The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation

Berry J. Brosi *
Department of Biology, Stanford University, 385 Serra Mall, Stanford, CA 94305, USA

1. Introduction

Despite ongoing controversy over pollinator declines and a concomitant increase in studies on the effects of anthropogenic environmental change on pollinators (e.g. Chazoul, 2005; Steffan-Dewenter et al., 2005), we still do not have a comprehensive view of how bee communities respond to land-use change. This problem is particularly acute in the tropics, where most tropical forest trees are animal-pollinated (Bawa, 1990), where pollination limitation is most severe (Vamosi et al., 2006) and where land-use change is the largest driver of biodiversity loss (Sala et al., 2000).

The meliponine, or social stingless, bees (Apidae: Meliponini) are a critically important group of tropical bees. They are the most diverse group of eusocial tropical bees (Michener, 2000: p. 779), and may be the most abundant clade of bees on earth (Roubik, 1992). All meliponine bees are eusocial, with perennial hives consisting of a single queen and thousands of workers. Meliponine workers recruit foragers to rich sources of floral forage, thus allowing them to efficiently pollinate tropical plants whose blooming period is brief, including crops such as coffee (Klein et al., 2003a; Ricketts, 2004). This efficient exploitation of floral resources, along with their high densities, means that they are also major players in the cycling of nutrients in tropical forests (Roubik, 1989: p. 354).

This importance carries over to the human enterprise as well, since meliponines contribute to the pollination of >60 tropical crops. They are the primary wild pollinators of coffee (Klein et al., 2003b); and contribute to the effective pollination of avocado, sweet pepper, tomato, cucumber, strawberry, and rambutan (Slaa et al., 2006); as well as coconut, mango, macadamia nuts, chayote, carambola (“star fruit”), and achiote (Heard, 1999) among many other crops. These meliponine-mediated pollination services likely contribute billions of dollars to tropical economies ever year (Kearns et al., 1998; Ricketts et al., 2004b; Klein et al., 2007).
importance of meliponines as pollinators of tropical crops is likely to increase given the ongoing problems of honey bees, including Africanization (Schneider et al., 2004) and parasites and disease (e.g. Oldroyd, 2007).

While the Maya and other indigenous peoples have managed meliponine bees for millennia (Chemas and Rico-Gray, 1991), and some efforts have been made to modernize techniques and promote the husbandry of meliponines, also known as “meliponiculture” (Cortopassi-Laurino et al., 2006), wild colonies account for the vast majority of crop pollination activities that are conducted by meliponines. Thus, nearly all meliponine pollination activity can be considered a true ecosystem service, rather than a managed human activity.

Given the central place of meliponine bees in provisioning tropical crop pollination services, it is critically important to understand how they respond to ongoing land-use changes. This is particularly true given that studies of bee communities in Central America and Southeast Asia have found that meliponine bees are strongly associated with native forest habitat (Klein et al., 2002; Ricketts, 2004; Brosi et al., 2007; Brosi et al., 2008). On one hand, this association with forest is not surprising given that many (but not all) meliponines are tree-cavity nesters that may rely on tropical forests for nesting habitats (Roubik, 1989). On the other hand, many meliponine species will forage and even nest in human-dominated habitats that have experienced high degrees of deforestation (Klein et al., 2002; Ricketts, 2004; Brosi et al., 2007, 2008).

This tendency of meliponines to forage in human-dominated habitats is a positive attribute when considering crop pollination—and also makes for a direct linkage between forest cover and meliponine-mediated crop pollination. For example, Ricketts et al. (2004a) found that two patches of tropical forest near a large coffee farm in southern Costa Rica supported meliponine bees which contributed approximately $60,000 a year to the value of the coffee harvest, through increases in both the quantity and quality of coffee beans produced.

In order to improve understanding the responses of meliponine bees to land use change, I sampled meliponines over 3 years in a largely deforested landscape in southern Costa Rica, along gradients of both distance to forest and also forest fragment size. I hypothesized that meliponines would be more diverse and abundant in sites with more forest cover surrounding them, and in sites with greater density and diversity of floral resources. I also hypothesized that meliponine species would respond differently to land use change, and that these differences would be reflected in measures of community composition.

