



## RESEARCH ARTICLE - BEES

## Annual survival rate of tropical stingless bee colonies (Meliponini): variation among habitats at the landscape scale in the Brazilian Atlantic Forest

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### Abstract

Stingless bees are abundant and generally numerically dominant in bee communities in the tropics. Given that the collective foraging of their colonies is driven by communication systems, the preferential use and sharing of productive and spatio-temporally concentrated floral sources, are probably at the center of the foraging economy of the colonies of these bees. This study analyzed the influence of habitat anthropization on spatial variation in the survival of tropical stingless bee colonies. We investigated how three categories of habitats affect the survival of colonies within communities in a landscape of large fragments of disturbed natural forest and a matrix of rubber agroforestry. Random sampling of replicates of each habitat type for two years located 118 nests of 14 species in the two natural forest habitats and 105 nests of six species in the anthropic habitat. Monitoring revealed significant differences in colony survival between young and old-growth forests and between old-growth forests and anthropic habitats. The highest annual survival rates, ranging from 87% to 93%, were associated with three medium-large sized bee species that were most abundant and exclusive to the two forest habitats: *Melipona scutellaris* Latreille, 1811, *Scaptotrigona xanthotricha* Moure, 1950 and *Scaptotrigona bipunctata* (Lepeletier, 1836). These three species had similar survival rates in the two forest regeneration stages. Another species abundant in the landscape was *Tetragonisca angustula* (Latreille, 1811), a small habitat generalist with the lowest survival rate among the three habitats in the anthropic (43%). Euclidean distance analysis based on this habitat-generalist placed young forests closest to anthropic habitat and grouped the replicates of old-growth forest together. Considering the observed spatial variation, we infer that the Atlantic Forest favors stingless bees with high colonial longevity. In contrast, habitat-generalists, such as *T. angustula*, with small body sizes, short colonial longevity and high reproduction rates are favored by deforestation and replacement of forest with anthropogenic habitats.

### Introduction

Although life histories arise at the intersection of ecological and evolutionary dynamics (Alonzo & Kindsvater, 2008), attempts to link life history to habitat and ecological contexts remain diffuse and lack a comprehensive theory after decades since the synthesis of Stearns (1997). Stearns (1997)

concluded that it would be necessary to avoid approaches to life history as a whole (e.g. the r-k continuum) and focus on the impact of habitats on specific attributes, particularly age- and size-specific fecundity and mortality. Similarly, the trade-off-centered approach among life history attributes proved unsatisfactory for understanding how the ecological context affects the overall fitness of individuals. In contrast,



Stearns (1997) concluded that an approach based on specific attributes and defined lineages (or organisms of a given basic design) relative to habitats will contribute to expose “sets of patterns that could prove useful in future attempts to relate life history evolution to community ecology” (Stearns, 1997).

Here, we adopt an exploratory approach to the ecological relationship between habitat and longevity for a lineage of tropical bees with perennial social colonies, known as stingless bees (Meliponini). We are not aware of any studies on trade-offs between the life history attributes of these bees. Slaa (2006) and Silva et al. (2014) analyzed, respectively, variation in longevity and reproduction rates between natural forest habitats and anthropogenic habitats. However, this group has broad variability in characteristics related to life history, including interspecific variation in worker body size, colonial population size and reproduction rates (Sakagami, 1982; Kleinert et al., 2012; Silva et al., 2013). Assumptions about the role of these characteristics in diet breadth, food sharing, and competitive hierarchy are often implicit in studies of foraging behavior, local coexistence and species abundance in ecological communities (Johnson, 1982; Johnson et al., 1987; Kleinert et al., 2012; Biesmeijer & Slaa, 2006; Silva et al., 2013; Lichtenberg et al., 2017). However, we are unaware of any ecological studies on the effects of these characteristics on individual or colonial fitness.

