The effects of forest fragmentation on bee communities in tropical countryside

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Summary

1. Despite ongoing concerns and controversy over a putative 'global pollination crisis' there is little information on the response of bees, the most important group of pollinators, to land-use change. In particular, there are no published studies of the effects of tropical forest fragmentation on entire bee communities.

2. We examined bee community responses to forest fragment size, shape, isolation and landscape context (forest variables) by sampling foraging bees at ground level using aerial netting within, and in pastures adjacent to, 22 forest fragments ranging in area from *c.* 0·25 ha to 230 ha, in southern Costa Rica. We sampled each site 13 times in total, in both wet and dry seasons.

3. Although there were no effects of forest variables on bee diversity and abundance, we did find strong changes in bee community composition. In particular, tree-nesting meliponines (social stingless bees) were associated with larger fragments, smaller edge:area ratios and greater proportions of forest surrounding sample points, while introduced *Apis* showed opposite patterns.

4. Community composition was also strikingly different between forests and pastures, despite their spatial proximity. In forests, even in the smallest patches, meliponines comprised a much larger proportion of the apifauna, and orchid bees (euglossines) were common. In pastures, *Apis* was much more abundant and no euglossine bees were found.

5. These results agree broadly with other studies that have found contrasting responses to habitat fragmentation from different bee groups. Conserving meliponine bees, important for pollination of coffee and other crops, and euglossine bees, critical in long-distance pollen transport, will require forest.

6. *Synthesis and applications.* In the first study of the effects of tropical forest fragmentation on entire understorey bee assemblages, we found bee community resilience to land-use change, as deforested sites and small forest fragments can have a diverse component of bees. While bees as a whole show some degree of resilience to land-use change, there are taxon-specific responses and, in our study area, there is clear value to conserving native forest, particularly for the ecologically and economically important meliponine and euglossine bees.

Key-words: agro-ecosystems, Apoidea, conservation, ecosystem services, Euglossini, landscape ecology, Meliponini, pollination

Introduction

Continuing scientific controversy over an alleged 'global pollination crisis' (Ghazoul 2005; Steffan-Dewenter, Potts & Packer 2005) highlights how little we know about the responses of bees, the most important taxon of pollinators, to ongoing global change. Land-use changes, including deforestation, have potentially major impacts on bee

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communities (Allen-Wardell *et al.* 1998; Kearns, Inouye & Waser 1998; Kremen, Williams & Thorp 2002; Klein *et al.* 2007; Kremen *et al.* 2007) but very few empirical studies have addressed the effects of habitat fragmentation on bees. This situation has changed little since Cane (2001) pointed out that the number of review papers on pollination and fragmentation nearly outnumbered the empirical studies on which the reviews were based. Given the importance of bees to both the maintenance of native plant communities and the human agricultural enterprise, it is vital that we better

understand how bee diversity, abundance and community composition are affected by land-use change.

The paucity of studies on bees and land-use change is particularly marked in tropical systems. While studies exist from subtropical areas (Aizen & Feinsinger 1994) and in tropical areas on specific bee groups, especially the euglossines (Powell & Powell 1987; Becker, Moure & Peralta 1991; Tonhasca, Blackmer & Albuquerque 2002), there are, to our knowledge, no studies of habitat fragmentation and whole bee communities in tropical habitats. This is of concern for several reasons. First, biotic pollination is critical for the reproduction of the vast majority of tree species in moist tropical rainforest (Bawa 1990). Secondly, recent work has shown that pollination limitation is particularly marked in areas of high plant diversity, especially in the tropics (Vamosi *et al.* 2006). Thirdly, the potential of native habitat to provide bee pollination services to agriculture is particularly salient in the neotropics, where 'Africanization' of honeybees (*Apis mellifera* L.) has led to the disappearance of beekeeping in many locales (Brosi, Daily & Ehrlich 2007). Wild bees could help compensate for the loss of pollination services from no-longer managed honeybees (Kremen, Williams & Thorp 2002; Ricketts *et al.* 2004) but the habitat area requirements of wild bees are essentially unknown (Kremen *et al.* 2004). For example, in southern Costa Rica, Ricketts *et al.* (2004) found significant increases in coffee *Coffea arabica* pollination as a result of wild bees near two relatively large forest fragments (111 and 46 ha) but not near an 18-ha narrow riparian strip of forest.