2. Methods

2.1. Study region

I conducted this study in the Valle de Coto Brus, Puntarenas province, southern Costa Rica, in the landscape surrounding the Las Cruces Biological Station (8° 47’ N, 82° 57’ W), near the town of San Vito. The landscape was converted in the 1960s from mid-elevation tropical forest to a mosaic of pastures, coffee fields, rural dwellings, and subsistence plots of crops like corn, beans, and bananas. Locally collected pollen records, however, show a history of forest clearing and agriculture by indigenous people spanning several thousand years (Clement and Horn, 2001). Remnant tracts of forest comprise about 15% of land cover in the region, with the largest fragment the ~230 ha tract at the Las Cruces Biological Station.

2.2. Study sites

The sites and samples—and thus the data presented here—come from one of the larger systematically collected datasets on tropical bees (Brosi et al., 2007, 2008). With data from both studies and with restrictions I imposed on sites (detailed below), I used 35 sites in the Las Cruces landscape in this analysis. The results presented here are distinct from those in Brosi et al. (2007, 2008) in that analyses combine both datasets (though only including sites that were sampled in a minimum of two full field seasons), along with several new analyses. The sites used in Brosi et al. (2007) fell along a gradient of distance from forest and were sampled in the rainy season (July-September) of 2003 and in the dry season (February-May) of 2005. The sites from Brosi et al. (2008) were along a gradient of forest fragment size, with sample sites situated in pastures at the edges of the forest fragments. These sites were sampled in the rainy season (June-September) of 2004, and the dry season (February-May) of 2005, with the dry season samples being taken concurrently with those from Brosi et al. (2007). Sites ranged from 500 m to 13 km in geographic distance from one another and from 900 to 1300 m in elevation above sea level.

2.3. Bee and plant sampling

In each site, two field team members netted bees in a 20 m × 20 m square plot for a 15-minute period, focusing their efforts on flowering plants within the plot. The netting team caught bees in the order that they were seen, and thus would not pursue a relatively rare species at the expense of a common species seen first. The netting trials were focused across all bees in the bee community; in the analyses presented here, we include only the meliponine bees from these samples. We did not net bees in conditions of fog, precipitation, or high winds. For more on the sampling, see Brosi et al. (2007, 2008). Specimens were pinned, labeled, and identified to species using Roubik (1992). V. Gonzalez and I. Hinojosa, University of Kansas, evaluated and corrected species determinations. Specimens are housed in the Biology Department, Stanford University.

Blooming plants were counted along 5 parallel 20 m transects in each site, counting and identifying all plants in bloom within 50 cm of either side of the transect line. See Brosi et al. (2007, 2008) for more details on plant sampling.

2.4. Data analysis

I analyzed two responses (dependent variables) of meliponine communities to landscape structure and plant resource availability: (1) the species richness and abundance of meliponines (across all species, and also species-specific abundances for those species with >20 individuals recorded); and (2) meliponine community composition (similarity matrices between sites).

I analyzed data using the R statistical programming language (R Core Development Team, 2006); additional R packages I used are cited with the details of specific analyses. Sample size was 35 (i.e. the number of sites), except for analyses on forest fragment size, where N = 19.

I assessed the effects of (1) landscape structure and (2) local floral resources on meliponine species richness, abundance, and community composition. The primary measure of landscape structure used in the analyses was “forest cover”, or the proportional area of forest surrounding sample sites at a radius of 400 m. I used 400 m because earlier work showed this radial distance to have a consistently strong relationship with meliponine diversity and abundance (Brosi et al., 2007, 2008). In secondary analyses, I also looked at two additional measures of landscape structure: distance, i.e. whether a site was at the edge of a forest fragment or located in open countryside; “fragment size”, the log 10 of forest fragment area (for those sites at forest edges). Forest cover, distance to forest, and forest fragment area were all highly correlated with one another. I used forest cover in multivariate analyses because it is continuous (unlike
the meliponine community in the Las Cruces landscape is highly mean for both meliponine richness and abundance (e.g. Olofsson (GLM) with Poisson errors in the mixed-effects model, because the curve, Fig. 1).

