

1 **Foraging traits modulate stingless bee community disassembly under forest loss**

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3 Elinor M. Lichtenberg^{1,2,*}, Chase D. Mendenhall^{3,4,5}, Berry Brosi⁶

4
5 1) Department of Ecology and Evolutionary Biology, University of Arizona, PO Box 210088,
6 Tucson, AZ 85721, USA, elichten@utexas.edu

7
8 2) Department of Integrative Biology, University of Texas at Austin, 205 W 24th St. Stop C0930,
9 Austin, TX 78712

10
11 3) Department of Biology, Stanford University, 385 Serra Mall, Stanford, CA 94305, USA,
12 cdm@stanford.edu

13
14 4) Center for Conservation Biology, Stanford University, 385 Serra Mall, Stanford, CA 94305,
15 USA

16
17 5) The Nature Conservancy, Arlington, VA 22203, USA

18
19 6) Department of Environmental Studies, Emory University, 400 Dowman Drive, Suite E510,
20 Atlanta, GA 30322, USA, bbrosi@emory.edu

21
22 *Corresponding author: Elinor M. Lichtenberg

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25 **Running headline:** Foraging traits impact bee sensitivity to forest loss

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28 collected the data; EML analysed the data; EML led the writing of the manuscript. All authors
29 contributed critically to drafts and gave final approval for publication.

1 **Abstract**

2 1. Anthropogenic land use change is an important driver of impacts to biological communities
3 and the ecosystem services they provide. Pollination is one ecosystem service that may be
4 threatened by community disassembly. Relatively little is known about changes in bee
5 community composition in the tropics, where pollination limitation is most severe and land use
6 change is rapid. Understanding how anthropogenic changes alter community composition and
7 functioning has been hampered by high variability in responses of individual species. Trait-based
8 approaches, however, are emerging as a potential method for understanding responses of
9 ecologically-similar species to global change.

10 2. We studied how communities of tropical, eusocial stingless bees (Apidae: Meliponini)
11 disassemble when forest is lost. These bees are vital tropical pollinators that exhibit high trait
12 diversity, but are under considerable threat from human activities.

13 3. We compared functional traits of stingless bee species found in pastures surrounded by
14 differing amounts forest in an extensively deforested landscape in southern Costa Rica.

15 4. Our results suggest that foraging traits modulate competitive interactions that underlie
16 community disassembly patterns. In contrast to both theoretical predictions and temperate bee
17 communities, we found that stingless bee species with the widest diet breadths were less likely to
18 persist in sites with less forest. These wide-diet-breadth species also tend to be solitary foragers,
19 and are competitively subordinate to group-foraging stingless bee species. Thus, displacement by
20 dominant, group-foraging species may make subordinate species more dependent on the larger or
21 more diversified resource pool that natural habitats offer. We also found that traits that may
22 reduce reliance on trees – nesting in the ground or inside nests of other species – correlated with
23 persistence in highly deforested landscapes.

1 5. The functional trait perspective we employed enabled capturing community processes in
2 analyses and suggests that land use change may disassemble bee communities via different
3 mechanisms in temperate and tropical areas. Our results further suggest that community
4 processes, such as competition, can be important regulators of community disassembly under
5 land use change. A better understanding of community disassembly processes is critical for
6 conserving and restoring pollinator communities and the ecosystem services and functions they
7 provide.

8

9 **Keywords:** biodiversity, community disassembly, fourth-corner problem, functional traits, land
10 use change, Meliponini, pollination, stingless bees

1 **Introduction**

2 Human activities are major drivers of landscape change, leading to habitat loss,
3 fragmentation, and alteration of habitat composition. These landscape changes in turn can lead to
4 disassembly of biological communities, i.e., non-random species declines and losses (e.g.,
5 Leavitt & Fitzgerald 2013; Moser *et al.* 2015; Figuerola *et al.* 2015). Understanding which taxa
6 are better able persist in disturbed environments and the mechanisms underlying disassembly can
7 help guide taxon-specific conservation efforts. This understanding is necessary to predict how
8 community disassembly will alter or reduce ecosystem services (Zavaleta *et al.* 2009; Cardinale
9 *et al.* 2012).

10 One ecosystem service globally threatened by community disassembly is pollination.
11 Bees are considered the most important animal pollinators for most plants and ecosystems (Klein
12 *et al.* 2007; Ollerton, Winfree & Tarrant 2011). Habitat loss due to human activities reduces bee
13 abundance and diversity (Potts *et al.* 2010) and lowers plant reproductive success (Hoehn *et al.*
14 2008; Albrecht *et al.* 2012). Land use change is especially rapid in the tropics, marked by both
15 increasing cropland (Beddow *et al.* 2010) and decreasing forest area (Hansen *et al.* 2013). These
16 changes may have stronger ecosystem-level effects in tropical than in temperate areas due to
17 more severe pollen limitation (Vamosi *et al.* 2006) and a higher proportion of animal-pollinated
18 plants (Ollerton *et al.* 2011). Further, bee community disassembly patterns may differ between
19 temperate and tropical regions due to the high abundance and species richness of social bees in
20 the tropics (Roubik 1992a). It is thus critical to determine how land use change disassembles
21 communities of tropical bees and the plants they pollinate.

