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Effects of Ecological Fitting and Dispersal in a Generalist Stingless Bee: A Field Experiment

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Abstract

We tested the role of ecological fitting and dispersal in spreading a generalist stingless bee and its potential effects on forest bee assemblages. Phenotypic plasticity in two life history traits (colony reproductive rate and annual survival) together with colony density were used as measures of 'ecological fitting' of *Tetragonisca angustula* Latreille, 1811 (*Ta*) to three adjacent habitats: forest core (FC), forest edge (FE), and rubber tree matrix (RM). Swarms/ha were estimated six times over 12 months in four replicates/ habitat types. Generalized Estimating Equations were used to analyze the relationship between habitat type and swarm occurrence. Colony density (colony/ha) and annual colony survival (a proxy for longevity) were compiled from our previous studies. A total of 329 swarms were captured across the three habitats during the sampling period. The colony reproductive rate (swarm/colony/year) of Ta was high (4 to 6) among the stingless bees and did not vary between the habitats, so it is configured as a conservative trait in this species. The swarming rate/ha was significantly lower in FC than in RM and FE, indicating spatially structured dispersion (SSD). The SSD and significantly lower colony density in FC supported the premise of mass effect on FC. Ta's ecological fitting to FC involved increased colonial longevity and was successful. The ecological fitting of generalists and SSD is a process with rapid effects that probably drives the structuring of stingless bee assemblages in the Brazilian Atlantic Forest in a widespread deforestation and anthropization scenario.

Introduction

The 'ecological fitting' approach to biodiversity in ecological communities implies *a priori* acceptance that these systems are open and recognize the fundamental role of phenotypic plasticity and dispersal in species distribution. Ecological fitting results from the interaction between flexible organisms and changing ecological conditions, so its primary mechanism is phenotypic plasticity (Agosta & Klemens, 2008).

Phenotypic plasticity evolves when populations are exposed to different conditions in various environments, which affect individuals' survival. Consequently, different phenotypes are favored in each type of environment, ensuring that none of them has higher fitness in all environments (Ghalambor et al., 2010). This mechanism allows organisms or genotypes to obtain fitness under new ecological conditions (or selective regimes) without 'waiting for new mutations' (West-Eberhard, 2003).

Species with wide geographic distribution are expected to exhibit phenotypic plasticity (Schlaepfer et al., 2010). By analogy, it is expected that deforestation and anthropization of habitats in landscapes also tend to favor the expression of latent phenotypic plasticity in generalist species in habitat use, for example (Agosta & Klemens, 2008).

Many Neotropical social stingless bees (Tribe: Meliponini) have a wide geographic distribution, including different tropical

habitats and biomes. This pantropical bee group is diverse (more than 600 species) and often abundant in tropical lowland habitats (e.g., Kleinert et al., 2012; Grüter, 2020; Roubik, 2023), where they can play a central role in plant-pollinator networks (Gruchowski-Woitowicz et al., 2020). In the last two decades, field studies have analyzed the spatial variation in abundance, composition, and richness of stingless bees in landscapes with different levels of forest cover and anthropogenically disturbed forests (Eltz et al., 2002; Samejima et al., 2004; Brosi, 2009; Silva et al., 2013; Lichtenberg, 2017). However, species traits associated with such spatial ecological variation were rarely the focus of these studies. For instance, Lichtenberg et al. (2017) tested the hypothesis that foraging traits and dietary range were associated with the persistence of different stingless bee species in landscapes exposed to deforestation. Slaa (2006) observed a slight variation in colony longevity of species between habitats in a landscape with dry forest and deforested areas in Costa Rica. In the Brazilian Atlantic Forest landscape, Silva et al. (2021) detected spatial variations in annual colony survival between species of forest and adjacent anthropogenic habitats. Nevertheless, the role of latent phenotypic plasticity in these variations is still unknown.

In addition to ecological fitting, how a species occupies different habitats in a landscape also depends on the spatial structure of dispersal (that is, how each habitat influences the production and dispersal of propagules) and the spatial configuration of the habitats (Leibold et al., 2004; Ai et al., 2013). The process of dispersal and the choice of habitats by a species where it maintains its fitness is called 'ecological resource tracking' or ecological fitting sensu lato. In contrast, establishing a species in new habitats would characterize ecological fitting sensu stricto (Agosta & Klemens, 2008). In theory, a quality habitat in a central position in a dispersal dynamic favors "ecological resource tracking" (Ai et al., 2013), while a high influx of propagules (e.g., reproductive units) into a low-quality habitat from a nearby high-quality habitat (mass effect sensu Shmida & Wilson, 1985) would also favor ecological fitting sensu stricto, depending on the phenotypic plasticity of the species.

