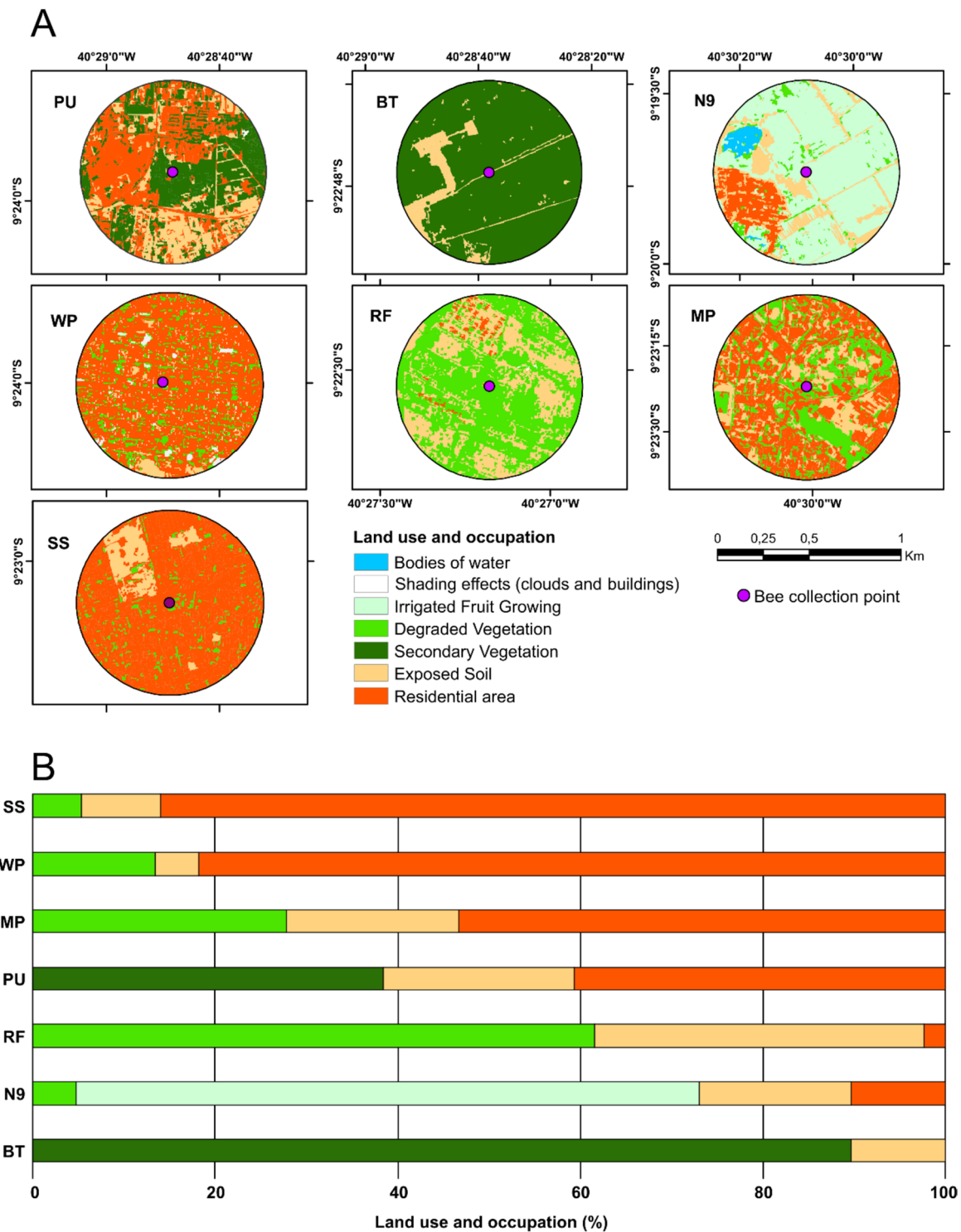


Fig. 2 Land use and land cover within the sampling areas of Euglossini bees in the urban area of Petrolina municipality, State of Pernambuco, Northeast Brazil. **A** Maps within a 500-m radius from the col-