22 Focusing on functional traits, characteristics of an organism that strongly influence its
23 fitness (McGill *et al.* 2006; Vandewalle *et al.* 2010), holds great promise for determining effects

1 of anthropogenic changes on community composition and functioning. Functional traits, which
2 are often shared by multiple members of a community, can better predict ecosystem functioning
3 than do purely species-based indices such as abundance and richness (Gagic *et al.* 2015). This is
4 proving true for pollination, where the degree to which bees interact with plants and provide
5 pollination services is best explained by specific traits of the bees (e.g., mouthpart size) and
6 flowers (e.g., whether open or tubular) (Garibaldi *et al.* 2015; Crea, Ali & Rader 2016).
7 Functional traits also effectively predict responses of communities to global change (e.g., Marini
8 *et al.* 2012; Pedley & Dolman 2014). This may be in part because traits strongly influence how
9 organisms interact with each other and their environments. Such interactions can be mechanisms
10 of community disassembly (Bregman *et al.* 2015) and of ecosystem functioning. For example,
11 Forrest *et al.* (2015) showed that reduced bee diversity on farms compared to natural areas is in
12 part due to a lack of sufficient nesting substrate on farms for species that nest above ground (e.g.,
13 in trees, stems or dead wood). In addition, studying land use change within a trait-based
14 framework facilitates determining general patterns that can be applied to related taxa or separate
15 geographic regions (Keddy 1992). Focusing on functional traits has helped identify general
16 disassembly patterns of temperate bee communities, such as increased losses of solitary bees
17 with disturbance (Jauker *et al.* 2013; Rader *et al.* 2014; Pisanty & Mandelik 2014; Forrest *et al.*
18 2015).

19 Despite their promise, the use of functional traits to study mechanisms of community
20 disassembly has been hampered by a methodological issue: the “fourth-corner” problem
21 (Legendre, Galzin & Harmelin-Vivien 1997; Dray & Legendre 2008). Standard analysis methods
22 are unable to directly analyse the relationship between a species’ traits and characteristics of the
23 environment where that species is found (Legendre *et al.* 1997). Because traits are properties of

1 species (Fig. 1, bottom left) while environmental variables are properties of sites (Fig. 1, top
2 right), there is an inherent challenge in estimating the joint effects of traits and the environment
3 (Fig. 1, bottom right) on community metrics such as species richness.

4 Several approaches attempt to work around the fourth-corner problem. Early approaches
5 involved interpreting species-environment relationships *a posteriori* in light of trait data (e.g.,
6 Cane *et al.* 2006) or species-trait relationships in light of environmental data (e.g., Mabry &
7 Fraterrigo 2009), which precludes testing mechanistic hypotheses. Another common approach is
8 assessing the frequency of different traits or mean trait values in different environments (e.g.,
9 Moretti *et al.* 2009). Summarizing trait distributions within a site often leads to low
10 discriminatory (Verberk, van Noordwijk & Hildrew 2013) and predictive (Wright *et al.* 2006)
11 power, and can yield data that are overly influenced by outliers or abundant species. A common
12 approach to minimising this unequal influence, weighting by abundance, is problematic when
13 data include species of varying degrees of sociality and thus expected group sizes (as is often the
14 case with bees). Summarising trait distributions also is better suited to answering questions about
15 changes in community composition than species-level responses to environmental change: the
16 focus of our study. Further, workarounds cannot explicitly test how trait and environmental
17 values simultaneously alter persistence probabilities (or other performance consequences)
18 because they do not explicitly include a trait-by-environment interaction (McGill 2015). This
19 makes it difficult to directly address mechanisms that determine how traits mediate community
20 disassembly (Pedley & Dolman 2014). In contrast, analyses that incorporate the fourth corner,
21 such as the one presented here, permit direct tests of mechanisms. We used the method
22 developed by Walker *et al.* (2012) to combine the three standard “corners” (Fig 1; site by species
23 matrix, species by traits matrix, site by environment matrix) into a long format that allows

1 regression of species occurrence by both traits and environmental data in the same dataset. This
2 approach avoids the pitfalls described above by 1) including both trait and environment data for
3 each site-species combination and 2) combining continuous and categorical trait variables. Our
4 regression-based method, which is not restricted to any one type of regression, provides an
5 additional benefit: flexibility. For example, it can be used to study non-linear effects, or to test *a*
6 *priori* hypotheses about combined effects of multiple traits and environmental variables (via
7 planned contrasts).

8 Here we examine whether functional traits are associated with the disassembly of
9 stingless bee communities under land use change. We focus on social stingless bees
10 (Hymenoptera: Apidae: Meliponini), which are thought to provide a large share of tropical insect
11 pollination (Heard 1999) and to suffer disproportionate abundance and richness losses from
12 human activities (Brosi, Daily & Ehrlich 2007; Brosi *et al.* 2008). The strong effect of habitat
13 loss on these social tropical species contrasts with land use change predominantly affecting
14 solitary species in temperate areas (Rader *et al.* 2014; Pisanty & Mandelik 2014; Gonçalves *et al.*
15 2014; Forrest *et al.* 2015). In addition to their high taxonomic diversity — over 500 species
16 (Michener 2000) — stingless bees within and across sites show high diversity in functionally-
17 relevant traits. For example, body size can range from a head width of 0.8 mm (Pedro &
18 Camargo 2009) to 5 mm (Roubik 1992b), and colony sizes from less than 100 (Wille &
19 Michener 1973; Roubik 1983a) to over 10,000 (Hubbell & Johnson 1977; Lichtenberg,
20 Imperatriz-Fonseca & Nieh 2010). Stingless bees typically nest in tree cavities or the ground,
21 although some species build nests on tree trunks or branches. All stingless bees are eusocial, but
22 some species forage as individuals while others tend to forage in large groups of nestmates
23 (Johnson 1983). With such high trait diversity and critical roles as pollinators, stingless bees are

1 a good system for studying the dynamics of system change in response to anthropogenic
2 disturbance.

3 We use data on the effects of forest loss on Costa Rican stingless bee communities to ask
4 two questions: (1) Does land use change cause trait shifts within stingless bee communities? And
5 (2) Does competition affect which species can persist in altered habitats? It is generally held that
6 specialized species and larger animals are more sensitive to habitat loss and prone to extinction
7 (McKinney 1997; Ewers & Didham 2006). Studies of temperate bee communities to date
8 typically support specialization effects (Cane *et al.* 2006; Kleijn & Raemakers 2008; Williams *et*
9 *al.* 2010; Bartomeus *et al.* 2013; Rader *et al.* 2014; Gonçalves *et al.* 2014; Forrest *et al.* 2015; but
10 see Otieno *et al.* 2015), but show mixed support for size effects (Winfree, Griswold & Kremen
11 2007; Williams *et al.* 2010; Bartomeus *et al.* 2013; Jauker *et al.* 2013; Wray, Neame & Elle
12 2014; Rader *et al.* 2014). Too little is known about stingless bee biology and responses to land
13 use change to formulate specific hypotheses about other traits. In terms of the second question,
14 competition with honey bees (Roubik *et al.* 1986; Paini 2004) and among stingless bees (Eltz *et*
15 *al.* 2002; Slaa 2006) have been hypothesized to be key factors shaping stingless bee
16 communities. Forest loss can reduce both nesting sites and food (flowers) available to stingless
17 bees (Roubik 1989; Batista, Ramalho & Soares 2003), potentially intensifying competition for
18 those resources. Thus competition may partially drive species persistence patterns under land use
19 change.