In this experimental field study, in a landscape of tropical forest and perennial crops, the ecological fitting of the social stingless bee *Tetragonisca angustula* (Latreille, 1811) is analyzed from two complementary perspectives: (1) the occurrence of phenotypic plasticity in two life history (LH) traits (reproduction rate and colony longevity) and (2) the influence of dispersal dynamics and possibly" mass effect" (Silva et al., 2014) on habitat occupancy across the landscape. *T. angustula* (*Ta*) has a wide distribution in tropical America and occurs from Panama to Southern Brazil (Oliveira et al., 2004; Camargo, Pedro & Melo, 2023), where it is often abundant in anthropic and disturbed habitats and not abundant or uncommon in extensive areas of preserved tropical forest (Nogueira-Neto, 1970; Pinheiro-Machado & Kleinert, 1993; Wilms et al., 1996; Batista et al., 2003; Ramalho, 2004; Slaa, 2006; Velez-Ruiz et al., 2013). It is a generalist both in foraging (Macêdo et al., 2023) and in habitat use and stands out among stingless bees for its high reproductive rates (Slaa, 2006; Silva et al., 2014; Grüter, 2020). This species is likely being favored by deforestation and anthropization of habitats (Batista et al., 2003; Silva et al., 2021), and therefore, it should be a suitable model for analyzing the effects of ecological fitting and dispersal processes on habitat occupancy.

Methods

Field Study

The Atlantic Tropical Forest (ATF) of Brazil originally covered the study area (Ribeiro et al., 2009). The local ATF landscape, on the coordinates 13º50'S - 39º15'W, comprises the Reserva Ecológica Michelin (REM), a privately protected area of 3,386 ha with a mosaic of rainforest, abandoned rubber plantations, riparian forest, wetlands, and mangroves, in northeastern Brazil (Flesher, 2015). The REM suffered deforestation, selective logging, and hunting in the mid-20th century. Today, the three largest forest remnants (140, 625, and 700 ha) of REM are immersed in an anthropogenic mosaic formed by rubber trees, rubber/cacao, and smallholder agroforestry farms with a 10,000+ ha contiguous forest block to the west. The topography is hilly with the relief between 40 and 586m above sea level. The average annual rainfall is 2,000 mm, with no defined dry season and monthly temperatures varying between 18 and 30 °C (Flesher, 2015).

Terminology and the measured variables

Two main variables in the analysis of LH traits are reproduction and longevity (Stearns, 1992). Here, the corresponding variables are swarms/colony and the colony's annual survival (a surrogate for colony longevity). The swarms/colony were also referred to as per capita fitness to emphasize the eventual phenotypic plasticity at the colony level. The population reproduction rate (swarms/ha) and population density (colony/ha) were jointly assumed as proxies for population fitness. Demographic variables are among the most suitable for measuring habitat quality (Johnson, 2007). In particular, we assume that demographic variables reflect the direct response of the population to habitat conditions, thus offering an integrated measure of habitat quality from the perspective of a given species.

The variation between habitats in the swarm/ha ratio was also taken as an indication of spatially structured dispersion (SSD). SSD was inferred from the measured number of swarms per habitat type (see below) and not through direct measurements of dispersal flux. Swarms are expected to disperse from source habitats that produce more swarms to those that produce fewer. Particularly, the mass effect (sensu Shmida & Wilson, 1985) would be characterized

by the large influx of swarms into a habitat with low swarm production due to the proximity of the source habitats. In the REM, dispersal between habitats is assumed to be favored by the co-occurrence of the three habitat types.

Swarms are the reproductive units of stingless bees, consisting of a group of workers and a newly fertilized queen, which leave the mother colony (reproductive adult colony) to occupy a new nesting substrate. Conceptually, a new daughter colony emerges as soon as a newly fertilized queen settles there, although the bond between the daughter and mother colonies can persist for several weeks (Engels & Imperatriz-Fonseca, 1990). In the occupancy analyses, we used newly established swarms in trap nests (see below).