Stingless bees are abundant and generally numerically dominant in bee communities in the tropics (Biesmeijer & Slaa 2006; Kleinert et al., 2012). In addition, these bee communities may be limited by food resources (e.g. Roubik, 1983; Biesmeijer & Slaa, 2004, 2006; Kleinert et al., 2012; Silva et al., 2013; Silva & Ramalho, 2014; Lichtenberg et al., 2017). Due to their abundance, colonial perenniality and generalized foraging behavior (Kleinert et al., 2012; Silva et al., 2013), these bees also tend to control the structure of mutualistic interaction networks between plants and pollinators in some tropical communities (Woitowicz-Gruchowski et al., 2020). Given that the collective foraging of their colonies is driven by communication systems (Nieh et al., 2004), the preferential use and sharing of productive and spatio-temporally concentrated floral sources, such as mass flowers, are probably at the center of the foraging economy of the colonies of these bees (Ramalho, 2004; Kleinert et al., 2012; Woitowicz-Gruchowski et al., 2020). This basic ‘colony foraging strategy’ should determine the ability to buffer food supply fluctuations in the restricted home range of a colony, and therefore affect colony longevity (e.g. annual survival rate) in the long run.

In contrast, the level and temporal pattern of floral availability in tropical habitats, and the high and continuous demand for food (Roubik, 1983; Eltz et al., 2002), would be critical to the survival of the perennial and highly populated colonies of stingless bees. In this scenario, worker body size arises as a key phenotypic constraint because it determines flight range (Araújo et al., 2004) and colony home range.

In other words, viability of colonies of stingless bees (with hundreds to tens of thousands of workers of small body size) would depend fundamentally on the relationship between food demand (e.g. colonial population) and supply of floral resources in the restricted home ranges of colonies. Therefore, the compromise between life history and local ecological conditions (Stearns, 1997) must be reflected in spatial variation of key attributes of stingless bee colonies, such as annual survival or longevity, according to habitat heterogeneity or among habitats in a landscape.

Empirical studies that have compared the survival of colonies of stingless bees among habitats under natural conditions are rare. Slaa (2006) detected similar survival rates between forest colonies and colonies in nearby cleared areas for most stingless bees in Central America, with the exception being generalist species. The premise that the choice of resistant nesting cavities by stingless bee colonies was under selection (such as hollows in live hardwood trees that would be less susceptible to degradation or predator attack) due to potential effects on differential colony survival (Roubik, 1989) was recently refuted by measures of non-selectivity of tree holes in a tropical forest of Brazil (Silva et al., 2014).

In general, we assume that measured values of longevity of stingless bee colonies in local communities and their spatial distribution among habitats should simply reflect changing spatial ecological contexts in a landscape. The longevity of a colony is taken as an integrated response to local ecological contexts or habitat categories, which, in the focal landscape here, include natural tropical forests and rubber agroforestry. Due to the perennial social lifestyle, and the aforementioned processes of structuring local communities, it is assumed that the expected corresponding variation in colony survival is inherent to “ecological fitting by phenotypically flexible genotypes” (sensu Janzen, 1985; Agosta & Klemens, 2008). This would be a common ecological process to which these bees are subjected in landscapes with rapid changes in natural habitats and the expansion of anthropogenic habitats. Thus, in this study, we tested the effects of habitats on colony survival rates in a landscape of native Brazilian Atlantic Forest and deforested areas with anthropogenic habitats. We also explored the argument that the spatial variation in the community of these bees in the landscape are closely related to variation in colonial survival and reproduction rates among species and habitats.

## Material and Methods

This natural field study was conducted in the northern portion of the Central Atlantic Forest Corridor of Brazil, in the area of the ‘Reserva Ecológica Michelin’ (REM) (13° 50’S, 39° 15’W). The REM consists of 992 ha of large remnants of legally protected tropical forest surrounded by extensive tropical forest to the north and numerous small fragments of dispersed forest and riparian forests to the south. The landscape

is dominated by extensive rubber agroforestry, with several small villages of rubber tappers. The sampled areas were distributed in a landscape of about 4,000 ha, of which 1,500 ha are covered by forest fragments of different extensions and in various stages of regeneration (including REM), and the rest by anthropogenic habitats, mainly due to rubber agroforestry. The natural forest is Dense Ombrophilous Tropical Forest at altitudes ranging from 150 to 330m (Flesher, 2006). The regional climate is Af (Köppen, 1948), with temperatures between 18°C and 30°C, and high relative humidity (between 80% and 85%) and rainfall (about 2000 mm annually) (CEI/CONDER, 1993).