lection points. **B** Bar chart illustrating the proportion of land uses and land cover in each area. (Details regarding the abbreviations of sampled locations can be found in Table 1 and Fig. 1)

vegetation (61.55%). The remaining areas display three land use types, which are degraded/secondary vegetation, exposed soil, and a significant portion of residential areas. SS has the highest residential occupancy (85.96%), followed by WF (80.30%), MP (53.30%), and PU (40.66%) (Fig. 2B).

The sampling areas also show a wide range of ATI values among them (Table 2). The ATI scores varies from 3.6 in the most preserved area (BT) to 9.5 in the most degraded/anthropized area (SS).

Abundance, richness, and diversity of Euglossini bee community

To sample the male euglossine bees, we employed scent baits, a well-known and widely used technique that allows for the standardization of the type of scent, the number of traps employed per unit area, and the sampling duration (Rebêlo 2001). The methodology involves exposing synthetic compounds that are attractive to these bees in the environment. After a few minutes, the male bees approach in an attempt to collect the synthetic compounds, providing the opportunity for bee collection (Becker et al. 1991; Oliveira et al. 1995).

For this study, we combined this technique with traps consisting of a two-liters PET bottle with two lateral openings. The cut-off upper parts of two other bottles were inserted as side entrances to the trap. The inner surfaces of the two entrances were scraped to facilitate bee adhesion and entry into the traps (Roubik and Hanson 2004; Nemésio 2009). Inside each trap, we placed a 2 ml glass vial (Analitica) filled with cotton and a synthetic compound. The vials were filled with 1.5 ml of the following synthetic compounds: scatol, methyl salicylate, β -ionone, vanillin, benzyl acetate, eucalyptol, eugenol, veratrol, (*E*)-methyl cinnamate, benzyl benzoate, and geraniol. The vials filled with the synthetic compounds were placed inside the traps immediately before they were hung in the field.

Using this method, monthly samplings were conducted between September 2021 and August 2022 for each selected area (N = 12 samplings for each location). On each sampling day, eleven scent traps were hung at least

2 m apart from each other. All collections were performed under similar weather conditions, on sunny days. The traps were set up at 8:00 a.m. and retrieved at 12:00 p.m., which corresponds to the peak foraging activity of male euglossine bees (Armbruster and McCormick 1990; Roubik and Hanson 2004).

After the exposure period in the field, the captured bees were euthanized in a 20 ml glass containing ethyl acetate and sorted according to the compound used, collection date, and location. The bees were then taken to the laboratory, where they were pinned, dried in an oven for 48 h at 40°C, identified, and labeled with collection information. Identification was done using taxonomic keys and by comparing the specimens with bees from the collection of the Laboratory of Ecological Interactions and Semiochemicals, UPE Campus Petrolina (Roubik and Hanson 2004; Nemésio 2009). Sampling was authorized by ICM-Bio (permit number: 78784–1, ICMBio).

Statistical analyses

Different metrics were used to analyze the euglossine communities, including abundance, richness, and diversity. The diversity of the communities in different areas was determined using the Shannon–Wiener index, which calculated species diversity per area using the formula: $H' = \sum pi * (\ln pi)$, where $Pi = n$ (number of individuals of a species) / N (total number of individuals in the area).

