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Distance and habitat drive fine scale stingless bee (Hymenoptera: Apidae) community turnover across naturally heterogeneous forests in the western Amazon

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Abstract

High tree species richness in the western Amazon has been attributed to heterogeneous soils, which harbor edaphic specialist trees. While rapid transitions in tree communities are well documented across these variable soils, few studies have investigated the role of habitat heterogeneity in structuring animal communities. Stingless bees are taxonomically diverse and important natural pollinators in Neotropical forests. However, little is known about their community structuring at local scales in naturally heterogeneous environments. We systematically sampled stingless bee communities found across three paired sites that included adjacent patches of white-sand and non-white-sand forest in the lowland Amazonian region of Loreto, Peru. We sought to understand: (1) How stingless bee species richness and abundance differ among white-sand and non-white-sand habitats and (2) The relative influence of fine scale geographic distance and habitat type in structuring stingless bee communities. We found that species richness did not differ between habitats and that species abundances were highest in white-sand habitats. Community analyses for sampling sites pooled across all months demonstrated that location and soil type played a significant role in structuring bee communities and that community turnover may be more strongly influenced by distance in white-sand habitats than non-white sand habitats. Our results suggest that distance and habitat play an important role in driving stingless bee community turnover at fine scales and that the interaction between habitat and geographic distance may promote higher stingless bee community turnover in white-sand habitats than non-white sand habitats.

Introduction

The lowland amazon basin is notable for its exceptionally high levels of species diversity across a wide range of taxa (Erwin, 1988; Kress et al., 1998; Pitman et al., 2001). High levels of species richness have been attributed to extreme habitat heterogeneity with particular emphasis on the mosaic of soil types found across the Western Amazon in Peru (Terborgh, 1985; Whitney & Alvarez, 1989). These variable soils create a patchwork of forest types differentiated by plant communities that have strong edaphic associations with nutrient poor white-sand soil patches and the more fertile brown-sand and clay soils which surround them (Tuomisto & Ruokolainen,

1994; Fine et al., 2010). White-sand forests differ from surrounding forests in that they harbor significantly less species richness, are shorter in stature, and experience higher temperatures on average below the canopy due to increased light penetration than forests found on surrounding soils (Medina & Cuevas, 1989; Fine et al., 2010). In the western Amazon white-sand forests exist as small habitat islands, usually no larger than a few square hectares (Fine et al., 2005).

While the majority of research examining the role of edaphic variation in species turnover in the Amazon has been centered on tree communities (Tuomisto & Ruokolainen, 1994; Fine et al., 2010; but see Alvarez Alonso et al., 2013) similar habitat specialization may also be present in ani-

mals. Because forests constitute the primary habitat and food source for many forest dwelling animals we expect that abrupt changes in floristic composition across habitats may in turn drive turnover in animal communities.

Animals that provide pollination services play a particularly important role in tropical ecosystems where the majority of trees are reliant on animal interactions for pollen transfer (Bawa, 1990). While turnover in bee communities across forest fragments and agriculturally modified landscapes has been well studied in relation to crop production (Tylianakis et al., 2005; Jha & Vandameer, 2010) the role of naturally heterogeneous habitats in driving species turnover in the lowland Amazon has largely been neglected (but see Abrahamczyk et al., 2010).

Stingless bees (Hymenoptera: Apidae: Meliponini) are an important taxon for studies of biodiversity and species turnover in the lowland Amazon because they are highly diverse (*ca* 500 species) with their center of diversity found in the Neotropics (*ca* 400 species) (Michener, 2013). Additionally, they are the most important native providers of pollination services in the Amazon, making them essential for ecosystem functioning (Engel & Dingemans-Bakels, 1980; Roubik, 1995).

Most stingless bee species are considered to be generalist pollinators and they exhibit a wide range of variation in nesting habits across species. Nests are usually arboreal or subterranean and are constructed using diverse construction materials including mud, wood pulp, feces, and plant exudates (Schwarz, 1948; Roubik, 1989). Foraging distance away from nest site is dependent on the size of the bee with distances ranging from less than 500 m to 2 km (Kuhn-Neto et al., 2009). Given the variation in nest site preferences between lineages relatively little attention has been paid to the fine scale distribution and ecology of Neotropical stingless bees and no studies have investigated species turnover across naturally occurring environmental gradients in undisturbed forest sites.