The 'operative environment' (OPEN) concept was used here to qualify the habitats occupied by *T. angustula* and compare its "ecological fitting" across the REM landscape. OPEN is an operational concept derived from the Hutchinsonian niche concept to categorize habitats according to a species 'realized fitness' (Agosta & Klemens, 2008). Ideally, OPEN requires identifying habitat features affecting individual survival and species-relevant features interacting with the habitat (Ghalambor et al., 2010). By definition, the OPEN ancestor configures the habitat with the best ecological conditions for a species and serves as a reference for analyzing the ecological expansion of the population in terms of relative success in occupying new habitats (Agosta & Klemens, 2008). According to these authors, when a species manages to occupy a new habitat through phenotypic plasticity, it is said to exhibit ecological fitting, strictly speaking.

Sampling design

The sampling was done in three habitat types of REM (Fig 1): (1) forest core (FC; ≥ 500 meters from the edge) with long-lived shade-tolerant trees; (2) forest edge (FE; 300m wide strip along the border of the forest), with young regenerating secondary forest dominated by short-lived and shade-intolerant trees; and (3) the anthropogenic habitats formed by rubber monocultures (*Hevea brasiliensis*), rubber/cocoa plantations (*Theobroma cacao*) and smallholder agroforestry farms, together, have been called the 'rubber tree matrix' (RM). RM + FE is also referred to as anthropogenic habitats (AH).

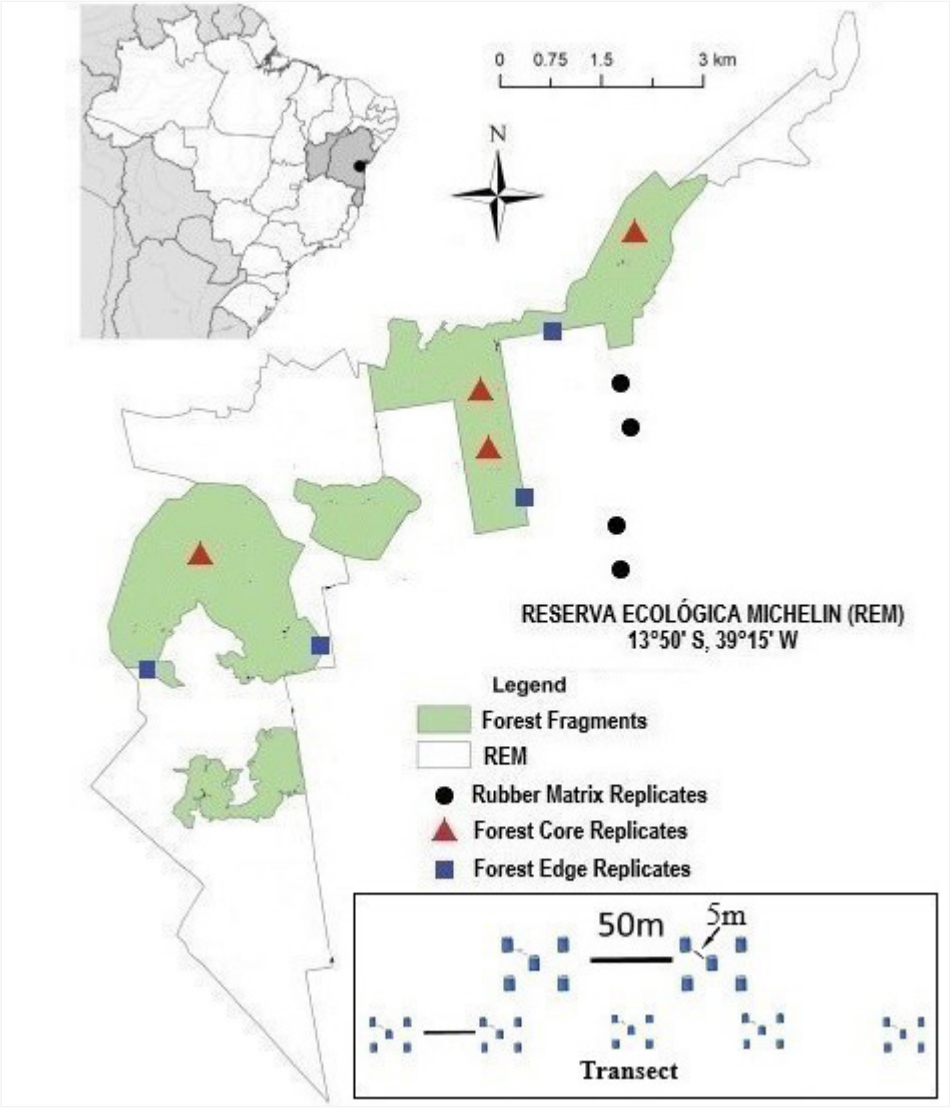

Fig 1. Reserva Ecológica Michelin in the Atlantic Forest of Brazil. Replicates are indicated by habitat type. The spatial arrangement of trap nests in each transect is indicated in a sketch below.