The effect of river distance and ATI on the richness and abundance of euglossine bees was assessed using Generalized Linear Mixed Models (GLMM) with a Poisson distribution. In these models, we included river distance and ATI, as well as their interaction, as explanatory variables. We also included the different months in which the collections were conducted as random variables. Each model had different response variables, which were richness, total abundance of bees, and abundance of the two main sampled species (see results). The analyses were performed

Table 2 Anthropogenic Transformation Index (ATI) of sampling areas for Euglossini bees in the city of Petrolina, Pernambuco, Northeast Brazil. (A zero value in the classes of the Anthropogenic Transformation Index indicates that this type of land use does not exist in the area, considering a 500 m radius)

Classes	Areas						
	BT	RF	PU	N 9	MP	WF	SS
Exposed soil	1	3,6	2	1,6	1,8	0,4	0,8
Residential area	0	0,2	4	1	5,3	8	8,5
Irrigated fruit growing	0	0	0	4,6	0	0	0
Degraded vegetation	0	2,4	0	0,1	1,1	0,5	0,2
Secondary vegetation	2,6	0	1,1	0	0	0	0
ATI	3,6	6,2	7,1	7,3	8,2	8,9	9,5

*The weights of the classes follow Nogueira et al. (2001), Rocha et al., (2009), Gouveia et al. (2013), and Almeida et al. (2022) (for details, see Supplementary Information)

using the lme4 package (Bates et al. 2015) implemented in the R software (RCoreTeam 2023).

Results

Abundance, richness, and diversity of euglossine bee community

We collected a total of 237 males of euglossine bees from eight species (Table 3). The most representative genus was *Euglossa*, with 172 individuals from seven species (of which, so far, only five have been adequately identified). *Euglossa cordata* was the most abundant species, with 150 individuals, representing 87.20% of the collected individuals of this genus. The other species were all rare, ranging from one (*Euglossa despecta*) to eight (*Euglossa melanotricha*) collected individuals. The other sampled genus was *Eulaema*, with 65 individuals of a single species, i.e. *El. nigrita*. Representatives of the other three Euglossini genera, namely *Aglae*, *Eufriesea*, and *Exaerete*, were not sampled.

The calculation of the Shannon–Wiener index indicated greater diversity for sampling areas near the river, i.e., $H' = 1.07$ in RF and $H' = 1.12$ in WF. The other areas presented an index ranging from $H' = 0.27$ in MP and $H' = 0.68$ in PU (Table 3).

When considering bee abundance, our results clearly demonstrate that areas close to the river have more bees compared to more distant areas. Regarding ATI, except for BT (which proved to be an outlier), lower values of this index were associated with higher bee abundance. In fact, we confirm that the total abundance of euglossine bees is negatively influenced by both the ATI (Estimate = -1.14; Std.error = 0.11; $Z = -10.80$; $P < 0.0001$; Fig. 3A) and the distance from the riverbank (Estimate = -4.10; Std. error = 0.39; $Z = -10.48$; $P < 0.0001$; Fig. 3B). There

is also an interaction effect between distance and ATI, where one variable intensifies the effect of the other (Estimate = 0.53; Std.error = 0.06; $Z = 9.25$; $P = < 0.0001$) (Figs. 4). It is important to note that the interaction effect is cooled at greater distances from the river with low ATI values (Fig. 4A, B), suggesting that the closer to the riverbank the greater the impact of degradation on bee abundance. The same pattern was found in terms of bee richness. In this regard, we confirm that euglossine bees are also negatively affected in their richness by both the ATI (Estimate = -0.31; Std.error = 0.15; $Z = -2.09$; $P < 0.01$; Fig. 3C) and the distance from the river (Estimate = -1.36; Std.error = 0.53; $Z = -2.57$; $P < 0.01$; Fig. 3D), as well as the interaction effect between these variables (Estimate = 0.15; Std.error = 0.07; $Z = 2.05$; $P < 0.05$; Fig. 4C).