### Sampling of nests in disturbed natural forests and anthropogenic habitats in the REM landscape

Disturbed natural forest was sampled within the largest forest fragments of REM. For comparative analyses, and according to regeneration stage, the forest plots were grouped into two categories: old-growth or advanced regeneration stage - AS; and young-growth or early regeneration stage - ES. The definition and field identification of forest regeneration stages in REM were based on historical data, plant physiognomy, stratification and the presence of key tree species (Flesher, 2006).

The two selected forest regeneration stages reflect different periods of forest restoration (secondary succession) after deforestation or selective logging. For example, in the young growth stage, fast-growing heliophytic trees are common and trees with diameters below 30 cm are very abundant. In the old growth stage, trees over 30 cm in diameter have the highest frequency and slow-growing centenary trees of over 1 m in diameter are common. The target anthropogenic habitat was of rubber agroforestry and associated with small villages of rubber tappers. The sampling of bee colonies in the anthropogenic habitat was concentrated on the walls of houses, other human structures and 'urban trees' widely dispersed over the total area of 1,500 ha of rubber agroforestry adjacent to the REM. This specific condition will here-on be referred to as 'anthropic habitat' (AH), while "REM landscape" will refer to the landscape formed by tropical natural forest and rubber agroforestry.

Bee colonies were sampled in 64 25x25-m randomly-distributed forest plots (32 plots per forest category) in three forest replicates (three large fragments, each > 300 ha) for a total of 32 ha sampled in the forest (16 ha / category of forest). Few nests located along access trails near the forest plots were included in the analyses. Replicates in the anthropic habitat were four villages of rubber tappers that were widely dispersed over an area of 1,000 ha of agroforestry.

All sites with potential nesting cavities (walls, posts, sidewalks, scattered 'urban' trees, etc.) were surveyed, for a total sampled area of 29.9 ha. Visual nest searches were performed between 07:00 and 15:00 h for five days per month in each habitat type (two forest categories and anthropic

habitat), between July 2007 and January 2010. Searches in the forest were more intensive in large trees (circumference > 60 cm), where most nests of species of Meliponini are expected to be found (Eltz et al., 2002; Batista et al., 2003; Silva et al., 2013).

The nests found in the three habitats (young and old growth forests and anthropic habitat) were marked and georeferenced for monitoring. All found nests were monitored monthly for two years to check if the colonies were still alive. There was wide application of insecticides in the anthropic habitat in the second year of monitoring, and so survival rates there were calculated for only one year.

Recorded stingless bee species were grouped according to body length into the following arbitrary size categories: small ( $\leq 6$ mm), medium ( $> 6 \leq 10$ mm) and large ( $> 10$  mm). Based on data from Silva et al. (2013), bee species with more than 0.2 nests/ha in at least one habitat category were considered abundant. Between five and 10 individuals per nest were collected to confirm species identification. Specimens were separated by morphospecies at the Pollination Ecology Laboratory of IBUFBA and identified by Favizia Freitas de Oliveira from IBIO-UFBA. Replicates of the collected material were deposited in the entomological collection of the Museum of Natural History of the Federal University of Bahia (MZUFBA).

### Annual colony survival rate

To estimate colony survival rate, all nests were monitored monthly for two years between July 2008 and January 2011. The presence or absence of a given species in the same nest each month was used as a measure of colonial survival. We were unable to monitor exceptional recolonizations of a nest by the same species following by colony mortality. Annual survival rate is used as a synonym for colony longevity.

### Data analysis

Multivariate analysis of variance (MANOVA) was used to compare annual survival rates of colonies among the three habitat types (AS, ES and AH). Annual survival rates were measured in each replicate of the three habitat categories: Habitat type and species were the independent variables. Survival rates were considered as dependent variables and were based on measures of presence-absence of colonies at each nest site. Each bee nest was taken as a sample unit and data on presence or absence of colonies after one or two years were used to construct the analysis matrix.