Furthermore, because the movement of animal pollinators directly influences the distance, direction and degree of pollen dispersal, they ultimately determine the spatial pattern of gene movement within and among plant populations (Garcia et al., 2007). If pollinators are restricted in their foraging area due to habitat preference (Dieckmann, 2004) then the question of ecological specialization in bee communities may be of particular interest to plant ecologists as well.

In this study we simultaneously examined the effect of habitat and distance in structuring stingless bee communities at a local scale. We systematically sampled native bee communities found across three paired sites that included adjacent patches of white-sand and non-white-sand forest across more than 100 km in the lowland Amazon in the region of Loreto, Peru in order to answer two questions (1) How does stingless bee species richness and abundance differ among white-sand and non-white-sand habitats? (2) What is the relative influence of fine scale geographic distance and habitat type in structuring stingless bee communities?

If stingless bees are generalist pollinators with relatively large foraging ranges, we expect that geographic distance will play a greater role in structuring bee communities than habitat type providing that trees exhibit similar flowering phenology across habitat types. Alternatively, if bees prefer floral resources provided by soil specialist trees, nesting sites that are more common in one particular habitat (*i.e.* large vs. small stems or clay vs. sandy soil in the case of subterranean nesters) or environmental differences such as temperature or predation risk then we may find that habitat type plays a stronger role than distance in structuring stingless bee communities.

Materials and methods

Study sites

Three primary study areas, each containing adjacent white-sand and non-white-sand forest patches, were established in the region of Loreto, Peru (Fig 1; Table 1). Area one and two are located within the Allpahuayo Mishana National Reserve in the Nanay River watershed and area three is located approximately 100km to the south in the Ucayali River watershed. We consider each forest patch a sampling site.

Sampling design

All trapping was conducted using bee pan traps. These traps are easily standardized and avoid collector bias (Westphal et al., 2008). Traps were created using 12-oz clear plastic soup bowls painted fluorescent blue, fluorescent yellow, or white in order to account for variation in color preference among bee species. Four trapping stations consisting of six bee pan traps were established in white-sand and non-white-sand forest sites at each of the three areas for a total of 24 trapping stations across six collecting sites (Fig 1). Within each collecting site each trapping station was established 200-250 m distant from any other trapping station.
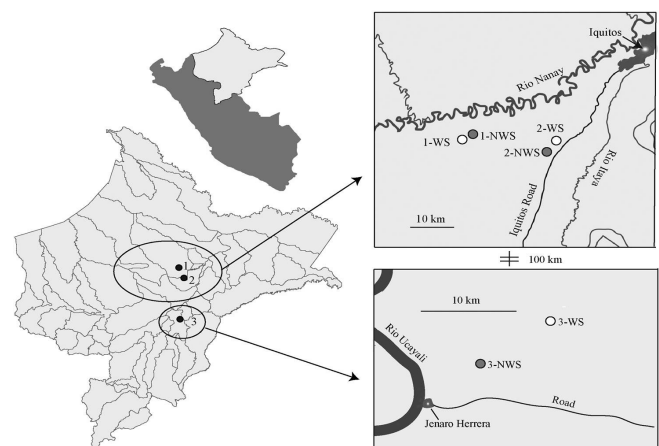

Fig 1. Sample sites and soil types where stingless bees were sampled in the region of Loreto, Peru. Numbered points represent the three areas where adjacent white-sand and non-white-sand forests were found. Each individual sampling site is displayed in the inset. Grey circles represent non-white-sand forests and white circles represent white-sand forests.

Table 1. Geographic coordinates, number of individuals, number of genera, and number of species collected at each trapping site as well as total abundance (A) and richness (S) for each habitat type and collection site.