To investigate the effects of tropical forest fragmentation on bee communities, we sampled bees within forest fragments of varying size, and in matrix habitats adjacent to them, at ground level in an extensively deforested landscape in southern Costa Rica. We also sampled in adjacent human-dominated habitats to assess whether the effects of forest on bee communities extend beyond forest edges, i.e. whether a forest-based landscape context affects bees in tropical countryside. We examined the effects of forest fragment size, shape, isolation and landscape context on bee diversity, abundance and community composition.

We hypothesized that different components of the bee community would respond differently to forest-based landscape factors, based on their life histories (Cane 2001; Cane *et al.* 2006). Previous work on the effects of distance to a large forest fragment in the same area (Brosi, Daily & Ehrlich 2007) showed strong shifts in bee community composition but no differences in bee diversity or abundance with distance. In particular, the meliponine bees (the social stingless bees of the tropics), which nest primarily in tree cavities, declined markedly away from forest edges. Similarly, pollination of coffee declines with distance to forest, primarily resulting from reduced numbers of meliponine bees, in a nearby southern Costa Rican landscape (Ricketts 2004; Ricketts *et al.* 2004). Therefore, we predicted that tree-nesting bees would respond positively to increases in forest size and proximity, while soil- or stem-nesting bees would be less sensitive.

Methods

OVERVIEW

We sampled bees in 22 forest sites along a gradient of fragment area, from *c.* 0·25 ha to *c.* 230 ha. We sampled the bee community using aerial netting at ground level at each site 13 times over 2 years. In the wet season (June–September) of 2004, we sampled bee communities both inside fragments and also in adjacent pastures. In the dry season (February–April) of 2005, we sampled bee communities only in pastures adjacent to the target fragments. Because all bees are dependent on flowers as a food source, we also measured samples of available floral resources within forest fragments and in the sampled pastures.

STUDY AREA

Our sites were located in the countryside surrounding the Las Cruces Biological Station (8°47′ N, 82°57′ W) in the canton of Coto Brus, Puntarenas State, Costa Rica, near the town of San Vito. The landscape in this area is largely (> 85%) deforested and primary land uses include pastures, coffee plantations and agricultural plots for subsistence crops such as corn and beans. Most of the current conversion from pre-montane tropical rainforest took place with a wave of European settlement in the 1960s, although pollen records show a 3000-year history of deforestation and agriculture by indigenous people (Clement & Horn 2001).

SITE SELECTION

We chose 22 sites centred on forest fragments varying in area from *c.* 0·25 ha to the *c.* 230 ha forest at the Las Cruces Biological Station. All fragments consisted of mature forest with a canopy of mostly primary trees. All had been subject to various forms of human disturbance, probably including some selective logging in all sites. Sites were located a minimum of 500 m apart (maximum distance 13·5 km) and at least 500 m from the nearest other forest fragment, and ranged in altitude from 900 to 1300 m above sea level. All forest sites were bordered by at least 50 m of actively managed cattle pasture. See Fig. 1 for photographs of representative forest fragments and adjacent pastures.

BEE SAMPLING

There are no standard protocols for sampling bee communities in tropical forests. Pan traps, which are used in a range of bee inventories, caught no bees in a pilot study in forests in our study area (B. Brosi, unpublished data) and generally perform poorly under tree canopies, particularly in the tropics (T. Griswold, personal communication). We also assessed the utility of Van Someren traps baited with rotten fish, which had been used to sample bees in Colombian semi-deciduous forest (Smith-Pardo 1999). Dozens of trapping trials, however, yielded < 1 bee specimen per trial, and we discontinued this effort and do not report results from those trials here.