The dependency between dependent variables is a premise of MANOVA, which therefore covered the time dependence related to the fact that the nests are the same from year 1 to 2. Tukey's HSD test was used for multiple comparisons. Nests of eight species with two or more occurrences were included in these analyses: *Lestrimellita* sp., *Melipona scutellaris* Latreille, 1811, *Nannotrigona* sp., *Paratrigona*

*subnuda* Moure, 1947, *Plebeia* sp., *Scaptotrigona bipunctata* Lepeletier, 1836, *Scaptotrigona xanthotricha* Moure, 1950 and *Tetragonisca angustula* Latreille, 1811. An exploratory analysis on the effect of bee size on colony survival was also conducted using MANOVA, with bee sizes as independent variables and survival after one and two years as dependent variables. It was used three size categories based on bee body length: Small ( $\leq 6$  mm), medium ( $>6\text{mm} \leq 10\text{mm}$ ) and large ( $>10\text{mm}$ ). This is a preliminary analysis, as there is an imbalance in the data in relation to the number of colonies/body size category. The analysis of variance and Tukey's test were performed with IBM SPSS Statistics software, version 25. The significance level adopted was 0.05.

## Results and Discussion

Annual colony survival rates were estimated based on monitoring 118 nests of 14 species in the two forest habitats (young and old-growth forest) and 105 nests of six species in the adjacent anthropic habitat in the landscape (Table 1). All species with more than 0.2 nest/ha were considered abundant and with sufficient data for specific analyses. Four species were in this category in the forest, and contributed 3.06 nest/ha to the total of 3.68 nest/ha; only one species, *T. angustula*, was abundant in the anthropic habitat, which stood out with 2.77 nests/ha out of the total of 3.5 nests/ha.

The highest survival rates were frequently associated with old-growth forest and the lowest rates with the anthropic habitat (Table 1). The greatest longevities were associated with three medium-large-sized species that are abundant and exclusive to natural forest in the landscape – *S. xanthotricha*, *M. scutellaris* and *S. bipunctata* – which had survival rates (weighted averages) of 87.2%, 89.4% and 93.1%, respectively. Lower rates were associated with a subset of non-abundant species ( $<0.2$  nests/ha), which were more frequent in, or unique to, the anthropic habitat (e.g., *Lestrimelitta* sp., *Nannotrigona* sp., *Plebeia droryana* (Friese, 1900) and *Trigona hyalinata* Lepeletier, 1836). *T. angustula* was abundant in all three habitats with high variation in survival rate among them.

During four years of natural nest monitoring, Eltz et al. (2002) observed high annual survival (85.5% – 85% or = annual mortality rates of 14.5% – 15.0%) of stingless bee colonies in dipterocarp forests with different levels of disturbance (different intensities of selective logging), in northern Borneo. In Central America, Slaa (2006) observed similar high survival rates (89% – 93%) in deforested and forested areas for colonies of the most abundant species, except for *T. angustula*. Thus, the data presented here for the REM landscape also support Slaa's generalization that high annual survival rates (between 80% and 90%) are common for stingless bee colonies.

There was no difference for the three most abundant bee species of the tropical forest of the REM landscape (*S. xanthotricha*, *M. scutellaris* and *S. bipunctata*), in colony

survival rates between the two stages of forest regeneration during the two years of monitoring (Table 1). These survival rates project low colony turnover with periods of over 10 years to completely replace colonies of the populations in these two forest habitats. This projection is very conservative considering estimates of about 20 years for total colony replacement (Slaa, 2006) for some stingless bee populations residing in dry tropical forest of Costa Rica.

The three most abundant species mentioned above also maintain similar abundances and very low reproductive rates in early and advanced stages of forest regeneration in the REM landscape (Silva et al., 2013; 2014). High abundance and low turnover of colonies (high annual survival) suggest that the populations of this bee group are resistant to the long process of forest regeneration (e.g., from 20 years for young forest to more than a hundred years for old-growth forest with centenary trees). This subset of abundant stingless bees is likely playing a prominent role in the resilience of the rainforest bee community as a whole, especially when the forest disturbance was caused by selective logging. This can be explained, first, by these abundant stingless bees playing a central role in structuring mutualistic networks in the rainforest region (Woitowicz-Grushowski et al., 2020) and, second, they have low selectivity for tree cavities in these natural forests (Silva & Ramalho, 2014), and thus would not be affected by the slow replacement of tree species throughout the forest succession process.