A more detailed analysis, considering the abundances of the only species present in all areas and the most abundant in this study, supported the same pattern. The abundance of *Euglossa cordata* is negatively influenced by the distance from the riverbank (Estimate = -4.05; Std.error = 0.50; $Z = -8.07$; $P = < 0.0001$) and ATI (Estimate = -1.04; Std. error = 0.12; $Z = -8.47$; $P = < 0.0001$), with an interaction between these variables (Estimate = 0.53; Std.error = 0.07; $Z = 7.44$; $P = < 0.0001$). Similarly, *Eulaema nigrita* was also negatively influenced by the distance from the riverbank (Estimate = -4.53; Std.error = 1.02; $Z = -4.44$; $P = < 0.0001$) and ATI (Estimate = -1.57; Std.error = 0.36; $Z = -4.39$; $P = < 0.0001$), showing also an interaction effect between distance and ATI (Estimate = 0.55; Std.error = 0.17; $Z = 3.20$; $P < 0.01$).

Discussion

The findings of the present study provide an in-depth exploration of the diverse land use patterns and the range of disturbance levels observed within the city of Petrolina.

Table 3 Species list and community parameters of sampling areas for Euglossini bees in the city of Petrolina, Pernambuco, Northeast Brazil

Bee species	Individuals	Individuals in each area							
		BT	RF	MP	SS	WF	N9	PU	
<i>Eulaema nigrita</i> Lepeletier, 1841	65	3	55	1	1	3	1	1	
<i>Euglossa cordata</i> Linnaeus, 1758	150	2	87	31	5	10	8	7	
<i>Euglossa despecta</i> Moure, 1968	1	0	1	0	0	0	0	0	
<i>Euglossa melanotricha</i> Moure, 1967	8	0	7	1	0	0	0	0	
<i>Euglossa stellfeldi</i> Moure, 1947	3	0	3	0	0	0	0	0	
<i>Euglossa truncata</i> Rebelo & Moure, 1996	2	0	0	0	0	2	0	0	
<i>Euglossa</i> sp. 1	5	0	2	0	0	2	0	1	
<i>Euglossa</i> sp. 2	3	0	3	0	0	0	0	0	
Total abundance	237	5	158	33	6	17	9	9	
Richness	-	2	7	3	2	4	2	3	
Diversity index (Shannon–Wiener)	-	0.67	1.07	0.27	0.45	1.12	0.35	0.68	

Fig. 3 Scatter plot showing the effects of Anthropogenic Transformation Index (ATI) and Distance from the São Francisco River on Total Abundance (A, B) and Species Richness of euglossine bees (C, D). (Blue lines indicate regression trend lines for the fitted models, and gray areas represent 95% confidence intervals; outliers corresponding to BAT locality have been removed from Figures A and C for better visualization of the trend line)