We sampled foraging bees using aerial netting in June–September 2004 (rainy season, six times per site) and February–May 2005 (dry season, seven times per site). In each netting session, two members of the field team aerially netted bees at ground level for a 15-min period, focusing on the flowers within a 20 × 20-m area in pasture directly adjacent to the fragment, while (in the 2004 samples only) two other team members simultaneously netted in an equal area at least 15 m within the target forest fragment. We did not repeat within-forest netting in 2005 because of very low catch rates. To

Fig. 1. Representative forest fragments with adjacent pasture habitats. Forest parcel of (a) 28·8 ha, (b) 3·3 ha.

reduce collection biases, bees were netted in the order seen (thus a netter would not pursue a rare bee at the expense of a common bee seen first); we rotated the order of sites within sampling days and the persons netting at each site. We did not net during conditions of precipitation, fog or strong winds.

SPECIMEN PROCESSING AND IDENTIFICATION

We collected all sampled bees and identified bee specimens in the laboratory to the finest taxonomic level possible, relying extensively on the expertise of bee systematists (M. Engel, V. Gonzales, I. Hinojosa, C. Michener, A. Smith-Pardo, University of Kansas, Lawrence, KS; B. Coelho, Universidade Federal do São Paolo, São Paolo, Brazil). Each specimen was identified to genus at a minimum; when lack of taxonomic treatments prevented identification to species, we used morphospecies designations that were carefully constructed, revised periodically, and also confirmed by specialists. We followed the taxonomic nomenclature of Michener (2000). We retained all bee specimens for future reference; some specimens are archived in the University of Kansas Entomology Museum (SEMC).

FLOWERING PLANT RESOURCES

We measured flowering plant resources in each site, both within the target forest fragment and in adjacent pastures. In each pasture site,

we recorded the species, number of individuals and $\log_{10}$ number of flowers of all plants in bloom in five parallel 20 × 1-m transects, spaced 10 m apart (thus sampling 100 m² at each site). The flora of these pastures is characterized by low species richness and low turnover of species in bloom (Brosi, Daily & Ehrlich 2007), so we therefore ran plant transects once in each site per year, immediately after finishing all rounds of bee sampling. We could not measure plant resources in four sites in 2005 because of disturbance (herbicide application and mowing) between the last bee sampling and our arrival to measure plants. To assess floral resources and characterize the vegetation in the forest fragments, we counted, identified and noted the flowering status of all trees > 10 cm d.b.h. and all plants in flower within a 10 × 20-m quadrat within each forest fragment (comprising half of the target netting area). We identified all plants to the generic level at a minimum, with > 90% of specimens identified to species in forest and 100% in pasture plots; L. Poveda and J. Sanchez of the Universidad Nacional de Costa Rica (Heredia, Costa Rica) assisted with particularly difficult determinations.

MEASURING LANDSCAPE ATTRIBUTES

We assessed the impact of forest fragment area, geometry, isolation and landscape context on bee communities. To measure these factors, we used a combination of geographic information systems (GIS) and ground-based surveys. We conducted GIS analyses using ArcGis 9 and ArcView 3·2 (ESRI, Redlands, CA, USA), with data from orthorectified aerial photographs (1998–2005; MINAE, Costa Rican Ministry of Natural Resources and Agriculture, San José, Costa Rica) and LANDSAT data (1998; 30 × 30-m pixels; classification details in Daily, Ehrlich & Sanchez-Azofeifa 2001). For fragments < 1 ha, we confirmed GIS area measurements by surveying the perimeter, using compass, laser range finder and clinometer; the two measurement techniques generated area estimates within 5% of one another.