On the other hand, there is some evidence that colony survival or longevity depends on habitat type or ecological context, as well as the stingless bee species (Table 1). The flexibility of this attribute and its involvement in ecological fitting (*sensu* Janzen, 1985; Agosta & Klemens, 2008) is particularly apparent in *T. angustula*, with low to moderate survival rates in the two forest habitats (between 58% in ES and 72% in EA) and very low survival in the anthropic habitat (43%) in the REM landscape. Slaa (2006) also observed a lower survival rate (40%) for this species in dry forest compared to adjacent deforested areas in the landscape. Therefore, the generalization that stingless bees invest more in colony survival (Slaa, 2006) needs to be considered with reservations, since it is valid mainly for species that are restricted to the natural habitats of tropical forest.

There were differences in the annual survival rate of colonies among species and between habitat types during the two years at REM (Tables 2), but there was no interaction between habitat type and species (Table 2). In any case, the spatial variation in longevity already described for *T. angustula* and the resulting similarities between habitats (Fig 1, see below) indicate that this generalist is probably fitting colonial fitness to the ecological context, that is, to the heterogeneity of habitat types in the same landscape. In a comparative analysis of forested and deforested areas in Costa Rica, Slaa (2006) also reported that the life history of stingless bees was affected by species or location.

**Table 1.** Variation of the annual survival rate of stingless bee colonies in two forest categories and in the anthropic habitat, in the landscape of the 'Reserva Ecológica Michelin' (REM) of the Brazilian Atlantic Forest. AS- old-growth forest or advanced stage forest regeneration; ES - young forest or early stage forest regeneration; AH - anthropic habitats. Body size (BS): large (L), medium (M) and small (S).

	BS	AS		ES		AH
		Tax. Sobr. (%)	Tax. Sobr. (%)	Tax. Sobr. (%)	Tax. Sobr. (%)	Tx. Sobr. (%)
		Year 1	Year 2	Year 1	Year 2	Year 1
<b>ANNUAL SURVIVAL</b>		**11±3,16	8,25±1,29	13±6	6±2,91	19,75±7,18
<b>Variation</b>		***9,75±3,03	7,5±1,65	10±4,30	5,25±2,68	17,5±6,34
<b>SPECIES</b>						
<i>Lestrimelitta</i> sp	S	*	*	*	*	50% (n=4)
<i>Melipona scutellaris</i> Latreille, 1811	L	83% (n=6)	100% (n=5)	100% (n=4)	75% (n=4)	*
<i>Nannotrigona</i> sp	S	*	*	*	*	66,6% (n=7)
<i>Partamona</i> sp1	M	66,6% (n=3)	100% (n=2)	*	*	*
<i>Partamona</i> sp2	M	100% (n=1)	0% (n=1)	*	*	*
<i>Paratrigona subnuda</i> Moure, 1947	S	50% (n=2)	0% (n=2)	0% (n=4)	*	*
<i>Plebeia droryana</i> (Friese, 1900)	S	*	*	25% (n=4)	100% (n=1)	14,2% (n=6)
<i>Scaptotrigona xanthotricha</i> Moure, 1950	M	92,8% (n=14)	100% (n=13)	81,8% (n=11)	66,6% (n=9)	*
<i>Scaptotrigona bipunctata</i> Lepeletier, 1836	M	100% (n=9)	88,8% (n=9)	83,3% (n=6)	100% (n=5)	*
<i>Scaura atlantica</i> Melo, 2004	S	0% (n=1)	*	*	*	*
<i>Schwarziana quadripunctata</i> Lepeletier, 1836	M	*	*	0% (n=1)	*	*
<i>Tetragonisca angustula</i> Latreille, 1811	S	85,7% (n=14)	58,3% (n=12)	59,3% (n=32)	57,8% (n=19)	42,6% (n=83)
<i>Trigona braueri</i> Friese, 1900	M	100% (n=1)	100% (n=1)	100% (n=1)	100% (n=1)	*
<i>Trigona fuscipennis</i> Friese, 1900	M	*	*	100% (n=1)	100% (n=1)	*
<i>Trigona hyalinata</i> Lepeletier, 1836	M	*	*	*	*	75% (n=4)
<i>Trigona spinipes</i> Fabricius, 1793	M	*	*	0% (n=1)	*	100% (n=1)

\*species nest is absent.

Variation of Annual Survival Rates among replicates of each habitat category: mean and standard deviation of total nests (\*\*) and most abundant species (\*\*\*).