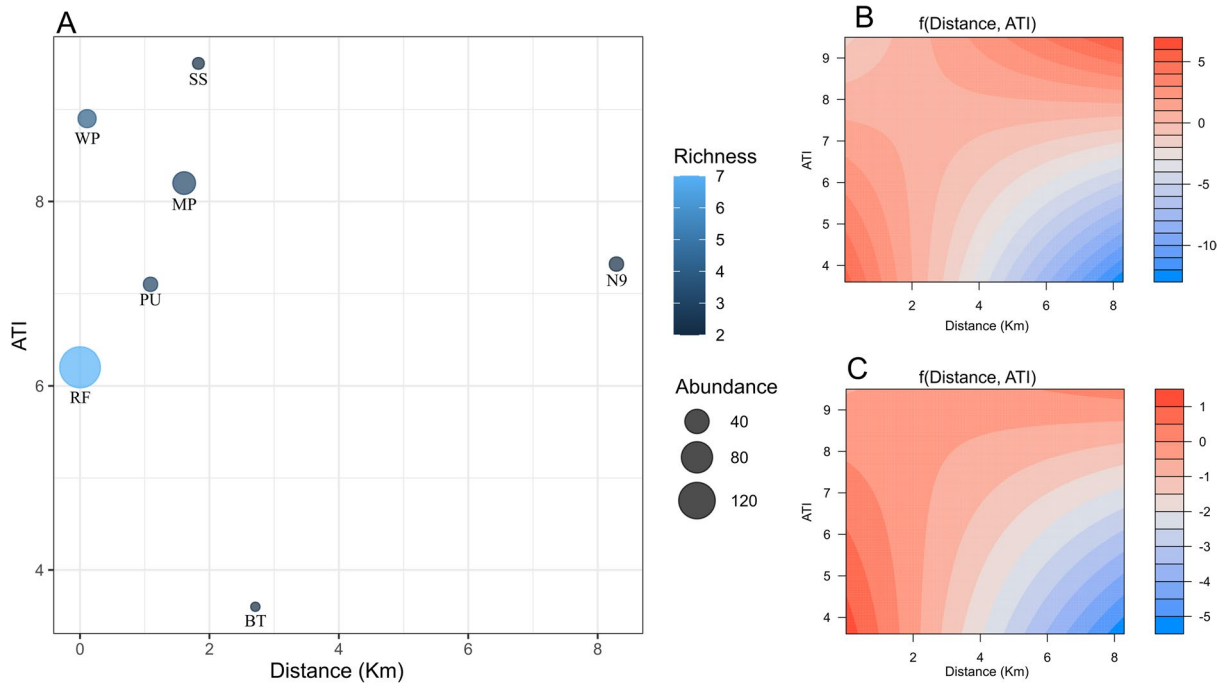
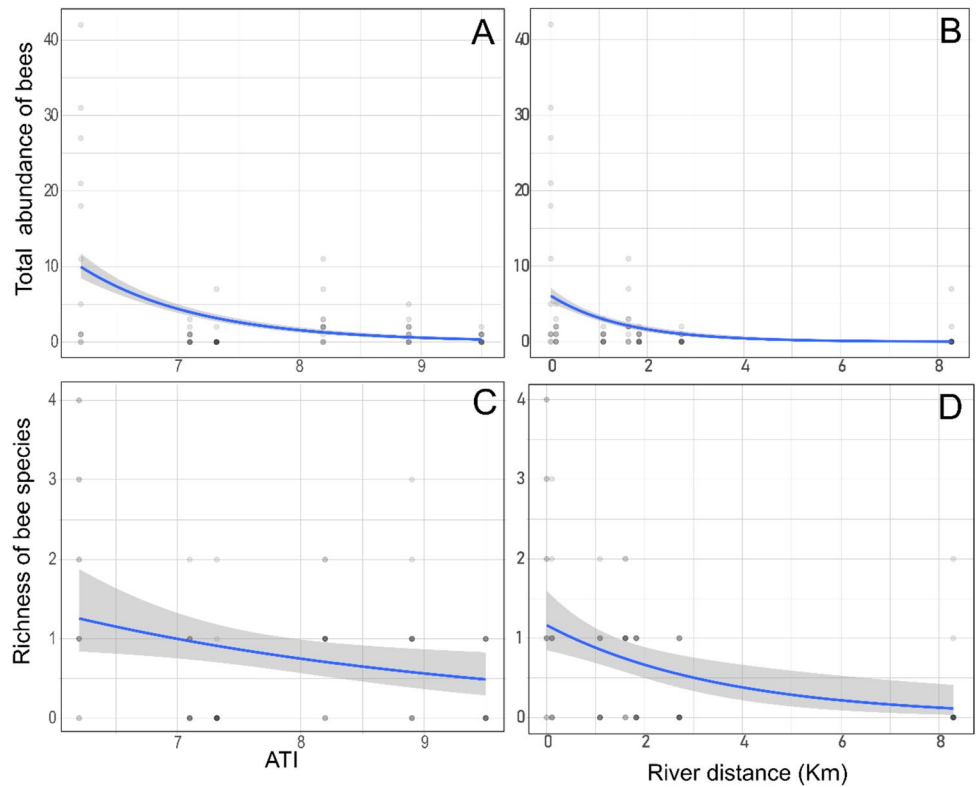