3.1. Overview

I sampled 1141 meliponine individuals representing 9 genera and 20 species (species list, Table 1). The rank abundance profile of the meliponine community in the Las Cruces landscape is highly uneven. One species, Trigona fulviventris, accounted for 45% of all sampled individuals; the next-most common species, Partamona orizabensis, represented 22% of all individuals (rank abundance curve, Fig. 1).

3.3. Meliponine diversity and abundance

Multivariate mixed-effects models showed that both meliponine abundance and species richness are strongly related to forest cover, but not to the abundance or richness of plants in bloom (Table 2; Fig. 2). When I re-analyzed these models without including Trigona fulviventris, the most common species, these results changed somewhat. Meliponine abundance was no longer significantly related to forest cover, though it remained unrelated to blooming plant richness or abundance. In contrast, meliponine richness was still related to forest cover, though more weakly, and showed marginal relationships with both plant richness and plant abundance (Table 3; Fig. 3). Thus, T. fulviventris appears to be a significantly spatially autocorrelated (p = 0.00031). Abundance and richness were both significantly altitudinally autocorrelated (abundance: p = 0.0031; richness: p = 0.0011). Community similarity, however, showed no significant relationship with either geographic distance (p = 0.22) or altitudinal differences between sites (p = 0.52), as assessed with Mantel tests. In subsequent analyses, I assumed sites were independent.

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### Table 1

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Abundance</th>
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</thead>
<tbody>
<tr>
<td>Melipona</td>
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<td>24</td>
</tr>
<tr>
<td>Nogueirapis</td>
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<td>Trigona</td>
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<tr>
<td>Trigonisca</td>
<td>sp</td>
<td>6</td>
</tr>
</tbody>
</table>

**Fig. 1.** Rank abundances of meliponine species.
driver of the results, particularly with regard to meliponine abundance and forest cover.

Separate univariate analyses showed strong positive relationships with meliponine richness and abundance and both distance to forest (abundance: $z = 3.26, p = 0.0011$; richness: $z = 3.31, p = 0.00094$) and forest fragment size (abundance: $z = 2.40, p = 0.016$; richness: $z = 3.13, p = 0.0017$).

### 3.4. Species-specific abundance

Because I separately analyzed the abundances of nine species, I used a Bonferroni-corrected significance cut-off $p$-value of 0.0005 in the species-specific analyses. At this level, I found only three significant associations between landscape or flowering-plant variables and species-specific abundances of meliponines. Two species showed positive relationships with forest cover ($T. fulviventris$ $z = 3.55, p = 0.00039$; $Plebeia jatiformis$ $z = 8.40, p = 8.69 \times 10^{-15}$). The abundance of $Paratrigona orniticeps$ was positively related to plant species richness ($z = 3.13, p = 0.00027$).

### 3.5. Community composition

The results of the multivariate matrix permutation tests were highly dependent on variable order, so I re-ran them for all possible

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Mixed-effects model results for meliponine abundance and species richness.</th>
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<tr>
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<td>Estimate</td>
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<td>Plant abund</td>
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<tr>
<td>Plant spp. rich</td>
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Significance levels are: $p < 0.1$; $^* p < 0.05$; $^{**} p < 0.01$; $^{***} p < 0.001$.

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Mixed-effects model results for meliponine abundance and species richness, excluding $Trigona fulviventris$.</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Abundance</td>
</tr>
<tr>
<td></td>
<td>Estimate</td>
</tr>
<tr>
<td>(Intercept)</td>
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<tr>
<td>Forest cover</td>
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<tr>
<td>Plant abund</td>
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<tr>
<td>Plant spp. rich</td>
<td>$0.073$</td>
</tr>
</tbody>
</table>

Significance levels are: $^* p < 0.05$; $^{***} p < 0.001$. 