Swarming rates (swarms/ha) were estimated by capturing swarms with standardized trap nests (Oliveira et al., 2013; Silva et al., 2014). Each habitat type receives four transects of 200 m, which contain five groups of nest traps, placed 50 m apart from each other (Fig 1). Each group was considered a sample unit. To enhance the chance of occupancy, as well as to avoid swarm occupancy failure, each group contains five nest traps, totalling 300 nest traps (see Data Analysis). All transects were established in the same week and maintained in a fixed position, with a minimum distance of 500 m between them. Between May 2015 and May 2016, all transects and trap nests were inspected simultaneously within a week, six times at two-month intervals. Nest trap occupancy by a swarm was considered successful when the typical cerumen tube and active workers (guards and foragers) were observed at the nest entrance. These swarms are considered established and included in the occupancy rate analysis (see below), regardless of subsequent mortality.

The swarms/ha were calculated by estimating the area sampled in each 200 m transect. Assuming the general relationship between the flight range and body size of the worker bees and the behavioral restrictions of progressive swarming in stingless bees (Engels & Imperatriz-Fonseca, 1990; van Veen & Sommeijer, 2000; Araújo et al., 2004), the highest dispersal distance for swarms in *T. angustula* was assumed to be 50 m. Thus, a 3 ha plot was sampled along each 200m transect (functionally 300m long x 100m wide).

Blue 5-liter plastic containers were used to standardize trap nests (Oliveira et al., 2013; Silva et al., 2014). The trap nests were hung with nylon thread on tree trunks, 1.5 meters above the ground. To improve the attraction of swarms, two baits were placed inside each trap nest and at the hole entrance: (1) alcoholic extract of propolis (from *Apis mellifera* Linnaeus, 1758) diluted in 96° GL ethyl alcohol (1: 4); (2) small portions of cerumen from colonies of *Melipona scutellaris* Latreille, 1811. At 2-month intervals, all unoccupied traps were kept attractive by spraying propolis extract and adding fresh portions of cerumen.

To estimate the number of swarms/colonies, we measured the number of swarms/ha in the field (this study).

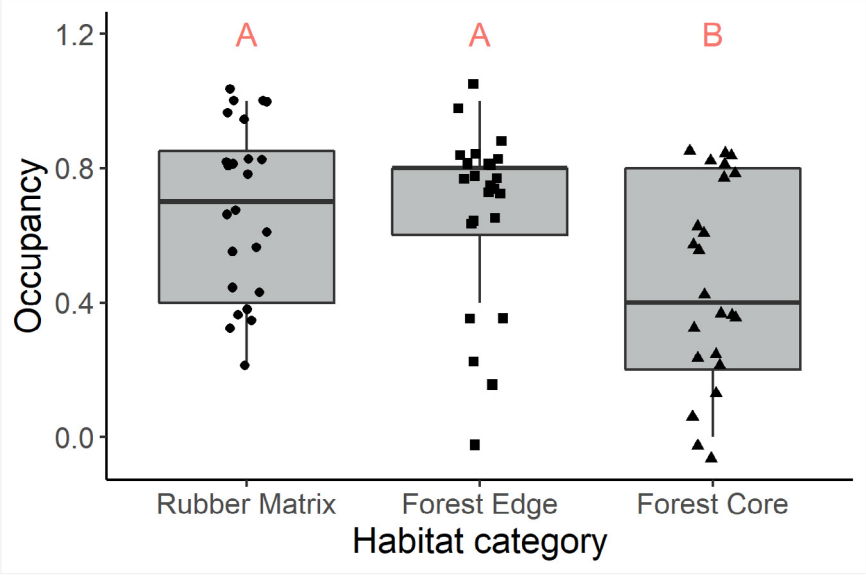

Fig 2. The occupancy rate of trap nests by swarms of *T. angustula* in each habitat (4 replicates/habitat x 6 times at 2-month intervals for 12 consecutive months): rubber tree matrix (RM), forest edge (FE), and forest core (FC). Different letters above bars indicate significant differences in mean occupancy.