Fig. 4 A Scatter plot depicting the variation in bee abundance and richness as a function of ATI and distance from the São Francisco River. (Details regarding the abbreviations of sampled locations can

be found in Table 1 and Fig. 1). B-C Heatmap illustrating the interaction between the explanatory variables, riverbank distance, and ATI, on Euglossini bee abundance (B) and richness (C)

These patterns are observed across different distances from the river. In this urban context, we identified eight species belonging to two genera of euglossine bees, which is a notably high number considering the arid Caatinga dry forest. As expected, our results reveal that proximity to the river and the level of disturbance significantly impact the euglossine bee community. Similarly, anthropogenic disturbance also exhibits a negative effect on the bee community. However, and perhaps the most alarming aspect of our findings, is the interaction effect between these two conditions, demonstrating that the distance from the riverbank determines how anthropogenic disturbance affect the euglossine bee community. As we approach the river, parameters such as abundance, species richness, and diversity of these bees become more compromised by disturbance. This effect holds true even for species that seemingly respond well to disturbance, such as *Euglossa cordata* and *Eulaema nigrita*. Below, we discuss the identified patterns and highlight their potential implications for the conservation of this distinct group of pollinating insects.

The euglossine community in the Caatinga concentrates in riparian forests

As discussed earlier in this paper, euglossine bees are known for their specific preferences for habitats and floral resources, and their occurrence can be influenced by a range of environmental factors. In the context of the Caatinga, the presence of euglossine bees has been observed to be concentrated in riparian forest areas, as confirmed here. However, this is not an isolated process. Studies conducted by Brito et al. (2017) in the Amazon rainforest identified indicator bees for primary forests, revealing that the composition of euglossine bee assemblages also varies according to vegetation cover. These findings indicate the crucial role of riparian forests and forest reserves in sustaining euglossine bees, even in landscapes affected by the presence of oil palm plantations in the Amazon region. This observation is further supported by the study conducted by Faria and Silveira (2011) in the Cerrado, where riparian forests play a crucial role as corridors for forest-associated euglossine bees. In all these contexts, riparian forests provide a connection between forested areas, allowing bees to move between these fragments and ensuring the dispersal and viability of their populations.

One of the reasons suggested to explain the abundance of euglossine bees in riparian forests is the year-round availability of floral resources. Studies have demonstrated that riparian vegetation harbours a rich diversity of flowering plants, ensuring a continuous and varied food source for these bees (Moura and Schindwein 2009; Montoya-Pfeiffer et al. 2020). Moreover, riparian forests provide suitable conditions for nesting, as demonstrated for both solitary and

social bees (Moura and Schindwein 2009; Brito et al. 2017). Another plausible explanation for the concentration of euglossine bees in riparian areas is related to the favourable environmental conditions found in these locations. According to Cândido et al. (2021), the temperature and humidity characteristic of riparian forests can be determining factors for the good development of the nests of these bees. Adequate temperature is essential for the successful reproduction and survival of euglossine offspring, and humidity also plays an important role in their life cycle. Thus, riverbanks, where humidity is usually higher and the temperature is more moderate than surrounding Caatinga areas, might offer better conditions for the nesting of these bees. However, despite these plausible explanations, there is still a lack of data and detailed studies on the diversity and ecology of euglossine bees in riparian forests (Moura and Schindwein 2009; Faria and Silveira 2011). Therefore, further research is still necessary to better understand the occurrence patterns of these bees and the factors influencing their preference for these habitats.