Fig. 2. Relationships between forest cover, floral resources, and meliponine species richness and abundance. These graphs are not constructed from the multivariate mixed-effects models, but rather show site-based averages with linear regression fit lines to show basic relationships. Solid regression lines depict significant relationships in the mixed-effects models, with dashed lines for non-significant relationships.
order combinations (15 combinations total for all three-way, all two-way, and all one-way combinations). This order specification dependency could be due in part to correlations between variables. Forest cover and plant variables were not significantly correlated with one another, though plant abundance and species richness were significantly correlated. Plant species richness had a consistently significant relationship with meliponine community composition, in all but two of the 11 trials (univariate: $F = 3.18, p < 0.001$). Forest cover was significant in the univariate test, in two of four bivariate tests, and in two of the six trivariate tests (univariate: $F = 1.72, p < 0.001$). Thus, forest is likely playing some role in the relationship, but not as strongly or consistently as plant richness. Plant abundance, on the other hand, was not significant in univariate tests or any bivariate tests, and was only significant in one of the six trivariate tests. Therefore, plant abundance overall does not seem to be an important factor in shaping meliponine community composition (univariate: $F = 0.48, p = 0.8$). Univariate tests showed no relationship between meliponine community similarity and forest fragment size ($F = 0.76, p = 0.6$) or distance category ($F = 0.87, p = 0.4$).

4. Discussion

4.1. Overview

Meliponine species richness and abundance are strongly and positively related to the proportion of forest surrounding sample sites, but are not correlated with blooming plant density or plant species richness. Much of the effect of meliponine abundance (but not species richness) is driven by the most common species, *Trigona fulviventris*. In analyses that omitted this species, abundance was no longer significantly related to forest cover, but species richness remained significantly correlated with forest cover. I also found species-specific responses: abundance of *T. fulviventris* and *Plebeia jatiformis* was significantly positively related to forest cover, while abundance of *Paratrigona orniticeps* was positively related to plant species richness. None of the six other species analyzed showed any relationship with forest cover or plant resources. Meliponine community composition was most strongly related to plant species richness, weakly related to forest cover, and not related to plant abundance.

4.2. Meliponine species richness and abundance

The results related to species richness and abundance are largely consistent with the few landscape-scale studies that have considered meliponine bees. Brown and Albrecht (2001), working in Brazil, found a strong relationship between the species richness of bees in the genus *Melipona* and forest cover, and further showed species-specific responses in that two *Melipona* species were not associated with the degree of forest cover, while another two species showed a very strong association with forest. In Indonesia, Klein et al. (2002) demonstrated a negative relationship between land-use intensity and the diversity and abundance of social bees, which there included meliponines as well as two species *Apis*. In southern Costa Rica, about 100 km NW of my study region, Ricketts (2004) showed significantly greater visitation to coffee flowers by meliponine bees, as well as enhanced bee species richness, near two large forest fragments, but not near a thin riparian strip of trees. Finally, earlier work in the same landscape did not directly show effects of distance to forest (Brosi et al., 2007) or forest fragment size (Brosi et al., 2008) on meliponine species richness and abundance. Both studies, however, did show a positive relationship between forest size and proximity and the proportion of the total bee community represented by meliponines. Comparing the results presented here with those from Brosi et al. (2007,
it is likely that in the present work, the larger true sample size (increased number of sites), as well as the larger number of samples considered within some individual sites, contributed to greater statistical power to detect trends within the meliponine community.

I did not find a relationship between meliponine species richness and abundance and the availability of floral resources within a site. While all meliponines in this region are dependent on nectar and pollen for essentially 100% of their dietary requirements, the relationship between the species richness and abundance of plants and bees is not straightforward, for several reasons. One factor is that different plant species have distinct pollen and nectar rewards, both in terms of quantity and quality, as well as access to those rewards, through both morphological (floral structure) and chemical (nectar and pollen chemistry) means (e.g. Chittka et al., 1999). It was beyond the scope of this study to quantify these rewards, and thus by necessity I used somewhat coarse measures of the availability of floral resources. Second, meliponines and many other pollinators, by virtue of their ability to fly, have large areas over which they can forage, and quantifying the floral resource base over the entire study area, let alone over a larger area in each study site, was beyond the scope of the study. Finally, there can be lag effects in the responses of bee communities to changes in floral resources. Due to the time constraints of provisioning larval cells, larval and pupal development, and (in some species) periods of dormancy, bee abundance can take several weeks to a year to respond to increases in the floral resource base (e.g. Tepedino and Stanton, 1981).