20

21 **Methods**

22 *Bee sampling*

1 We sampled stingless bees in the Valle de Coto Brus, Puntarenas province, southern
2 Costa Rica, in the landscape surrounding the Las Cruces Biological Station (8° 47' N, 82° 57'
3 W), near the town of San Vito. This region was covered by premontane wet tropical forest before
4 European settlement. It now consists of interspersed pastures, coffee, small (<1 ha) mixed-
5 agricultural plots, human settlements and small (mostly <10 ha) forest patches (see Brosi *et al.*
6 2007 for more detail). The dataset used here is identical to that described in Brosi (2009),
7 consisting of 35 sites in the Las Cruces landscape. All sites were in relatively open pastures
8 (mean area ~0.5 ha) with active grazing rotations. Sites ranged from 900 to 1300 m in elevation
9 above sea level and from 500 m to 13 km in geographic distance from one another, with no
10 spatial autocorrelation in community composition (Brosi *et al.* 2007; Brosi 2009). Sites were
11 surrounded by varying degrees of tree cover.

12 Each site was comprised of a 20 x 20 m plot, in which we sampled all bees detected in
13 15-minute netting samples with two field team members actively netting. We did not sample
14 bees in conditions of high winds, fog or precipitation. Bees were captured in the order that they
15 were seen (i.e., rare species were not sampled at the expense of a common species seen first).
16 This sampling effort was inclusive of all species in the bee community, but we used only the
17 stingless bees from these samples in the analyses presented here. We sampled foraging bees in
18 the rainy seasons of 2003 and 2004 (June–September) and in the dry season of 2005 (February–
19 May). In Costa Rica, stingless bee richness and species' abundances show little seasonality
20 (Heithaus 1979). Each site was sampled on 10-22 separate days over these periods. We pinned,
21 labelled and identified stingless bees to the species level using Roubik (1992b). V. Gonzalez and
22 I. Hinojosa, then at the University of Kansas, evaluated and corrected species determinations.
23 Some determinations are updated here following Camargo and Pedro (2013). Specimens are

1 housed in the Department of Environmental Sciences, Emory University. For more on the
2 sampling, see Brosi et al. (2007, 2008) and Brosi (2009).

3 For each site, we determined the presence or absence of each species from netting data
4 pooled across all sampling days. We focused on presence/absence, rather than species'
5 abundances, because abundances can reflect a species' propensity to recruit nestmates to rich
6 resources. Abundances thus do not consistently represent the number of nests in a region when
7 considering multiple species. To account for uneven sampling effort across sites (10-22 days),
8 we used sample-based rarefaction to calculate rarefied presence/absence: the probability a
9 species was present at a site in any set of 10 sampling days.

10

11 *Bee traits*

12 We selected seven life history and behavioural traits that are relevant to stingless bees
13 conservation and their role as pollinators, and for which we could find enough data in the
14 literature: body size (average head width), colony size (average number of workers), diet
15 breadth, group foraging, nesting in the ground, inquiline nesting (nesting in other species' nests)
16 and nesting in man-made structures. The traits we selected can reasonably be assumed to impact
17 stingless bee nesting and foraging, even though little is known about pollinator functional traits
18 in general. The first three are continuous and the latter four categorical (yes/no). Because diet
19 breadth data are limited, we used diet breadth data from congeneric Brazilian stingless bees
20 (Biesmeijer & Slaa 2006). Following Lichtenberg et al. (2010), we used descriptions of bees
21 foraging on natural food sources (citations in Table 1) to characterize foraging strategies. These
22 foraging strategy classifications consider numbers of nestmates visiting the same food source
23 rather than recruitment. Species whose colonies can forage in large groups at the same spatial

1 location (typically the same mass-flowering tree) were categorized as group foraging, and those
2 whose workers forage as solitary individuals at different spatial patches were categorized as
3 solitary foraging. For the three nesting variables, species were categorized as “yes” if at least one
4 instance of the relevant nest type has been reported and “no” otherwise. Ground-nesting species
5 may also nest in trees. We did not include a tree-nesting variable because almost all of the
6 species we recorded are known to nest in or under trees (Camargo & Pedro 2013).

7

8 *Site-specific data*

9 In addition to bee traits, we assessed the impact of landscape context, bee community
10 context and flowering plant resources on stingless bee communities. To quantify landscape
11 context, we calculated the proportion of forest around sample points at radii ranging from 10 to
12 1350 m in 10-50 m increments. We classified ecosystem elements manually, by digitizing Costa
13 Rica Airborne Research and Technology Applications (CARTA) orthorectified aerial
14 photographs from 2003 and 2005 with two-meter resolution. Forest elements included: primary
15 and secondary forest fragments of all sizes, single trees, charral (early secondary forest), live
16 fences, hedgerows, non-native timber and fruit tree plantations, and non-native garden
17 ornamentals. These data are much finer resolution than the 30×30 m pixel LANDSAT data
18 previously used by Brosi (Brosi *et al.* 2008; Brosi 2009). We determined the most appropriate
19 radius to use in analyses by assessing the correlation between percentage forest cover and
20 stingless bee richness at each distance. Because stingless bee richness was significantly related to
21 forest cover up to approximately 250 m (Fig. S1), further analyses quantify landscape context as
22 the percentage of forest within a 250 m radius circle around each sample point.