Anthropogenic disturbance in urban areas negatively affects the euglossine community

Our results demonstrate that anthropogenic disturbance resulting from human activities significantly influences the euglossine bee communities in the Caatinga. Habitat destruction is a crucial factor that affects the composition and diversity of these bees, as indicated by the Anthropogenic Transformation Index (ATI) and supported by previous studies (Nemésio and Silveira 2006; Rasmussen 2009; Allen et al. 2019). Increased disturbance is associated with a decrease in the abundance, richness and diversity of euglossine bees, highlighting the importance of conserving their natural habitats. Landscape modification in urban areas and agricultural use emerge as significant causes of reduction in the wetter areas of the Caatinga. The continuous growth of urban areas results in the depletion of natural resources, including nesting sites and food sources such as pollen and nectar (Santos et al. 2019), and this resource limitation strongly impacts the richness and abundance of euglossine bee species (Zanette et al. 2005; Storck-Tonon et al. 2013). The effect of habitat destruction in Caatinga areas is not limited to euglossine bees but also affects various other groups of pollinators and insects in general, such as flies, butterflies, and ants (Almeida et al. 2011; Barbosa et al. 2021; Melo et al. 2023).

In addition to the reduction in natural resources, anthropogenic disturbance can result in abiotic alterations in the environment. Increased wind incidence, higher temperatures, and reduced shading are some of the new abiotic conditions associated with habitat destruction (Zanette et al. 2005; Storck-Tonon et al. 2013; Cardoso and

Gonçalves 2018). These environmental changes have a substantial impact on bees, particularly on solitary and native species. Consequently, even small or highly disturbed natural areas situated in urban environments can serve as crucial refuges for a variety of euglossine species (Aronson et al. 2017). Interestingly, our study demonstrated that even the dominant euglossine species, i.e. *Eg. cordata* and *El. nigrata*, are also sensitive to anthropogenic disturbances, despite their general ability to persist in disturbed areas (Silva and De Marco 2014; Oliveira et al. 2015).

The distance from the river determines the effect of disturbance on euglossine bees in urban areas of Caatinga

The proximity to rivers plays a crucial role in determining the impact of anthropogenic disturbance on Euglossini bee populations in urban areas of the Caatinga. This suggests that the riverine environment provides certain advantages and mitigates the detrimental effects of anthropogenic activities. One particular point worthy of mention is that the BT area exhibited low abundances and species richness of bees, despite being the area with the lowest level of disturbance. This exemplifies that the hyper-xerophilous native vegetation of the Caatinga, even in good condition, may not be the most suitable environment for the maintenance of these insects. In contrast, even in the more disturbed areas at some distance from the river, such as the MP or the SS, for example, there are often artificial irrigation systems in place, ensuring the presence of larger cultivated trees. This condition could result in higher humidity in these areas, a significant abiotic factor determining the occurrence of euglossine bees.

One possible explanation for this pattern is the availability of resources. Riverside areas often harbour a greater diversity and abundance of flowering plants, providing a continuous and reliable food source for euglossine bees throughout the year (Moura and Schlindwein 2009; Montoya-Pfeiffer et al. 2020). Additionally, the proximity to water sources alone ensures higher humidity levels, which are crucial for the survival and reproductive success of these bees (Silva and De Marco 2014; Cândido et al. 2021). The combination of abundant floral resources and favourable environmental conditions near the river contributes to the resilience of euglossine bee populations in the face of anthropogenic disturbance.

Furthermore, as already mentioned, the riverine landscape often acts as a corridor, facilitating the movement and dispersal of bees between fragmented habitat patches (Brito et al. 2017). This connectivity enables gene flow and maintains population viability, allowing for the persistence

of euglossine bee communities in urbanized areas. The riparian vegetation along the riverbanks serves as a refuge and steppingstone habitat, facilitating the movement of bees and providing opportunities for nesting and foraging (Faria and Silveira 2011).

Euglossine bees highlight the need to protect and monitor riparian areas in the Caatinga cities

Riparian forests in the Brazilian Caatinga play a crucial role in sustaining biodiversity, as exemplified by our findings with euglossine bees. However, their significance extends beyond supporting wildlife. These forests also serve as guardians of water quality, ensuring an adequate water supply for both ecological systems and human communities. Moreover, they contribute to soil stability and regulate water flow, safeguarding the well-being and resilience of local populations (Camporeale et al. 2013; Ellison et al. 2017; Nóbrega et al. 2020). Recognizing the multifaceted benefits of riparian forests emphasizes the urgency of their conservation efforts in the Caatinga region.