We compiled raw data on the number of colonies/ha from our earlier studies (Silva et al., 2021) using the first year dataset, when all three habitats were sampled simultaneously. In the latter case, all living colonies established in natural cavities (mainly tree hollows in the forest) were sampled, based on the recognition of workers active in collecting food and protecting the nest entrance. The combination of these data was considered adequate because: first, during the four-year interval between these two field studies, there were no relevant changes in the proportion of the three habitats defined in the REM landscape (Flesher, 2015; Dechner et al. 2018); second, the REM remaining forests have not been exposed to logging since the end of the 20th century and have been continuously protected by Michelin forest rangers (Flesher, 2015). To standardize habitat types or categories in both studies in the REM scenario, we used the corresponding terms: young forest = forest edge; old forest = forest core.

Data analysis

We constructed Generalized Estimating Equations (GEE – Prentice & Zhao, 1991) to analyze the effect of habitat type on the occurrence of Ta. As mentioned, to enhance the detection of swarms, each group had five nest traps, and any number of swarms (1 to 5) in each group generates a single swarm occurrence called occupancy. Each transect with five

groups was treated as a binomially distributed variable with five trials (each group as a unit trial) used as an estimate of the occurrence probability of swarms. In total, we had sixty groups in the three habitat categories, which had six sequential observations over 12 months. This design generates repeated and dependent measurements in space (transect dependent) and time. To deal with spatial and temporal dependencies, the transects were considered as random variables, and we built a conditional dependence variance structure, considering the autocorrelation between samples of the same group over time, to generate a working matrix of variance and covariance (AR-1 type of autocorrelation – Zuur et al*.,* 2009). In the final model, both the variance-covariance dependency structure and the average effect of habitat on swarm occurrence were fitted to the data.

To fit the GEE model, we used the "geepack" package (Højsgaard et al., 2006). Wald statistics were used to test the significance of each term in the model through a sequential test of the model's terms (Højsgaard et al*.,* 2006). Inspection of a standardized residual distribution for remaining trends in the residuals was used to validate the final model. Multiple comparisons of swarm occurrence means between habitats were made with Tukey contrasts using the "multcomp" package (Hothorn et al*.,* 2008). All models and graphics were built in the R environment (R Core Team, 2020).

Results

Out of the total 329 swarms of *T. angustula* (*Ta*) recorded over the twelve-month study, 17 (5%) died as a result of attacks by a honey-eating predator (*Eira barbara*) and by the kleptobiotic stingless bee *Lestrimelitta limao* (Smith, 1863). On average, at each inspection (six inspections at 2-month intervals), 18% of the available traps were occupied by swarms of Ta and 12% by other animals, mainly ants, small wasps, and spiders. Both swarm attacks and trap occupations by other animals were widely distributed across habitat types; therefore, total swarm occupancy estimates were considered unbiased by these factors. Furthermore, potential small deviations would also be mitigated by the data analytical procedure, in which occupancy analysis dealt with swarms established per group of five traps (and not the number of swarms/group) along the transects, regardless of whether the swarms were targets of subsequent attacks.

Table 1. Comparisons of colony-level and population-level data of the *T.angustula* stingless bee in the three habitat types of the REM landscape.

	Rubber Tree Matrix – RM	Forest Edge – FE	Forest Core – FC
Swarms/ha	11.2 ± 1.70 (N = 133)	11.2 ± 3.62 (N = 125)	5.8 ± 2.83 (N = 71)
Colonies/ha*	2.7 ± 1.00 (N = 83)	2.0 ± 1.86 (N = 32)	1.0 ± 0.20 (N = 14)
Swarms/colony	4.1	5.6	5.8

*Colony density was estimated from published raw data. See methods and Silva et al. (2013, 2021) for details of estimating of colonies/ha.

According to the occupancy rate analysis, the swarms/ha were significantly lower in the FC compared to the other two habitats (Figure 2). Multiple tests showed that the FC had a lower swarm occurrence than RM ($p = 0.01$) and FE ($p = 0.02$), while RM and FE did not show a difference between them ($p = 0.99$). The GEE model confirmed that habitat type had some effect on swarm occurrence ($X^2 = 8.46$, d.f. = 2, $p = 0.01$). The number of colonies/ha (Table 1) was significantly lower in FC than in RM ($p = 0.017$), with no significant differences between FC and FE ($p = 0.32$) and between FE and RM ($p = 0.55$).