1 To quantify the bee community context as an explanatory variable for our analyses of
2 competition, we used two approaches. First, we calculated the abundance and richness of all bees
3 sampled at each site. Second, we separately calculated abundance and richness values for
4 stingless bees, honey bees (abundance only) and all other bees. Because sampling effort was
5 uneven across sites, we applied sample-based rarefaction to estimate bee abundance and richness
6 at each site if they had been sampled only 10 times (the fewest times any one site was sampled)
7 (Gotelli & Colwell 2011).

8 To quantify flowering plant resources available to stingless bees at each pasture site, we
9 counted flowering plants along five parallel 20 m transects in each site. We counted and
10 identified all plants in flower within 50 cm of either side of the transect line. See Brosi et al.
11 (2007, 2008) for more details on plant sampling.

12

13 *Data analysis*

14 We tested effects of trait values, landscape context, bee community context and flowering
15 plant richness on the presence or absence of each stingless bee species using logistic regression
16 and the R statistical system v. 3.1.3. (R Core Team 2014). Scripts and data are available online
17 (Lichtenberg *et al.* 2017). We used presence or absence of each species at each site (as described
18 above) as the response variable.

19 In order to include interactions between traits, which describe bee species, and landscape
20 context, which describes sites, we combined data on sites and species into a data list (Walker *et*
21 *al.* 2012). This data structure organizes multiple table data (here, site by species matrix, species
22 by traits matrix, site by environment matrix) into a long format with one row per site-species
23 combination, and all site and trait variables as separate columns. This data list can be used by

1 standard R regression functions. It thus overcomes the “fourth-corner problem,” the difficulty in
2 linking species’ traits to environmental variables (Legendre *et al.* 1997). This yields nested data,
3 since environmental variables are properties of the site and traits are species-specific. However,
4 the tight correlations between our fixed effects and potential random effects (site, species) would
5 violate the assumption that fixed and random effects are orthogonal (Wooldridge 2010). We thus
6 used fixed effects models to more accurately measure relationships between traits, site
7 characteristics and a species’ presence (Townsend *et al.* 2013).

8 To identify potential drivers of stingless bee presence in our sites, we used a four-step
9 information theoretic model selection approach. First, we ran logistic regressions (in a
10 generalized linear modelling framework) relating the presence/absence of stingless bees at
11 particular sites to both trait and environmental variables, with rigorous assessment for
12 collinearity and overdispersion (relative to a binomial distribution). We assessed collinearity
13 using regressions that included all environmental and trait variables as main effects, but no
14 interaction terms. These independent variables were: flowering plant richness, abundance of the
15 bee community (one or three variables), richness of the bee community (one or two variables),
16 forest cover as landscape context, body size, colony size, diet breadth, group foraging, ground-
17 nesting, inquiline nesting, and nesting in man-made structures. Regressions with rarefied
18 stingless bee presence/absence data (presented here), which were proportions, included sampling
19 effort (10 sites) as a weight, while regressions with unrarefied presence/absence data (see R
20 scripts) included the number of times a site was sampled. Models with both classifications of bee
21 community context (all bees together vs. bees split into groups) showed evidence of collinearity
22 (high variance inflation factors; see R scripts). Collinearity was no longer present when we
23 removed colony size, which had strong relationships with diet breadth (Spearman’s rank

1 correlation: $r = -0.70$, $S=618.46$, $p = 0.008$) and group foraging (Mann-Whitney U test: $U=0$, N_1
2 $= 14$, $N_2 = 12$, $p = 0.004$). Further analyses thus excluded colony size. We next re-ran models
3 with the terms described above plus the interaction between each trait and forest cover. Models
4 with the bee community split into groups additionally included the interaction between honey
5 bee abundance and the group foraging trait, since honey bees may be in stronger competition
6 with group-foraging than solitary-foraging species. Regressions that included interaction terms
7 but excluded colony size showed overdispersion. We thus used the quasibinomial link in
8 regressions, and assessed model fit via quasi-AIC, since quasi-distributions do not allow for the
9 strict calculation of likelihood that is needed for classic AIC calculations. Because these models
10 included multiple parameters, we used the second-order quasi-Akaike Information Criterion
11 (QAICc) for smaller sample sizes (Burnham & Anderson 1998; Bartón 2013).

12 The second step was to determine the best classification of bee community context (all
13 bees together vs. split into groups)(Table S1). Splitting the bee community into three categories
14 yielded the best fit (QAICc smaller than other models by at least 2.0) with unrarefied
15 presence/absence data (Table S1). It also enabled us to investigate potential competitive effects
16 of honey bees on group- versus solitary-foraging stingless bee species. Thus further analyses are
17 based on the model with the bee community split into groups.

18 The third step, after establishing which richness and abundance estimates to use, was to
19 use QAICc-based model selection to remove terms from the full model using the MuMIn
20 package (Bartón 2013). To control for sampling effort all potential models included stingless bee
21 abundance, and models with unrarefied presence/absence data included the number of times a
22 site was sampled (Gotelli & Colwell 2011).

1 Fourth, because the second step yielded multiple “best” models (QAICc within 2.0 of the
2 smallest QAICc value) and these best models all had relatively low weights (Grueber *et al.*
3 2011), we used model averaging to obtain one summary model. To assess effects of forest cover,
4 plant richness, the bee community and stingless bee traits, we tested whether each averaged
5 coefficient was significantly different from zero. We estimated coefficients using a “full”
6 average with shrinkage, which assumes each term is included in every model but in some the
7 coefficient is set to zero. This avoids biasing coefficient estimates away from zero (Burnham &
8 Anderson 1998) and facilitates out-of-sample prediction (Hooten & Hobbs 2015).

9

10 **Results**

11 *Bee traits overview*

12 Tables 1 and S2 shows species’ trait values. Head widths ranged from 1.2-4.01 mm
13 (mean 2.39 mm), colony sizes from 185-13,625 workers (mean 3,950) and diet breadth from
14 0.26-0.56 (mean 0.45). Seven of the 12 species for which we could find information are group
15 foragers. Of the 18 species studied, seven nest in the ground, five are nesting inquilines and six
16 nest in man-made structures.