	White-Sand					Non-White-Sand						Totals per site	
Site	Lat.	Long.	Ind. (N)	Gen. (N)	spp. (N)	Site	Lat.	Long.	Ind. (N)	Gen. (N)	spp. (N)	A	S
1-WS	-3.91	-73.55	215	8	16	1-NWS	-3.90	-73.55	92	9	15	307	20
2-WS	-3.95	-73.40	112	5	6	2-NWS	-3.97	-73.42	236	9	12	348	14
3-WS	-4.86	-73.61	415	9	16	3-NWS	-4.88	-73.64	31	6	9	446	20
A			742			A			359				
S			27			S			24				

Each trapping station contained two sets of yellow, blue and white traps. One set was suspended one meter above the ground with each individual bowl spaced at a distance of five meters to avoid bowl competition (Droege, 2010). The second set of bowls was suspended at a height of 15–20 m in the canopy directly above the ground traps. Bowls were filled with six ounces of soapy water solution (one tsp blue Dawn brand soap per two liters of water).

Pan traps were set out at each site once per month for 24 h between March-July 2010. While Loreto, Peru exhibits very little seasonality our sampling period extended from the high water season, when rivers rise substantially, through the low water season. All trapped specimens were collected in the field and transferred to 96% ethanol. Specimens were separated, pinned and identified and have been deposited at the Essig Museum of Entomology at University of California, Berkeley. Identification of all specimens was done by C.R. by direct comparison with a large synoptic collection of Peruvian stingless bees previously identified by J.M.F. Camargo.

General diversity

We assessed the effectiveness of our sampling method using species accumulation curves and the Chao estimator (Chao, 1987). Rarefaction curves were calculated using the individual-based species matrix and the species accumulation curve and Chao estimates were calculated using the 'specacum' and 'specpool' functions respectively within the package 'vegan' (Oksanen et al., 2013). We assessed the dominance structure within our dataset by ranking the relative abundance of each species using a regular base plot (Magurran, 2004).

Fine scale community structure

We investigated the influence of trap height, trap color, month collected, soil type and trapping site on species richness and abundance using generalized linear models (Dobson, 1990). The full model was constructed using trap height, trap color, month collected, soil type and trap site as a fixed effect. Poisson distribution and logarithmic link function were selected as an error distribution and link function, as it has shown to work well with

count data (Bolker et al., 2009). The significance of each explanatory variable was then tested using Chi-square test to compare the reduction of deviance from the residual deviance (Hastie & Pregibon, 1992). We then identified the best-fitting model using backward step-wise model selection with AIC criterion, using function "stepAIC" in package MASS.

Broad scale community structure

In order to assess the broad scale effects of soil type and location as defined by the three sampling areas (Fig 1), we combined all monthly collection data for each of the four trap stations within each of the six collecting sites for a total of 24 sample units. We transformed the data by first applying square root to the abundance data followed by standardization using the Wisconsin method (Bray & Curtis, 1957), which reduces the effect of overly dominant species in the data set and controls for sampling effort at each trap site (Legendre & Gallagher, 2001). We first quantified relative contributions of soil type and location to the community structure by performing variance partitioning with the function 'varpart'. The analysis partitions the explained variation in community structure into different components based on the studied environmental factors (Borcard et al., 1992). Then, in order to visualize results and specifically test the significance of effects of soil and location, as well as their interaction in driving community structure, we used a distance-based Redundancy Analysis (db-RDA) with soil and location as constraints. This method allowed us to carry out constrained ordinations using non-Euclidean distance measures (Gower, 1966; Gower, 1985; Legendre & Anderson, 1999; Legendre & Legendre, 2012). Our distance matrix was created using Bray-Curtis distance, which only accounts for shared presences between two sites (Anderson et al., 2011), and the redundancy analysis was carried out using the 'capscale' function (Anderson & Willis, 2003). The significance of constrained ordination was assessed using a permutation test for Constrained Correspondence Analysis (Legendre et al., 2011; Legendre & Legendre, 2012) using the function 'anova.cca'. The P-value is calculated by comparing the observed F-value with the values from 999 permutations of community data.