The number of swarms per colony or swarm per capita remained high and similar across the landscape (Table 1). However, due to the lower colony density in FC, the number of swarms/ha in this habitat reached about half the value observed in FE and RM. This significant spatial variation in swarm production/ha (Table 1; Fig. 2) suggests spatially structured dispersal (SSD) across the landscape, with a likely directional flow from anthropized habitats (RM and FE) to FC.

However, assuming the combination of swarms/ha and colonies/ha as a proxy for population-level fitness and thus an integral measure of habitat quality (see methods), the ecological fitting of 'Ta' to the forest core is shown to be less effective than to anthropogenic habitats.

Discussion

Occasional variations in the availability of natural nesting cavities for stingless bees between habitats could produce biases in the sample of swarms with trap nests. However, tree hollows are the main nesting cavities for stingless bees in the forest, and their availability did not vary between the forest edge and the forest core in the REM landscape (Silva & Ramalho, 2014). Therefore, this potential source of variation in swarm/colony and swarm/ha estimates of Ta should be disregarded in this analysis.

Phenotypic plasticity in colony life history traits

Although comparative data on LH traits in stingless bees are still scarce, what we have indicates that Ta's per capita reproductive rates are higher than those of other species in this group of bees (Slaa, 2006; Silva et al*.*, 2014, 2021; Grüter, 2020). Producing about 4 to 6 swarms/colony/year in a variety of habitats, Ta deviates from the dominant tendency of stingless bees to produce less than one swarm/colony/year (Slaa, 2006; Roubik, 2006; review in Grüter, 2020). Furthermore, the lack of variation between habitats suggests that the high reproductive rate must be a conservative trait of this species, unlike annual colony survival. Annual colony survival (here a proxy for longevity) was significantly higher

in FC (Silva et al., 2021) and is likely the life history trait involved in ecological fitting to this habitat.

Maintaining the swarm/colony ratio by Ta would be compatible with a similar availability of nesting sites (mainly tree holes) in FE and FC, as measured by Silva e Ramalho (2014). On the other hand, a reduction in the per capita swarm rate (swarm/colony) to compensate for the increased annual colony survival in FC was an expected trade-off, especially when there is competition (Stearns, 1992), a common scenario in stingless bee assemblages (Hubbell & Johnson, 1977; Johnson et al., 1987). Particularly, these bee assemblages should be more stable in the forest (Silva et al., 2013), so that foraging pressure would remain high in the long term, favoring a reduction in investment in swarm production, with some gain in colonial longevity, for instance. Given that Ta maintains swarm/colony numbers across all habitats, the aforementioned trade-off may still involve a reduction in mean swarm size in FC with increased mortality (not measured here). Smaller swarms would imply lower reproductive cost for the mother colony, but would also be more susceptible to mortality during the initial establishment period (greater difficulties in social regulation/task allocation within the nest; lower defense capacity against invaders; lower foraging capacity for floral resources; and, through negative feedback, longer exposure time to all these variables due to slower population growth of the young colony, etc.). This expected increase in very early swarm mortality would also explain the lower measured density of Ta colonies established in FC, despite their greater longevity (Silva et al., 2013)..

Assuming most "stingless bees invest more in colony survival than reproduction" (Roubik, 2006; Slaa, 2006), selecting for high colonial longevity must be extreme in rainforest habitats. For example, in the ATF landscape, the highest annual colony survival was associated with species abundant in the forest and not with the set of species abundant in adjacent anthropogenic habitats (Silva et al., 2013, 2021). Therefore, Ta's expression of phenotypic plasticity would also be in the right direction, promoting increased colony longevity in the interior of the tropical forest.

Whatever the biological variables associated with the complex responses of stingless bees to deforestation (Brosi, 2009), it seems certain that the traits of Ta's life history and particularly its high reproductive rate adjust well to anthropogenic habitats (Batista et al., 2003).