17

18 *Trait shifts within stingless bee communities*

19 Results from analyses with rarefied and unrarefied presence/absence data were
20 qualitatively similar. We thus focus on rarefied presence/absence results here, and show
21 unrarefied presence/absence results in published R scripts (Lichtenberg *et al.* 2017). The
22 averaged model included the number of times a site was sampled, plant richness, abundance and
23 richness of the three bee categories (honey bees, stingless bees, other bees), forest cover, all six

1 bee traits (excluding colony size, as described in the Methods), interactions between forest cover
2 and all bee traits, and the interaction between honey bee abundance and group foraging (Table
3 2).

4 As stingless bee communities disassembled, effects of forest loss depended on a species'
5 diet breadth (Table 2). Species with narrower diet breadths were less likely to be present at sites
6 with more forest nearby, while species with broader diets were more likely to be present at such
7 sites (Figs. 2a, S2). Further investigation showed that diet breadth was narrower for group-
8 foraging species than for those that are not known to forage in large groups (Fig. 2b; Mann-
9 Whitney U test: $U = 30$, $N_1 = 5$, $N_2 = 6$, $p = 0.007$).

10 The averaged model also indicated several traits that affected the probability that a
11 species is present at a site, independent of forest availability (Table 2). Species with larger body
12 size were more likely to be found in pastures (Fig. 3a). In addition, ground-nesting (Fig. 3b) and
13 inquiline-nesting (Fig. 3c) species were more common in pastures relative to species with other
14 nesting habits.

15

16 *Competition and stingless bee persistence*

17 Competition with other bee taxa did not appear to have a strong impact on whether
18 stingless bees were found in pastures. Stingless bee species' presence was not affected by the
19 richness or abundance of honey bees or other bees, or by stingless bee abundance (Table 2).

20 While a given species was more likely to be found in samples if the site had higher stingless bee
21 richness (Table 2), this is likely to be a sampling artefact rather than reflecting facilitation among
22 stingless bees. Further, plant richness (food availability) in the sampled pastures did not affect a
23 stingless bee species' presence in that pasture (Table 2).

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Discussion

It is increasingly clear that functional traits underlie general patterns of community disassembly with anthropogenic change. Such predictions will be useful for conservation of bees and the pollination ecosystem service they provide, but the geographic bias in bee biodiversity research (Archer *et al.* 2014) may affect assessment of community disassembly patterns. The results of this study show that social tropical bees respond to land use change differently than do temperate bees. In contrast to the majority of studies to date (e.g., Cane *et al.* 2006; Williams *et al.* 2010), we found that species with narrower diets better persisted in disturbed areas. Further investigation of species’ traits led us to propose the mechanistic hypothesis that foraging traits such as group foraging, and associated abilities to dominate resources, can modulate effects of land use change. Specifically, subordinate species may be frequently displaced from rich food sources and thus depend on the larger resource pool that forests offer. This analysis also found that ground and inquiline nesting, and larger body size increased the probability of finding a bee species in pastures.

Disturbance is generally predicted to reduce the abundance or diversity of more specialized species (McKinney 1997; Vandewalle *et al.* 2010). Contrary to this, we found that species with the broadest diets were more sensitive to habitat loss while species that visit fewer plant species were largely absent in sites with high forest availability. The only other trait-based study to date of anthropogenic effects on tropical bee communities similarly found that habitat degradation reduced abundances of polylectic bees that collect pollen from a broad range of floral sources (Otieno *et al.* 2015). Temperate studies, on the other hand, do follow the expected pattern (Cane *et al.* 2006; Kleijn & Raemakers 2008; Williams *et al.* 2010; Rader *et al.* 2014;

1 Gonçalves *et al.* 2014; Forrest *et al.* 2015). This contrast suggests that lower dietary
2 specialization of pollinators in the tropics (Schleuning *et al.* 2012) and decreased risk of
3 extinction in communities with more generalists (Stroud & Feeley 2015) could leave more room
4 for community processes to modify effects of land use change in tropical than in temperate
5 pollinator communities. It is also worth noting that even the most “specialized” stingless bees are
6 still generalists who visit a diverse pool of flowering plant resources, although the diversity of
7 plant species that different stingless bee genera visit spans a factor of two (Shannon index:
8 $H' = 0.26-0.56$, Biesmeijer & Slaa 2006).

9 The trait-based approach we used suggests a mechanism through which forest loss
10 reduces persistence of species with broader diets in communities of social, tropical bees:
11 interspecific competition and dominance-related foraging traits. In this study, species with more
12 diversified diets and a negative response to forest loss also tended to forage as individuals or in
13 small groups. Such species are generally subordinate (Lichtenberg *et al.* 2010), and thus subject
14 to displacement by group-foraging, dominant species. We propose, therefore, that stingless bee
15 species’ diet breadths are plastic responses to competitive interactions rather than the evolved
16 preferences hypothesized by earlier work (Johnson & Hubbell 1975). This may be true even
17 though our analyses did not detect effects of community context. Such facultative expansion of
18 diet in response to competition is common (Futuyma & Moreno 1988), and may help animals
19 avoid unsustainably long food search times (Prinzing 2003). Under this scenario, species with
20 broader diets may tolerate disturbance poorly if they require the larger or more diversified
21 resource pool that natural habitats offer, or cannot compete with more dominant stingless bee
22 species in areas with a reduced floral resource pool. The dominant species with wider diet
23 breadths, meanwhile, may have been largely absent from sites surrounded by more forest if those

1 forest fragments provided sufficient quantities of one preferred food resource for stingless bees:
2 mass-flowering trees (Ramalho 2004). Our results thus highlight the importance of including
3 behavioural traits in studies of community disassembly.