To quantify fragment shape, we first assessed the ratio of (perimeter)² to area, which remains constant for circles of varying area. For our sites, however, this measure was still significantly positively correlated with fragment area (linear regression, $F_{21} = 12\cdot30$, $P = 0\cdot0024$, $r^2 = 0\cdot39$). We thus used the residuals of (perimeter)²:area regressed against area as a measure of forest fragment shape independent of area (hereafter shape). To quantify landscape context, we calculated the proportion of both forest and pasture around sample points at radii from 200 to 2000 m in 200-m increments (Ricketts *et al.* 2001; Steffan-Dewenter *et al.* 2002). We calculated isolation by measuring the distance from each site to the nearest forest pixel from the classified LANDSAT data, using the Nearest Features 3·8a extension (Jenness 2004) for ArcView 3·2. We ran tests with raw and square root-transformed isolation data, which returned the same patterns; we report only the raw data results.

DATA ANALYSIS

We tested the effect of forest area, isolation, geometry and landscape context on bee relative abundance (number of individuals captured), raw species richness, diversity (Shannon–Weiner diversity index; SWDI) and estimated species richness (Chao 2 estimator; Colwell & Coddington 1994; Chazdon *et al.* 1998; calculated following Colwell 2005). We tested these bee community responses against landscape metrics and forest characteristics using linear regressions, with $\log_{10}$-transformation of distances and areas to meet assumptions of homoscedasticity. We also grouped sites into $\log_{10}$ area classes and assessed differences in bee diversity and abundance between

groups with Kruskal–Wallis tests, as data did not meet assumptions of normality. For the Chao 2 species richness estimator, we tested differences between groups using 95% confidence intervals, calculated following Colwell (2005).

To assess changes in bee community composition, we compared the distribution of taxonomic tribes (*sensu* Michener 2000), which group bees into ecologically meaningful units, across landscape and forest variables using logistic regression and Fisher's exact test. We did not use community similarity indices (e.g. Jaccard and Bray–Curtis) because of the prevalence of rare species in our sample and the failure of such indices (using analyses of similarity) to find differences in similar previous analyses (Brosi, Daily & Ehrlich 2007). To test the effect of landscape context, we calculated the correlations between bee response variables and the proportions of forest and pasture at varying scales (Ricketts *et al.* 2001; Steffan-Dewenter *et al.* 2002). Except where noted, we calculated the above statistics using JMP 5·0 (SAS Institute, Cary, NC). We used Moran's *I*, calculated with the VEGAN package (Oksanen *et al.* 2006), for the R statistical programming language, to test for spatial autocorrelation between sites.

We pooled all observations by site for all tests to avoid statistical pseudoreplication. We tested the 2004 and 2005 pasture netting data both separately and together. Where the data showed the same patterns across years (the majority of cases), we present only the combined data; otherwise, we present both years separately. We did not combine netting data from forest interior and pasture, nor did we combine data from the 2 years for our analyses on flowering plants because plant resources varied within some sites between years, in part as a result of active pasture management between the two sampling periods.

Results

BEE ASSEMBLAGES

We sampled 1858 bees in four families, 16 tribes, 34 genera and 117 morphospecies (species list in Table 1). Species accumulation curves did not approach an asymptote, as is typical in tropical insect inventories (Fig. 2). We found no evidence of spatial autocorrelation in bee abundance, species richness,
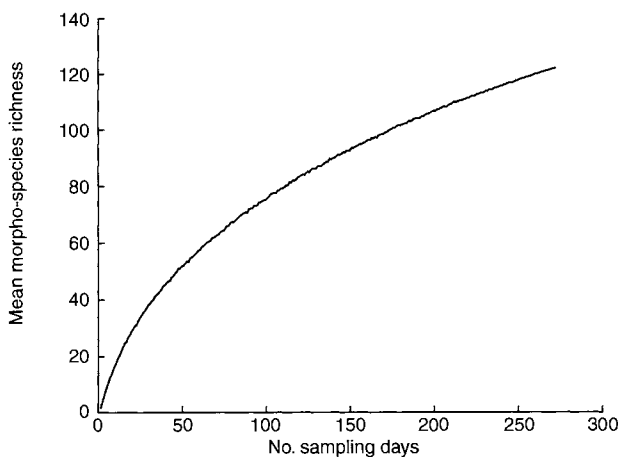
estimated richness or diversity (SWDI) using Moran's *I*. We thus assumed samples (always pooled by site) to be independent for the purposes of the statistical analyses presented here. We found no significant statistical interactions within or between any forest or floral resource variables. As in many bee inventories, our samples were marked by very high variability, both within and between sites (see Table S1 in the supplementary material).