We also used a Permutational Multivariate Analysis of Variance (PERMANOVA) to further test the effects of soil, location, and their interaction using the function 'adonis'. This analysis is analogous to parametric Multivariate Analysis of Variance (MANOVA), but has been shown to be more robust for community data, as the P-value is derived from permutation, as opposed to the comparison against a known distribution (Anderson, 2001).

Finally, using the function 'mantel' we implemented Mantel tests (Legendre & Legendre, 2012) individually on white-sand and non-white-sand populations to determine if geographic distance was more important in structuring bee communities in one habitat or the other. All functions for community analysis are available the R package 'vegan.' All statistical analyses were carried out in R 3.0.3 (R Development Core Team 2013).

Results

General diversity

We trapped a total of 1109 bees representing three families, 17 genera and 39 species. All but three taxa were Apidae (Appendix S1). Thirty-one species (79%) were identified to the species level and the remaining eight were sorted to morphospecies. Eight of the collected specimens representing six species were identified as solitary bees and were therefore discarded from the dataset for further analysis. All other specimens for the remaining 33 species were stingless bees and were included in all analyses (Table 1).

The species accumulation curve approached, but did not reach an asymptote (Fig 2) suggesting that our sampling was adequate but not exhaustive. The estimated species richness across all habitats and sites was 38.6 species (Standard Error: ±3.85) meaning we captured approximately 77 percent to 95 percent of the estimated total number of stingless bee species.

Plebeia minima (Gribodo) and *Plebeia* sp. A were particularly abundant in our data set (N=584, N=235). 29 species were represented by medium to low abundances. Six species were represented by singletons (Table 2; Fig 3). Preliminary analyses showed little to no effect when singletons were omitted from the data. As a result, all further analyses were carried out with the inclusion of singletons. A total of 19 species (N=1,048) were found in both white-sand and non-white-sand habitats, five species (N=13) were found only in non-white-sand habitats and nine species (N=40) were found only in white-sand habitats (Table 2). Total abundance (A) and species richness (S) for each habitat type and sampling location are reported in Table 1.

Fine scale community structure

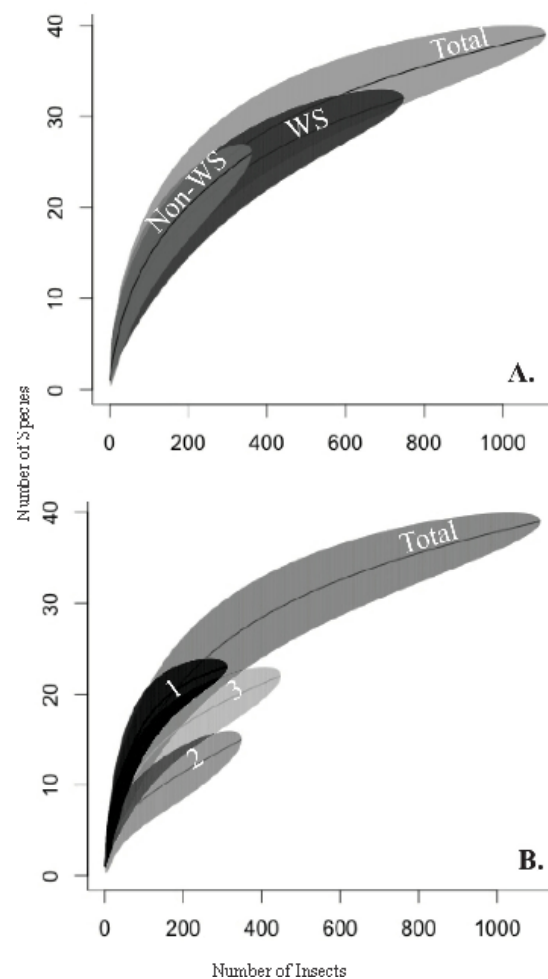Soil type and trapping site had a significant effect on species richness and abundance, while trap height, and month