The importance of these ecosystems was widely acknowledged by the original Brazilian Forest Code of 1965 (Law N° 4.771/1965), which established protected areas based on the highest water level of the stream, ensuring comprehensive protection of riparian wetlands. Regrettably, the revised Forest Code of 2002 (N° 12. 651/2012) defines the protected area from the stream bed, corresponding to the area occupied during low-water levels. This definition significantly reduces the extent of riparian zone protection, posing a significant challenge for the conservation of these critical habitats (Campagnolo et al. 2017). For the semi-arid regions in Brazil, such as the Caatinga and Cerrado, this issue becomes even more concerning as the current law fails to account for the significant fluctuations in stream discharge that occur both within and across years (Andrade et al. 2017).

Despite recent changes in the forest code, which have had a significant impact on riverine zones, it is evident that riparian forests have long been confronted with substantial anthropogenic threats, primarily driven by agricultural and urban expansion. The current estimates indicate that the original cover of riparian forests in the semi-arid Caatinga region would have accounted for approximately 3% of the total area. However, it is important to note that most of this original cover has been completely removed or extensively modified (Junk et al. 2022), highlighting the inadequate efforts of Brazilian environmental policy institutions in properly safeguarding these ecosystems (see for example (see for example, Oliveira et al. 2018). As a consequence, the ecosystem services provided by these forests are severely compromised.

Euglossine bees provide key ecosystem services in neotropical regions, pollinating not only native plant

populations (Dressler 1982; Roubik and Hanson 2004), but also agricultural crops (Darrault and Schlindwein 2005). In our study, we found a drastic decline in euglossine bee populations—and thus of their pollination service effectiveness—in areas where the riparian vegetation has been completely removed. The negative effect of disturbance on riparian vegetation may be observed in other pollinating insects, including meliponini bees (Vossler 2019), wasps (Souza et al. 2010), flies (Ober and Hayes 2008), nocturnal moths (Ober and Hayes 2008), butterflies (Cabette et al. 2017), as well as insect groups that contribute to other important ecosystem services, such as pest control (e.g. hymenopteran parasitoids; Silva et al. 2020b). Therefore, the decline in insect populations resulting from the disturbance/removal of riparian vegetation poses a serious threat to the ecosystem services they provide. This is particularly concerning for the city of Petrolina, where fruticulture and other agricultural crops represent one of the primary economic activities (Prefeitura de Petrolina 2022).

The removal of the riparian forests also resulted in a reduction of 50% of the euglossine bee richness. In our study, *Euglossa cordata* and *Eulaema nigrita* dominated the euglossine bee community and were reported in all sampling areas. However, other species, such as *Euglossa despecta* and *Eg. stellfeldii*, were exceptionally rare and confined to the river margin where a native riparian vegetation still persists. This emphasizes the critical role of riparian forests as refuge areas for these species within urban and agricultural landscapes and indicate that their removal could trigger a cascade of local extinctions. Similar cases of local extinction in euglossine bees due to intense human disruption of habitats have been documented in the Atlantic and Amazonian Rainforests (Nemésio 2011; Storck-Tonon and Peres 2017) and the risk of such extinction might be more accentuated in semi-arid regions, where euglossine populations are much smaller. Overall, our study shows the urgent need to implement effective conservation strategies and sustainable management practices to protect and restore riparian forests in the Caatinga region, aiming to ensure the preservation of its biota and the valuable ecosystem services they provide.

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Data Availability All data supporting the findings of this study are available within the paper and its Supplementary Information.

Declarations

Competing interests The authors declare no competing interests.

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