FRAGMENT AREA

Bee abundance (Fig. 3) and diversity (species richness, Fig. 4; estimated species richness and SWDI) were not significantly related to forest fragment area, when considered either as a continuous variable or divided into area classes. The distribution of bee tribes, however, did change significantly with fragment size for pasture-netted bees (Fig. 5; logistic regressions on continuous area, $\chi_4^2 = 46·87$, $P < 0·0001$; area classes, $\chi_4^2 = 48·87$, $P < 0·0001$) but not for forest-interior bees. The meliponines (tree cavity-nesting social stingless bees) showed the strongest individual response, comprising increasing
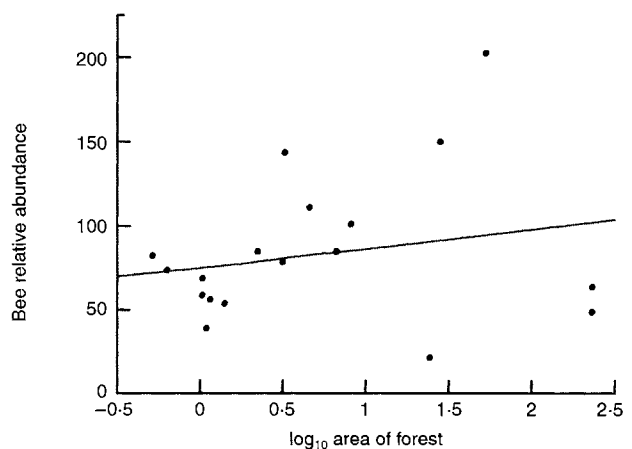

Fig. 3. Bee abundance with log-area of forest, for exterior sites. Each point represents one study site; relationship NS.

Fig. 2. Species accumulation curve for pooled sampling days; data were resampled without replacement 500 times.
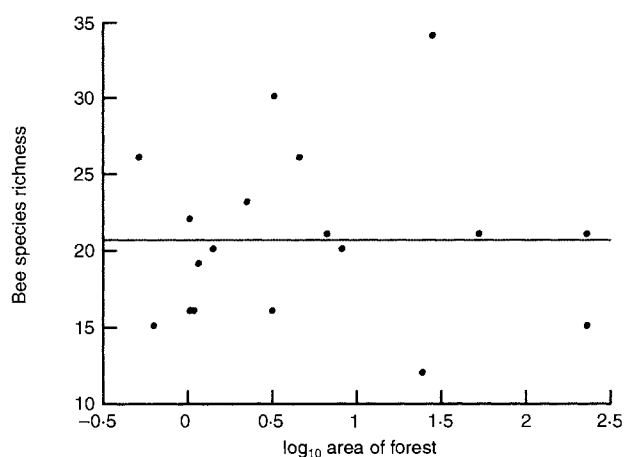

Fig. 4. Bee species richness and log-area of forest, for exterior samples. Each point represents one site; relationship NS.