The variables of the stingless bee's operative environment – OPEN

The lower population fitness of Ta in the forest core (FC) suggests that increased colony longevity is necessary but insufficient to achieve ecological fitness similar to that of this species in adjacent anthropogenic habitats. In addition to identifying specific traits relevant to species-habitat interactions (Ghalambor et al., 2010), e.g., phenotypic plasticity in colonial longevity, a detailed understanding of the process of ecological fitting of Ta to the rainforest would also require the identification of relevant habitat traits that diverge from its OPEN ancestor (sensu Agosta & Klemens, 2008; see methods). This is beyond the scope of this paper. However, considering the generalist foraging of stingless bees and the high and continuous demand for floral resources by colonies (Roubik, 1993; Gruchowski-Woitowicz, 2020), it is reasonable to consider that the abundance of competitors, availability, and sharing of floral resources are relevant habitat characteristics for stingless bees as a whole.

Over and above the measured direct influence of the availability of floral resources on bee populations in general (Roulston & Goodell, 2011), countless studies on diversity, food ecology, foraging traits and strategies of stingless bees (e.g., Johnson et al., 1987; Eltz et al., 2002; Biesmeijer et al., 2005; Biesmeijer & Slaa, 2006; Kleinert et al., 2012; Hrcnir & Maia-Silva, 2013; Lichtenberg et al., 2010; 2017; Gruchowski-Woitowicz et al., 2020, 2024), taken together, allow some generalizations: (1) due to their generalist year-round foraging and abundance, stingless bees tend to play a central role in structuring bee-plant networks (high nestedness and robustness) in the tropics, therefore, the direct and main competitor of a stingless bee is usually another stingless bee; (2) sharing floral resources is one of the bases for structuring coexistence among stingless bees, whose competitive interactions are actively mediated by foraging traits and the foraging hierarchy. Similarly, although nest site availability is expected to be a relevant habitat characteristic because most stingless bees require large pre-existing cavities to house their colonies, there is a scarcity of comparative data on this aspect (Eltz et al., 2002; Silva et al, 2013; Silva & Ramalho, 2014; Lichtenberg et al., 2017).

Any assumptions about the relative advantages of foraging strategies in stingless bees depend on patterns of resource availability and species-habitat interactions. Mass-flowering plants are frequent in the rainforest canopy, where they are essential floral resources for the populous and perennial colonies of stingless bees (Eltz, 2002; Ramalho, 2004) and mainly the large colonies of some group-foraging species (Silva et al., 2013; Silva e Ramalho, 2014). In particular, small solitary foragers, such as Ta, tend to be at a disadvantage when directly sharing spatially and temporally concentrated floral resources, such as mass flowerings, with group-foraging species (Lichtenberg et al., 2010). On the other hand, for cost-benefit reasons, territorial group-foraging species are expected to concentrate in larger floral patches (Johnson et al., 1987), so smaller patches of mass-flowering resources would tend to be less occupied and therefore more accessible to solitary foragers. Indeed, concentrating foraging in mass flowerings is expected to reduce the overall group-foraging pressure on other stingless bees in sparser blooms (Gruchowski-Woitowicz, 2024). However, the hyperdispersed pattern of mass-flowerings in the Neotropical forest canopy (Lieberman & Lieberman, 1994) should primarily reduce the chances of access for stingless bee colonies with smaller home ranges and, therefore, smaller species such as Ta (Van Veen & Sommeijer, 2000; Araújo et al., 2004).

In anthropized habitats, the high occurrence of annuals and ruderal plants likely implies a sparser supply of floral resources, a general condition favorable to solitary foragers. In this scenario, colonies with thousands of solitary foragers, such as Ta, should increase the chances of finding new resources, avoiding exposure to the risks of sharing (competition through interference or exploitation) with group-foraging species. Furthermore, solitary foragers of small-bodied stingless bee species, such as Ta, may also take relative advantage of sparse or depleted blooms simply because they have a greater pollen load capacity (carrying more pollen per unit body weight than larger bees; Ramalho et al., 1994).

There is some consensus on the relevance of nest site availability to stingless bee colony density, partly due to the dependence of most species on large, preexisting cavities (Eltz et al., 2002; Lichtenberg et al., 2017; Silva et al., 2013; Silva & Ramalho, 2014). Although the availability of nest sites in the forest (mainly tree hollows) does not limit colony density (Eltz et al., 2002; Silva et al., 2013; Silva & Ramalho, 2014), access to potential nest sites is likely affected by active patrolling by workers of territorial and aggressive species (Hubbell & Johnson, 1977), which can be abundant in this habitat.