Meliponines as a group are associated with the quantity of forest cover, as evidenced by both the results presented here as well as those reported by others, from a range of disparate and distant locations (Brazil, Brown and Albrecht, 2001; Indonesia, Klein et al., 2003a,b; and Costa Rica, Ricketts, 2004; Brosi et al., 2007, 2008). This pattern is likely driven by two primary life-history requirements: nesting and feeding needs. While meliponines have diverse nesting habits and substrates, many species prefer to nest in tree cavities, as is befitting of their evolution in tropical forest habitats (Roubik, 1989). In addition, while many meliponine species will forage both within tropical forests and also in deforested areas, some of the rich floral resources within forests (such as mass-blooming tropical trees) likely help support meliponine species richness and abundance. Measuring floral resources within tropical forests is logistically daunting and was beyond the scope of this study.

Another factor that could have contributed to the association between meliponines and forest is human exploitation and destruction of stingless bee nests. In many parts of the tropics, including southern Costa Rica, stingless bee honey is valued for its medicinal properties and carries a high price (Souza et al., 2006); nests are often destroyed in the process of harvesting this honey. Additionally, meliponine nest defense mechanisms (hair pulling; flying in the eyes, ears, and mouth; etc.) can present a nuisance to people (Roubik, 1989: p. 196), and nests near human habitation are often purposefully destroyed for this reason.

4.3. Community composition

The community composition of meliponines was consistently related only to the species richness of blooming plants in the sampled pastures, and consistently not related to plant abundance. There was a more complex response of forest cover, which showed inconsistent evidence of being an important factor in shaping meliponine communities. In about half of the combinations of variable order, it was significant, whereas it was not in the other half. Univariate tests on the effects of forest fragment size and proximity to forest on meliponine community composition did not show any significant effects, as was expected given the correlation of those values with forest cover. Thus, there is only very weak evidence to support my hypothesis that meliponine species would be grouped into sets of species that are more or less resilient to deforestation.

The result that meliponine community composition is driven primarily by blooming plant diversity is somewhat surprising, given the complex relationship between bee and plant communities discussed previously. One potential mechanism that could cause plant richness to structure bee communities is the interference competition and dominance hierarchy that meliponines display, which is thought to contribute to resource partitioning (e.g. Hubbell and Johnson, 1978). Such a mechanism may lead, for example, to an increased likelihood of some “submissive” bee species appearing in species-rich plant communities, where they can exploit floral resources that are not being used by more dominant species.

Potts et al. (2004) showed that nectar resource diversity, which is strongly related to plant species richness, is a major factor structuring pollinator community composition. They also found a significant relationship, however, between nectar resource diversity and bee diversity. Perhaps quantifying the species-specific floral rewards in the flowering plant community would strengthen the association between plants and bees, both in terms of diversity and abundance and also in terms of community composition.

4.4. Meliponine foraging behavior and land use change

Meliponine foraging strategies are extremely diverse and are a major driver of the distribution of workers of a given species on the landscape. In the context of this study, this is a particularly important point because some the strategy of some meliponine species is geared toward the efficient exploitation of “bonanza”-type resources, by having a few scouts locate resources, followed by massive recruitment. Foraging workers of such species are not distributed evenly across the landscape, which means that my sampling strategy would not have detected such species proportionally to their abundance. By contrast, other meliponine species forage in a primarily or exclusively solitary manner, and others are facultative recruiters, which forage in a solitary mode but will sometimes recruit nestmates to high-density floral resources (e.g. Hubbell and Johnson, 1978; Roubik et al., 1986; Slaa et al., 2003).

Foraging strategy, however, is closely tied to the distribution of flowering plant resources (Johnson and Hubbell, 1975), which is in turn strongly associated with land cover. Forested and deforested habitats contrast strongly in the spatiotemporal distributions of flowering plant resources in many places in the tropics. In particular, tropical forest trees often bloom in intense, short bursts, leading to an extremely patchy distribution of floral resources in both space and time (Bawa, 1990). By contrast, many deforested habitats, such as the rustic pastures I sampled meliponines in, have low densities of flowering herbs and shrubs, many of which are in bloom for much of the year (Brosi et al., 2007, 2008).