Table 1. Species list

Family	Tribe	Genus	Subgenus	Species	No. specimens
Apidae	Apini	*Apis*		*mellifera*	321
	Bombini	*Bombus*		[3 morphospecies]	71
	Centridini	*Centris*		*agiloides*	2
				dichrootricha	1
	Ceratinini	*Ceratina*	(Calloceratina)	sp.	1
			(Ceratinula)	[6 morphospecies]	45
			(Zadontomerus)	[3 morphospecies]	9
	Eucerini	*Melissoptila*	(Ptilomelissa)	[2 morphospecies]	3
		Peponapis		sp.	2
		Thygater		sp.	2
	Euglossini	*Euglossa*		sp. (female)	1
				cyanura	2
				flammea	1
				gorgonensis	1
				igniventris	1
		Eulaema		*bombiformis*	11
				cingulata	3
				meriana	2
				nigrifacies	3
	Exomalopsini	*Exomalopsis*	(S. str.)	[4 morphospecies]	12
	Meliponini	*Melipona*		*fasciata*	31
				marginata	1
		Oxytrigona		*mellicolor*	5
		Paratrigona		*isopterophila*	1
				ornaticeps	18
		Partamona		*orizabaienses*	133
		Plebeia		*frontalis*	6
				jatiformis	44
		Scaptotrigona		*mexicana*	32
				pectoralis	11
		Trigona		*almathea*	33
				angustula	26
				corvina	99
				dorsalis	9
				ferricauda	1
				fulviventris	444
				perangulata	7
			(Tetragonisca)	sp.	2
		Trigonisca		sp.	3
	Osirini	*Osiris*		sp.	3
	Tapinotaspidini	*Paratetrapedia*		*calcarata*	22
			(Paratetrapedia)	[5 morphospecies]	14
	Xylocopini	*Xylocopa*		*varipuncta*	1
Colletidae	Caupolicanini	*Mydrosoma*		sp.	1
	Colletini	*Colletes*		[2 morphospecies]	9
Halictidae	Augochlorini	*Augochlora*		*aurifera*	9
				nigrocyanea	4
			(S. str.)	[4 morphospecies]	10
			(Oxystoglossella)	[10 morphospecies]	52
		Augochlorella		*comis*	23
				seniaurata	95
		Augochloropsis		aff. *auriventris*	3
				auriferina	2
				ignita	2
			(Paraugochloropsis)	sp.	9
			(S. str.)	sp.	1
		Caenaugochlora		[2 morphospecies]	4
		Neocorynura		aff. *cribrita*	4
				pubescens	2
				rufa	21
				tica	3
		Pseudoaugochlora		*graminae*	1
	Halictini	*Agapostemon*	(S. str.)	sp.	1
		Habralictus		[3 morphospecies]	3
		Halictus		*ligatus*	1
				seladonia	2
		Lasioglossum	(Dialictus)	[10 morphospecies]	111
			(Lasioglossum)	[3 morphospecies]	39
Megachilidae	Megachilini	*Megachile*		[4 morphospecies]	6
Total					1858
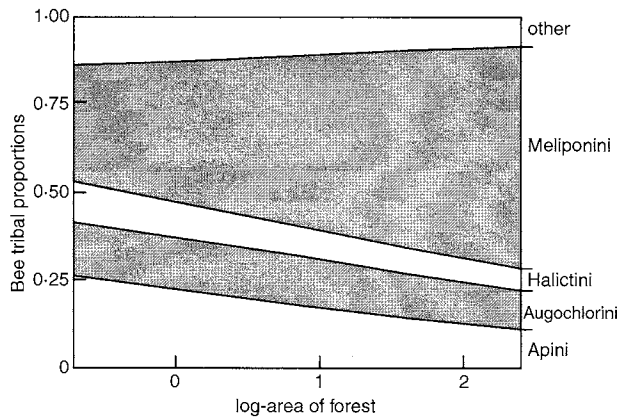
Fig. 5. Logistic regression of bee tribal composition with forest fragment area, for pastures adjacent to forests ($\chi_4^2 = 46\cdot87$, $P < 0\cdot0001$). Logistic regression output from JMP 5·0; lines are regression lines representing least-squares projections of tribal proportions, not bounding polygons.
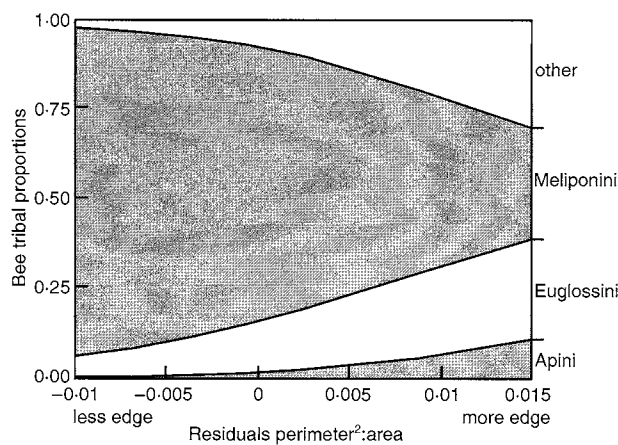