4 Our results show that ground- and inquiline-nesting stingless bee species are more likely
5 to be found in pastures. Such species may more easily disperse through disturbed landscapes and
6 persist in pastures than tree-nesting stingless bee species. Stingless bees establish new nests only
7 after multiple trips between the current and the new site (Roubik 1989), so are restricted in how
8 far the next generation can disperse from the natal nest. Nesting in the ground, or inside the nests
9 of taxa such as subterranean termites or mound-producing ants, may thus facilitate bee dispersal
10 across disturbed habitat. Consistent with this hypothesis, termite mounds were common in the
11 pastures we sampled (B. Brosi, pers. obs.). Beyond stingless bees, ground nesting encompasses
12 many nest types and is not closely linked to a dispersal mechanism. Reflecting this diversity,
13 ground-nesting bee species have mixed responses to disturbance (e.g., Cane *et al.* 2006;
14 Williams *et al.* 2010; Bartomeus *et al.* 2013; Fortel *et al.* 2014; Forrest *et al.* 2015). Species that
15 nest above ground in trees or stems, in contrast, are often harmed (e.g., Winfree *et al.* 2007;
16 Williams *et al.* 2010; Pisanty & Mandelik 2014; Forrest *et al.* 2015).

17 We also found that species with larger body size were more common in pastures. This
18 pattern likely reflects flight range capabilities. As central place foragers, bees have a stationary
19 nest to which they return after each foraging trip. Larger bee species are able to forage further
20 from the nest (Araújo *et al.* 2004; Greenleaf *et al.* 2007), and thus large stingless bees in the
21 present study were more likely to be seen in pastures even if their nests were in forest fragments.
22 A stronger effect of disturbance on small than large bee species has sometimes been found in
23 temperate studies (Winfree *et al.* 2007; Williams *et al.* 2010), although other patterns have been

1 reported as well, including stronger effects of disturbance on larger bees (Bartomeus *et al.* 2013;
2 Jauker *et al.* 2013; Wray *et al.* 2014; Rader *et al.* 2014; Pisanty & Mandelik 2014; Kormann *et*
3 *al.* 2015) and no differential effect of disturbance based on body size (Cane *et al.* 2006; Kleijn &
4 Raemakers 2008; Ekroos, Rundlöf & Smith 2013; Fortel *et al.* 2014; Forrest *et al.* 2015).

5 Trait-based approaches, as we have employed here, have some important limitations.
6 Researchers are often restricted to traits that are already published, or that are straightforward
7 and economical to measure in the field. Thus trait-based analyses may overlook important
8 ecological processes due to missing data. Analyses may also be biased towards more easily
9 measured traits (e.g., size) or taxonomic groups (e.g., plants). Recent efforts to standardize trait
10 measurement (e.g., Cornelissen *et al.* 2003; Fountain-Jones, Baker & Jordan 2015) and the
11 increasing popularity of trait-based studies (Martin & Isaac 2015) should help overcome these
12 issues in the future. The narrow scope of our study avoids taxonomic biases, but the differences
13 we find between effects of disturbance on bee traits in tropical and temperate regions highlights
14 that studies assessing broader effects on all bees need to incorporate more tropical bees.
15 Although the traits we could analyse were limited by what has previously been published, the set
16 of traits we used is sufficiently diversified to reasonably describe stingless bees' niches. The
17 traits we used described species' nesting requirements, movement patterns and food needs. Data
18 availability did limit us to assigning diet breadths at the genus rather than the species level.
19 However, several studies find higher diet similarity within than among stingless bee genera
20 (Imperatriz-Fonseca, Kleinert-Giovannini & Ramalho 1989 and sources therein; Ramalho,
21 Kleinert-Giovannini & Imperatriz-Fonseca 1990; Biesmeijer & Slaa 2006). Another limitation of
22 trait-based approaches is subjective assessments of whether a trait is functional in the absence of

1 data relating trait values to fitness. While we do not know the degree to which each trait affects
2 fitness, all the traits we used have a logical connection to pollinator functioning.

3 One of the key challenges of the ongoing biodiversity crisis is understanding the
4 ecosystem-level consequences of the losses of populations and species (e.g., Hooper *et al.* 2005).
5 This is particularly true in the case of pollinators, which are undergoing global declines (Potts *et*
6 *al.* 2010) and which also play a key functional role in the pollination of both crops (Klein *et al.*
7 2007) and wild plants (Ollerton *et al.* 2011). Loss of habitat is one of the key drivers of pollinator
8 — and more specifically bee — diversity (e.g., Potts *et al.* 2010). The work we present here
9 shows that stingless bee functional traits likely mediate, at least in part, their responses to habitat
10 loss. It is particularly important that we continue to work to better understand how pollinator
11 communities disassemble with habitat loss, and what the resulting consequences for pollination
12 of both crops and native plants will be. Such an understanding could provide key insights for
13 conserving and restoring both pollinator communities and the ecosystem services and functions
14 that they provide.

15
16

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8

9 **Data Accessibility**

10 Data and R scripts are archived at Zenodo (DOI: 10.5281/zenodo.843615).

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4

1 **Table 1:** Trait values for Costa Rican stingless bee species used in this study