Fig 2. Species accumulation curves for stingless bees. A. Species accumulation curves for white sand habitat, terrace habitat and total across habitats. B. Species accumulation curves by sampling sites 1, 2 and 3 and total across all sampling sites.
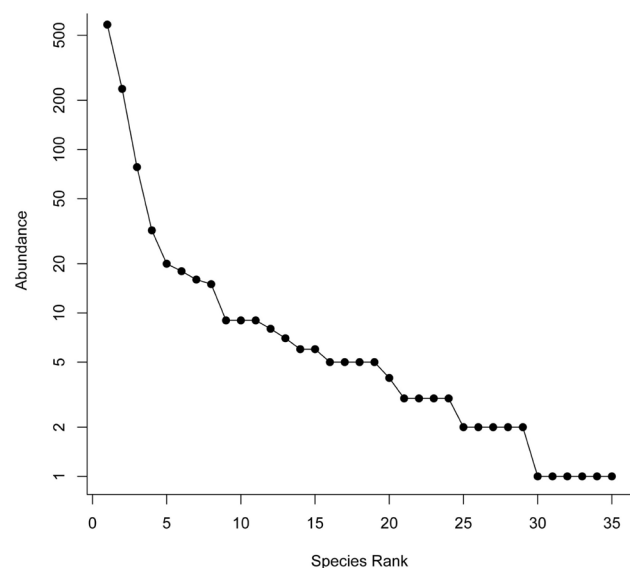

Fig 3. Species abundance distribution for all stingless bee species for all sites sampled.

Table 2. Bee species collected by soil type

Species	N ind. collected on WS	N ind. collected on non-WS
Leurotrigona pusilla	1	1
Leurotrigona muelleri	0	1
Melipona bradleyi	2	0
Melipona crinite	5	0
Melipona gr. *rufiventris*	1	0
Nannotrigona melanocera	73	5
Nannotrigona schultzei	4	1
Nogueirapis butteli	3	5
Partamona epiphytophila	3	2
Partamona testacea	0	1
Plebeia minima	342	242
Plebeia sp. A	200	35
Plebeia sp. B	18	0
Plebeia sp. C	3	1
Plebeia sp. D	13	3
Plebeia sp. E	1	0
Ptilotrigona lurida	7	2
Ptilotrigona pereneae	6	0
Scaura latitarsis	1	0
Scaura tenuis	0	6
Schwarzula coccidophila	4	11
Schwarzula timida	33	1
Tetragona clavipes	6	3
Tetragona dissecta	2	0
Tetragona gr. *dorsalis*	1	8
Tetragona handirschii	0	3
Tetragonisca angustula	3	0
Trigona amalthea	0	1
Trigona cilipes	0	7
Trigona guianae	3	2
Trigona williana	2	1
Trigonisca bidentata	4	15
Trigonisca gr. *ceophloei*	1	1

Table 3. Results of the generalized linear models for the effects of soil type, location, month, trap height and trap color on stingless bee richness and abundance at the smallest scale.

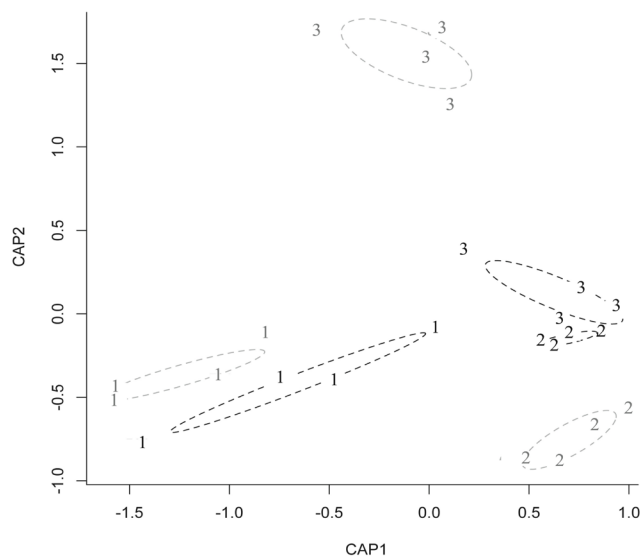|	Bee species richness			Bee abundance		
	df	Deviance	P	df	Deviance	P
Null model	252	108.92		252	1326.7	
Soil type	1	6.37	0.010	1	62.55	<0.001
Location	2	12.45	0.002	2	64.01	<0.001
Month	1	1.59	0.200	1	49.38	<0.001
Trap height	1	0.17	0.670	1	21.75	<0.001
Pan color	2	0.27	0.870	2	2.72	0.25