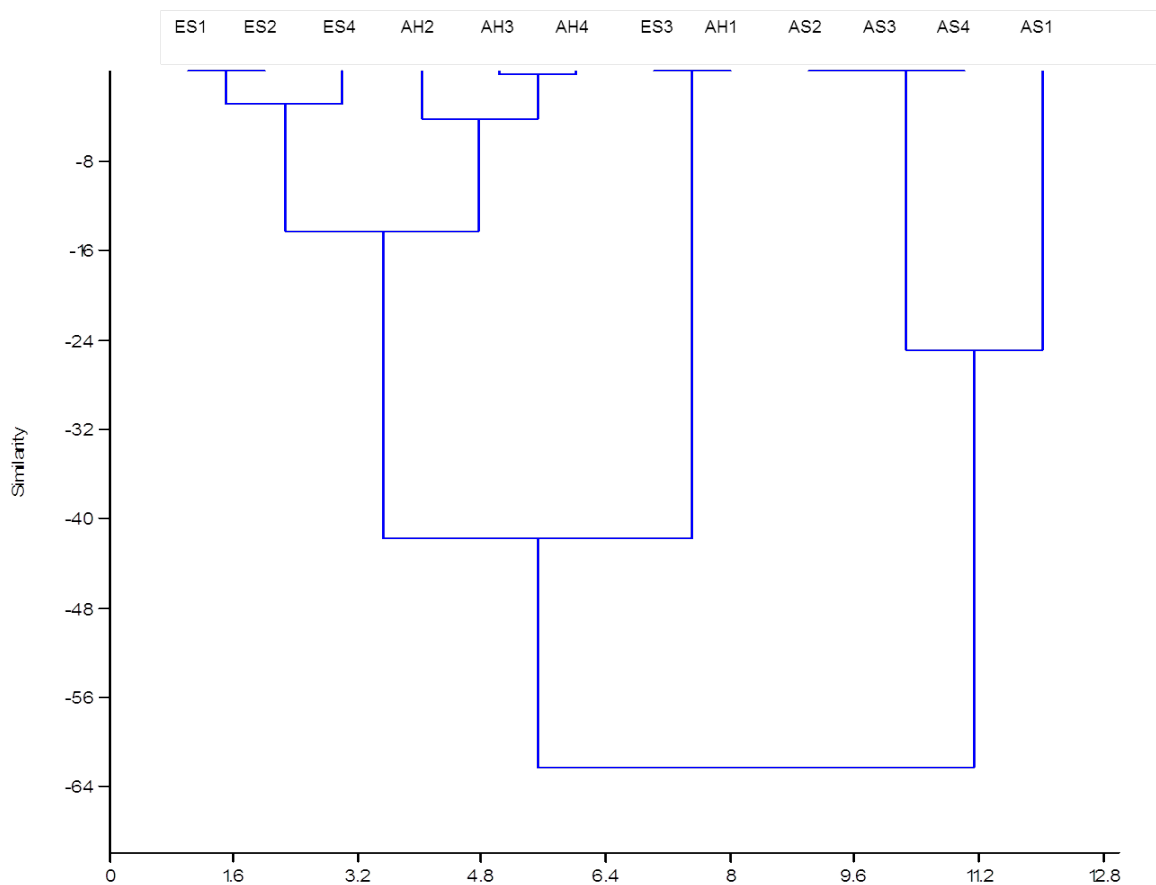
*T. angustula* was the only abundant species (> 0.2 nests / ha) in all the three habitat types in the REM landscape. The distance (similarity) analysis based on the survival of this habitat-generalist species places the young forest closer to the anthropic habitat than to the old forest (Fig.1) and groups the old-growth forest replicates together. At the same time, the colonies of this species reproduce at higher rates in the anthropic habitat than in the adjacent old growth forest (Silva et al., 2014; P.C.L. Gouvêa personal inf. Gouvêa & Ramalho, n.p.). These patterns of survival and reproduction produce a spatially structured population, which is finding better

conditions for growth in the anthropic habitat. Therefore, *T. angustula* also has a mass effect on the bee community in the remnants of old-growth forest, which tends to increase with progressive loss of natural forest cover (Personal information from PCLGouvêa, Gouvêa & Ramalho, np).