2

Species	Name in Brosi 2009 ^A	Head width (mm) ^B	Colony size (# workers) ^C	Diet breadth ^Z	Group-foraging? ^D	Nests in ground? ^E	Inquiline nesting? ^E	Nests in man-made structures? ^E
<i>Aparatrigona isopterophila</i>	<i>Paratrigona isopterophila</i>	2.17 ^l	185 ^h	0.56		no	yes	no
<i>Melipona costaricensis</i> or <i>panamica</i>	<i>Melipona fasciata</i> ^{cc}	4.01 ^{l,p,ee}	1092.84 ^{b,h,j,n,o,dd}	0.44	no ^k	no	no	no
<i>Oxytrigona mellicolor</i>	<i>Oxytrigona</i> sp. ^{l,w}	2.7 ^l	5442 ^h		yes ^u	no	no	no
<i>Paratrigona ornaticeps</i>	<i>Paratrigona ornaticeps</i>	1.795 ^{l,l}	1710 ^h	0.56		no	no	no
<i>Partamona orizabaensis</i>	<i>Partemona orizabaensis</i>	2.46 ^s	2950 ^{b,c}	0.37	yes ^{g,k}	yes	yes	yes
<i>Plebeia frontalis</i>	<i>Plebeia frontalis</i>	1.8 ^{i,ee}	1500 ^{b,c,f,h}	0.51	no ^{c,g}	no	no	yes
<i>Plebeia jatiformis</i>	<i>Noguerapis</i> sp., <i>Plebeia jatiformis</i>	1.5 ⁱ	805 ^h	0.51	no ^k	no	no	no
<i>Ptilotrigona occidentalis</i>	<i>Trigona</i> c.f. <i>ferricauda</i>	3.055 ^{l,v}				no	yes	no
<i>Scaptotrigona pectoralis</i>	<i>Scaptotrigona</i> c.f. <i>pectoralis</i>	2.5 ^l	4375 ^{c,f}	0.26	yes ^{c,d,g,t}	no	no	yes
<i>Scaptotrigona subobscuripennis</i>	<i>Scaptotrigona mexicana</i>	2.6 ^l		0.26	yes ^{c,d,g,m,r,t,aa}	yes	no	no
<i>Tetragona perangulata</i>	<i>Trigona</i> sp. 2, <i>Trigona perangulata</i>	2.7 ^l		0.53		no	no	no
<i>Tetragona zieglerei</i>	<i>Trigona dorsalis</i>	2.3 ^l	2647.75 ^{c,f,t}	0.53	no ^c	yes	no	yes

<i>Tetragonisca angustula</i>	<i>Trigona angustula</i> ^{w,bb}	1.8 ⁱ	2715 ^{a,h,n,x,y}	0.5	no ^g	yes	no	yes
<i>Tetragonisca buchwaldi</i>	<i>Trigona</i> sp. 1 ⁱ	1.9 ⁱ	1376.25 ^b	0.5		yes	yes	no
<i>Trigona corvina</i>	<i>Trigona corvine</i>	2.5 ⁱ	13,625 ^{b,c,h,y}	0.43	yes ^{d,e,t}	yes	no	no
<i>Trigona fulviventris</i>	<i>Trigona fulviventris</i>	2.7 ⁱ	9375 ^{c,f,h}	0.43	yes ^{g,t}	yes	yes	yes
<i>Trigona silvestriana</i>	<i>Trigona amalthea</i>	3.3 ^{i,ee}	7500 ^{c,f,h}	0.43	yes ^{c,d,e,g}	no	no	no
<i>Trigonisca</i> sp.	<i>Trigonisca</i> sp.	1.2 ⁱ				no	no	no

1 A – Stingless bee taxonomy and systematics have recently undergone revisions. Name changes were made following the Moure bee
2 catalogue (Camargo & Pedro 2013) unless otherwise indicated.
3 B – Head width indicates body size. We based *Trigonisca* body size on *Trigonisca atomaria*, the only *Trigonisca* species with
4 published head width. Measurement of several sampled *Trigonisca* confirmed a close match with the *T. atomaria* measure.
5 C – Colony size represents a species’ average.
6 D – We used a functional definition of group foraging that considers numbers of nestmates visiting the same food source, and defines
7 group foraging species as those whose colonies can forage in large groups at the same spatial location (Lichtenberg *et al.* 2010).
8 E – Nest characteristics determined by searching the Moure bee catalogue (Camargo & Pedro 2013), with a species defaulting to “no”
9 if it has not been reported to nest in the ground, in other species’ nests or in man-made structures. We could not find data for
10 *Scaptotrigona suboscuripennis*, but classified it as a group forager since all five congeners that have been classified for this variable
11 are group foragers.
12 Sources: (a, Lindauer & Kerr 1960; b, Wille & Michener 1973; c, Johnson 1974, d, 1983; e, Johnson & Hubbell 1974; f, Hubbell &
13 Johnson 1977, g, 1978, h, Roubik 1983b, i, 1992b; j, Roubik & Buchmann 1984; k, Howard 1985; l, Camargo & Moure 1994; m, Kerr
14 1994; n, Biesmeijer 1997; o, Nieh & Roubik 1998; p, Biesmeijer *et al.* 1999; q, Jarau *et al.* 2000, r, 2003; s, Pedro & Camargo 2003; t,
15 Slaa 2003; u, Slaa, Wassenberg & Biesmeijer 2003; v, Camargo & Pedro 2004, w, 2013; x, Tóth *et al.* 2004; y, Aguilar, Fonseca &
16 Biesmeijer 2005; z, Biesmeijer & Slaa 2006; aa, Menezes *et al.* 2007; bb, Rasmussen & Cameron 2010; cc, JMF Camargo, pers.
17 comm.; dd, M Eckles, pers. comm.; ee, see Table S2)

18

1 **Table 2:** Weights, coefficients and Wald test results for the averaged model. Terms in bold had a
 2 statistically significant effect on a species' presence in pasture sites.

Covariate	w	Predicted coefficient (\pm SE)	z	p -value
Intercept	--	-7.42 (2.98)	2.49	0.013
Plant richness	0.29	-0.01 (0.02)	0.29	0.77
Honey bee abundance	0.37	-0.003 (0.01)	0.21	0.84
Stingless bee abundance	1.00*	-0.0007 (0.007)	0.10	0.92
Stingless bee richness	1.00	0.59 (0.10)	5.91	<0.0001
Other bee abundance	0.38	-0.01 (0.02)	0.42	0.68
Other bee richness	0.33	-0.01 (0.06)	0.11	0.91
Forest cover	1.00	-3.75 (7.02)	0.53	0.59
Body size	0.94	1.19 (0.56)	2.12	0.035
Diet breadth	1.00	-0.62 (4.15)	0.15	0.88
Group foraging?	0.89	0.47 (0.81)	0.58	0.56
Ground-nesting?	1.00	1.78 (0.66)	2.71	0.007
Inquiline-nesting?	1.00	2.34 (0.94)	2.50	0.013
Man-made nests?	0.94	0.08 (0.82)	0.10	0.92
Forest cover: body size	0.94	-1.96 (1.16)	1.69	0.09
Forest cover: diet breadth	1.00	22.33 (11.38)	1.96	0.049
Forest cover: group foraging?	0.89	1.10 (2.00)	0.55	0.59
Forest cover: ground-nesting?	1.00	-1.56 (1.57)	0.99	0.32
Forest cover: inquiline-nesting?	1.00	1.37 (2.34)	0.59	0.56
Forest cover: man-made nests?	0.94	-2.68 (2.07)	1.30	0.20
Honey bee abundance: group foraging?	0.15	0.004 (0.01)	0.30	0.76