Thus, it is likely that meliponine species that employ a solitary or facultative-recruiting foraging style will fare better in deforested habitats, and forage more in those habitats, than will species that use intensive forager recruitment. For example, Trigona fulviventris, by far the most commonly sampled bee in this study, is a facultative recruiter that conducts a great deal of solitary foraging (Johnson and Hubbell, 1975; Hubbell and Johnson, 1978; Slaa et al., 2003). While T. fulviventris can apparently efficiently utilize the low-density floral resources of the deforested habitats in the study region, its distribution is also strongly linked to forest habitat. Its need for relatively large tree cavities for nesting sites (Hubbell and Johnson, 1977) likely drives this pattern.
Considering foraging patterns in meliponines, the sampling strategy that I used is appropriate for the deforested habitats I sampled in due to their relatively consistent, low-density floral resources. At the same time, this sampling strategy would not serve well for understanding the meliponine community in tropical forest habitats with a much patchier distribution of floral resources; such a goal was beyond the scope of this study.

Foraging strategy is also a very important aspect of meliponine biology in the context of crop pollination services. Crops with mass-blooming phenology, particularly those with a short flowering duration, should theoretically be particularly well pollinated by meliponines with strong recruitment behavior. Coffee (Coffea arabica L.), a cornerstone of tropical export agriculture, fits this exact profile with a typical blooming period of three days (e.g. Drinnan and Menzel, 1995). In a study of coffee pollination near San Isidro del General, Costa Rica (about 100 km north-northwest of my study site), Ricketts (2004) found that ten species of meliponines, along with feral honey bees (Apis mellifera) were the most common visitors to coffee flowers. While foraging-strategy data are not available for all species, of the four most common meliponines in the Ricketts (2004) study, one is a solitary forager (Plebeia frontalis, the second-most common floral visitor) and another is a facultative group forager (T. fulviventris, the fourth most common floral visitor). Thus, while foraging recruitment can play a role in meliponine-mediated crop pollination services, it is not the only factor in determining the density of flower visitors. It is possible that land-use change, and the concomitant change in the distribution of floral resources, reduced the abundance of mass-recruiting meliponines in the San Isidro landscape.

4.5. Management recommendations

Based on my results and those of others, several recommendations for landscape management to support meliponine bees and their crop pollination services can be made:

- Preserve even small patches of forest near pollination-dependent crops to support meliponine nesting. I recorded meliponines in fragments as small as ~0.25 ha.
- Consider conserving forest even when not adjacent to pollination-dependent crops, for their option value if land use were to change. This is particularly important given ongoing problems with honey bee declines.
- Work to re-connect isolated forest patches. While I did not find an effect of forest isolation on meliponine communities, the maximum isolation distance between forest fragments in this landscape was short. <2 km in all cases (Brosi, 2009). More extreme isolation distances may have strong impacts on meliponines, since their colonies do not swarm. Instead, workers take thousands of trips between old and new nests to transport nest material and provisions (Michener, 2000), which likely makes them particularly susceptible to habitat isolation at scales greater than normal foraging distances.
- Work to reduce human destruction of meliponine nests, for honey harvests or otherwise.
- Reduce use of agrochemicals; though this study did not focus on the effects of agrochemicals on meliponine bees, bees as a group are particularly susceptible to pesticides (Gross, 2008).

4.6. Future research

Future research should include the effects of species traits (such as flight range, nesting substrate, foraging and recruitment strategies, position in foraging dominance hierarchies) on meliponine responses to habitat loss and change. Specifically, there is little known about how foraging strategy may condition the effects of land use change on different species of meliponines. For example, do mass-recruiting meliponines fare worse in deforested habitats? Will crop fields near very large tracts of tropical forest receive higher levels of crop pollination services, due to a greater abundance of meliponine species that exhibit mass-recruitment?

In addition to questions on meliponine species traits, we also know little about the particular attributes of tropical forest that support their foraging and nesting. In particular, there is little information on how meliponines respond to re-growth forest, or how to design ecological restoration programs to support meliponine bees and the crop pollination services they provide.

5. Conclusion

Meliponine bees are important both ecologically and economically, and more work is needed to both understand their complex responses to habitat change, and to conserve their populations, over the long term. Given the increasing concern over the status of pollinators worldwide, conserving this critically important group of bees in the most biodiverse habitats on Earth should be prioritized.

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