In anthropized habitats, controlling access to nesting sites would be less effective due to their variety and fluctuating supply (most are not associated with long-lived trees, e.g.). Under these conditions, species that selectively nest in tree cavities would be placed under population pressure (Lichtenberg et al., 2017), negatively impacting colony density. For example, some forest-dwelling *Melipona* species are more susceptible to deforestation than others (Brown & Albrecht, 2000), and this may be associated with the degree of nesting fidelity in tree cavities (Silva & Ramalho, 2014). Species that selectively nest in trees would also be less effective at patrolling access to other cavities that may be abundant in the AH but are neglected by them. The availability and types of cavities in the AH should favor the high density of Ta colonies, considering their widely recognized generalist and flexible use of nesting sites (e.g., Batista et al., 2003) and their high reproductive rate. Overall, these latter assumptions still require further support through quantitative and comparative measurements.

Therefore, considering demographic variables as an effective and integrated measure of habitat quality from a species perspective (Johnson, 2007), it should be assumed that the lower fitness of Ta in FC also indicates that this habitat is the most divergent from the OPEN ancestor (Agosta & Klemens, 2008; see methods) of this species. The hyperdispersed pattern of essential floral resources (mass-flowering trees) together with the abundance of group-foraging species on them are likely relevant variables. Even so, given that Ta's population abundance in FC is equivalent to the three most abundant forest resident species (Silva et al., 2013), it can also be stated that this habitat generalist is already ecologically fitted to the forest (ecological fitting sensu stricto*;* Agosta & Klemens, 2008; see also methods), where phenotypic plasticity in colonial longevity contributes to this process. The ecological fitting of Ta to AH must be associated with the greater supply of sparse floral resources and the variability of nesting cavities.

Spatial dispersion structure across the landscape

The ecological fitting of Ta in the REM landscape is likely favored by the continuous influx of propagules into the forest from surrounding anthropogenic habitats. Structured spatial dispersal and directional influx of swarms from AH to FC are inferred from the significant differences in swarm production between these habitats and their spatial proximity. The continuous and cumulative year-to-year effects of this directional dispersal likely resulted in a mass effect (sensu Schmida & Wilson, 1985) over core areas of the forest. In an intermediate spatial position in this dynamic, FE probably acts as a spatial amplifier of dispersal towards the forest core. First, because a reinforced effect of ecological resource tracking on habitat patches in the central position of mosaic dynamics is expected when dispersal is high (Ai et al., 2013), a condition likely satisfied by the high reproductive rate of Ta. Second, due to the severe spatial constraints of progressive swarming in stingless bees as a whole (Engels & Imperatriz-Fonseca, 1990) and in smaller stingless bees like Ta in particular (van Veen & Sommeijer, 2000), the forest edge, but not the FC, should be directly accessible to swarms dispersing from the adjacent rubber tree matrix.

Conclusion

The primary variable in Ta's ecological fitting to forest habitats involves increased colonial longevity, consistent with the trend observed in forest-dwelling stingless bee species. The conservative nature of the per capita reproductive rate (swarm/colony) suggests an evolutionary history strongly linked to habitats with variable conditions, which could perhaps be better explored with genetic markers. A detailed analysis of the relationship between size and probability of death in swarms/habitat is also needed, given that the substantial reproductive investment distinguishes the species from other stingless bees. Further analysis of the effects of SSD and the likely mass effect would benefit from direct measurements of propagule fluxes across the landscape, where the forest edge probably participates as a powerful amplifier of the process. Finally, future work modeling regional scenarios of the effects of ecological fitting and the expansion of Ta in forest habitats should contribute to improving the quality of projections of the impacts of deforestation and climate change on native pollinator diversity.

Along the 3,000 km (north-south) extension of the Brazilian Atlantic Forest (Ribeiro et al., 2009), only approximately 12% of forest cover remains, and it is highly

fragmented. In such a scenario, forest edge conditions predominate (Tabarelli et al., 2004). Across the ATF landscape, the diagnosis is that the functioning of stingless bee metacommunities (sensu Leibold et al., 2004) is primarily affected by ecological fitting and SSD dynamics of habitat-generalists, such as *T. angustula*.

Authors' Contributions

PCLG: Conceptualization, methodology, writing-original draft, writing-review & editing
MR: Conceptualization, methodology, writing-original draft, writing-review & editing
EM: Formal analysis, visualization, writing-original draft, writing-review & editing

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