Fig 4. Results from distance-based redundancy analysis. Gray ellipses correspond to white-sand habitat and black ellipses correspond to non-white-sand habitat. 1, 2 and 3 refer to sampling sites. CAP refers to 'Constrained Analysis of Principal Coordinates'.

collected only significantly affected on abundance (Table 3). The multiple linear model that best explained species richness included soil type and trap site (ΔAIC=6.28). The model that best explained species abundance included soil type, month collected, trapping site and height, but it was only marginally better than the full model with the trap color (ΔAIC=0.96). Mantel tests suggests that geographic distance is correlated with species turnover in both habitat types (white-sand, r=0.4, P<0.001; non-white-sand, r=0.3, P=0.02).

Discussion

To our knowledge this is the first study to examine the role of geographic distance and forest type in structuring stingless bee communities at local scales across a naturally heterogeneous landscape in the Western Amazon. We found that both location and habitat were important in structuring stingless bee communities even over extremely small spatial scales. Our results were consistent with other tropical bee studies, which demonstrate changes in bee communities across a variety of spatial scales and environmental gradients (Tylianakis et al., 2005; Abrahamczyk et al., 2011; Batista Matos et al., 2013). While the total amount of variance explained by these two factors seems relatively small these results are in line with other studies of community turnover particularly those using natural gradients.

White-sand forests exist as small patches or habitat 'islands' surrounded by a matrix of non-white-sand forest. Accordingly, factors such as migration, colonization and local extinction may play a stronger role in structuring white-sand bee communities than non-white-sand bee communities. If non-white-sand habitat is less favorable for bee species found in white-sand forests then these communities may experience higher levels of isolation due to the compounded effect of habitat and distance. In this case metacommunity dynamics could play an important role in

increasing turnover among white-sand forests effectively amplifying the effect of geographic distance and habitat alone.

While our results demonstrated that stingless bee community structure is influenced by location, habitat type also plays significant role particularly at very fine geographic scales. We found that variation across sampling sites was driven in part by soil type however, species specific to one forest type tended to be rare in our collections, making it difficult to discern between true habitat specificity and insufficient sampling. Species abundances were much higher in white-sand-forests than non-white-sand forests suggesting that while many stingless bee species utilize both forest types habitat preferences may dictate where they are more commonly found. Floral and nesting resources are both important in structuring bee communities across habitats (Tependino & Stanton, 1981; Petanidou & Ellis, 1996). Fierro et al. (2012) found that stingless bee species show preferences for particular tree taxa, which commonly provide ideal nesting sites, as well as species-specific foraging behavior suggesting that turnover in tree diversity likely drives changes in stingless bee distributions. While we did not quantify differences in floral or nesting resource availability between habitat types in this study marked differences in floristic composition, forest structure, microclimate and abiotic resources are likely driving differences in these neighboring bee communities.

Habitat based differences in stingless bee communities may also reinforce tropical tree specialization across habitat boundaries. Many tree species that are endemic to white-sand forest patches in Peru have congeners associated with parapatric non-white-sand forests (Fine et al., 2010) and divergent natural selection across adjacent white-sand and non-white-sand habitats has been shown to play an important role in maintaining boundaries between ecologically divergent tree populations (Misiewicz & Fine, 2014). If pollinators forage less frequently outside of their preferred habitat type they may indirectly limit pollen flow between ecologically divergent plant populations increasing reproductive isolation.

This study indicates that geographic distance, forest type and the interaction between the two are important in structuring stingless bee communities supporting the hypothesis that dispersal processes such as migration and colonization interact with niche specialization in determining local patterns of community composition.

Acknowledgements

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