3 * Included in all models to control for effects of unequal sampling on our response variable
 4

1 **FIGURE LEGENDS**

2

3 **Figure 1:** The “fourth-corner problem” refers to the difficulty of analysing joint effects of
4 environment and trait, because the former is a property of sites and the later a property of
5 species. Here, each grey box represents a data matrix or table (modified from Fig. 1 in Walker *et*
6 *al.* 2012).

7

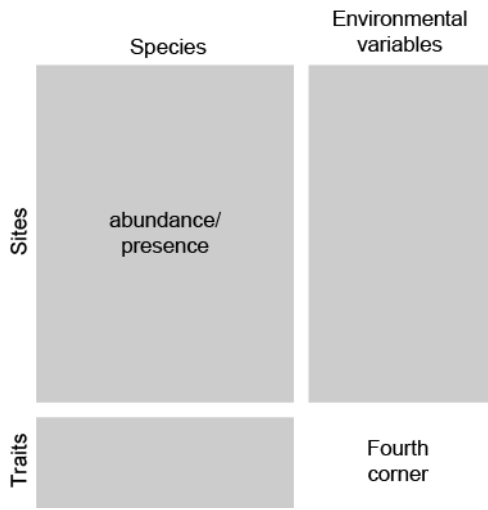
8 **Figure 2:** (a) Predicted probability that a species was present in a pasture as a function of the
9 site’s natural habitat availability (x-axis) and the bee species’ diet breadth (individual curves).
10 Curves show the predicted probability averaged across all values of the traits other than forest
11 cover and diet breadth. Fig. S2 shows curves with 95% confidence intervals. (b) Species that
12 forage as solitary individuals rather than in large group of nestmates tend to have wider diets
13 than group-foraging species.

14

15 **Figure 3:** Predicted probability that a species was present in a pasture as a function of (a) the
16 species’ body size, as indicated by head width (95% confidence interval in grey), (b) whether the
17 species nests in the ground and (c) whether the species exhibits inquiline nesting.

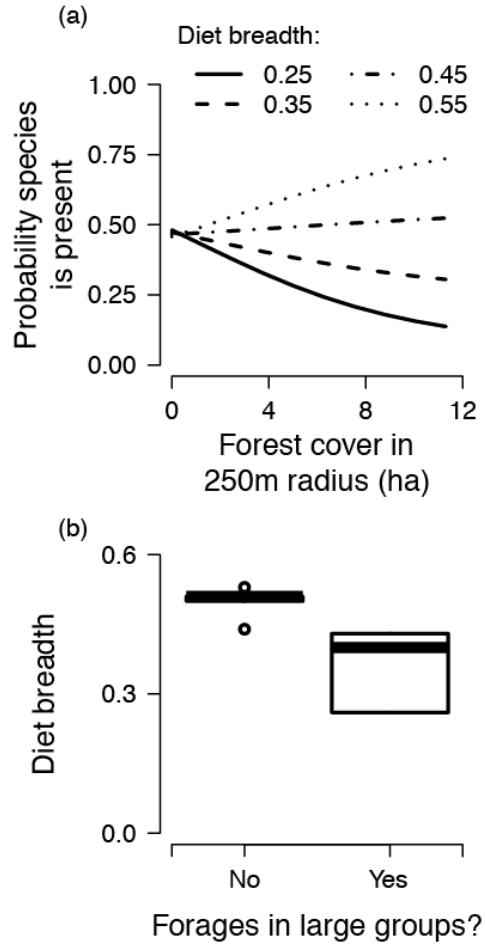
18

1 **Figure 1**
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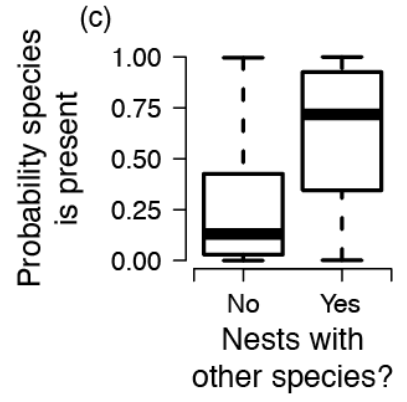
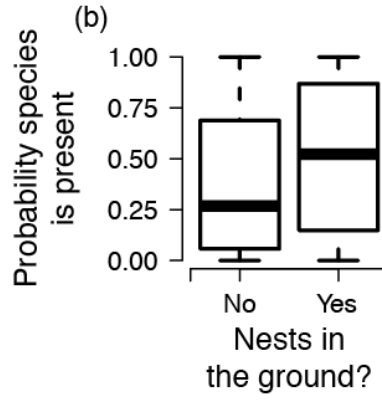
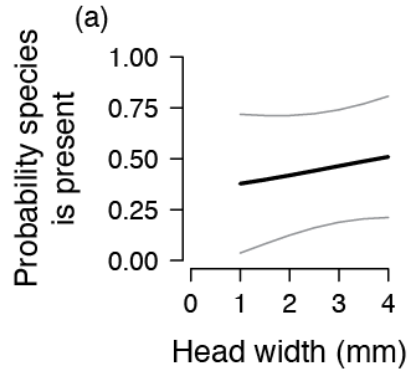
1 **Figure 2**
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1 **Figure 3**

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