The expected trade-off between survival (longevity) and reproduction (Stearns 1997) is apparent in all abundant stingless bee species residing in the Atlantic Forest: high survival rates (Table 1) are related to low reproduction rates and, more specifically, to very low rates of swarming in trap nests (Silva et al., 2014). Again, the above detailed information about *T. angustula* supports phenotypic plasticity and opposing trends in spatial variation in survival and reproduction rates between anthropic habitat and the old growth forest. Worker bee size had an apparent effect on colony survival. The multiple comparison tests revealed that small size differed from large ( $p < 0.0001$ ) and medium ( $p < 0.0001$ ) size but no difference between medium and large size ( $p = 0.9$ ). These results, however, are preliminary and should be interpreted with some reserve as the number of colonies for the different sized classes differed, such as a much greater

**Table 2.** Effect of habitat type and species on annual survival rate of stingless bee colonies. p = probability significance level.

Independent variables	Dependent Variable (Survival)	
	After 1 year (p)	After 2 year (p)
Species	0,084	0,001
Habitat	0,000	0,002
Interaction (species x habitat)	0,158	0,150



**Fig 1.** Dissimilarities among the three habitat types (old-growth forest or advanced stage regeneration - AS; young forest or early stage regeneration - ES, and anthropic habitat – AH), as a function of variation in *T. angustula* annual survival rate. Euclidian distances.

number of colonies of small species than of large species. The greatest longevities were associated with the three medium-large-sized species exclusive to natural forest. Often, lowest rates were associated with the small-sized species more frequent in the anthropic habitat (see Table 1) and the habitat generalist *T. angustula*.

On the one hand, the relationship between worker size and colony survival was not expected, since perennial colonies of social stingless bees were presumed to persist as long as they were able to replace their long-standing laying queens (Engels & Imperatriz-Fonseca, 1990). On the other hand, given a general relationship between body size and foraging area (e.g., Araújo et al., 2004; Kleinert et al., 2009), smaller bees are likely to be more exposed to seasonal or unpredictable variation in flower supply within the small home range of their colony.

The implications of the central-place foraging and small colonial home range for the survival of stingless bee colonies become apparent considering that, first, these perennial colonies have very high rates of pollen consumption to maintain very high biomass replacement rates throughout the year (Roubik, 1993), and, secondly, these bee communities are structured through the sharing of floral resources (Kleinert et al. 2012). Indeed, variation among colonies in stored food can lead

to marked differences in the amount of sexuals produced by different colonies (Moo-Valle et al., 2001), which in turn causes variation in fitness. Annual survival or longevity probably also depend on the specific resilience of colonies after seasonal population collapses, such as when they are exposed to critical unfavorable foraging conditions, as observed for species of *Melipona* in Brazilian dry forest (Hrncir et al., 2019).

In summary, it is likely that perennial colonies of stingless bees with smaller workers are more vulnerable to fluctuations in food supply that affect colony survival, due to implications of central-place foraging in very restricted colonial home range. An expected trade-off in such cases of unavoidable reduction in colony longevity would be an increase in reproduction rate, as the spatial pattern of *T. angustula* seems to confirm.

Based on independent empirical data on stingless bee species in various tropical vegetation types (Brown & Albrecht, 2001; Ricketts, 2004; Brosi et al., 2007; Williams et al., 2010; Silva et al., 2013; Lichtenberg et al., 2017), we infer that deforestation and habitat anthropization contribute to increased species turnover among habitats, but reduce the number of stingless bee species at the landscape scale. The loss of species due to anthropic disturbances can not be compensated by the expansion of generalist species,

such as *T. angustula*, for example Foraging traits and diet breadth are probably associated with interspecific variation in susceptibility to reduced forest cover due to anthropization (Lichtenberg et al., 2017). The flexibility (phenotypic plasticity or reaction norm) of critical life history attributes (longevity and reproduction) can also contribute to the ‘ecological fitting’ (Agosta & Klemens, 2008) of habitat generalists to fast anthropogenic changes in the landscape. In this scenario, it is also expected that stingless bees, with high colonial longevity living in the forest, will be exposed to increased dispersal pressure from abundant generalists, and their mass effects, from adjacent anthropogenic habitats.

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### Authors' Contribution

MDS: Conceptualization, methodology, investigation, data curation, project administration, visualization, writing.

MR: Supervision, conceptualization, methodology, project administration, resources, funding acquisition, writing

JFR: Methodology, formal, analisys, writing

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