Fig. 6. Logistic regression of bee tribal composition with forest fragment shape, for forest interior samples ($\chi_4^2 = 11\cdot61$, $P = 0\cdot0088$). Logistic regression output from JMP 5·0; lines are regression lines representing least-squares projections of tribal proportions.

sample proportions with increasing forest area. In contrast, *Apis mellifera*, the introduced European honeybee, decreased with increasing forest area. In our study area, all *Apis* are feral; they are no longer managed because of the dangers of working with 'Africanized' honeybees (J. Ilama, Copal de Agua Buena, Costa Rica, personal communication). Two tribes, Meliponini and Euglossini, dominated the within-forest samples (> 90% of individuals) and within-forest tribal proportions did not change significantly with forest fragment area.

FRAGMENT GEOMETRY AND ISOLATION

We found no statistically significant relationship between fragment shape and bee diversity or abundance for samples from either forest interior or exterior. The distribution of bee tribes, however, changed with fragment shape for samples from forest interior and exterior (Fig. 6; exterior, $\chi_4^2 = 12\cdot41$, $P = 0\cdot015$; forest interior, $\chi_4^2 = 11\cdot61$, $P = 0\cdot0088$). Meliponines
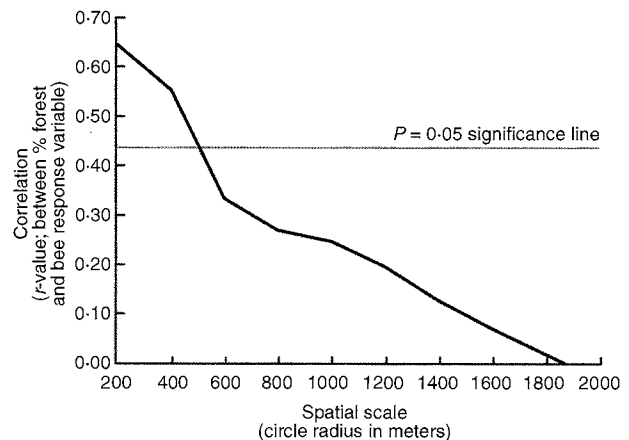
Fig. 7. Landscape context: correlation between proportion of forest and meliponine abundance in pasture at various spatial scales.

decreased in prevalence with increasing edge, while the pooled aggregate of minor tribes showed a concurrent increase. We found no statistical patterns of bee diversity, abundance or community composition with regard to fragment isolation.

LANDSCAPE CONTEXT

The proportion of forest surrounding sample points did not affect overall bee species richness or abundance at any scale. When bee tribes were considered independently, none showed significant trends except the meliponine bees. Landscape context did not affect forest-interior meliponines and the response for pasture-sampled meliponines changed with sample season. In 2004 (wet season) there were no significant correlations with forest cover; in 2005 (dry season) the abundance of meliponines was related to forest from 200 to 600 m; when the data sets were combined, meliponine abundance was significantly related to forest cover from 200 to 400 m around sample points (Fig. 7).

FLORAL RESOURCES

Examining all relationships between pasture plant and bee diversity and abundance, four comparisons for each of the 2 years, considered separately, we found one statistically significant relationship (see Figs S1 and S2 in the supplementary material). For pasture netting data, there was a positive trend between bee richness and plant richness in 2005 only (see Fig. S2D in the supplementary material; $F_{17} = 11\cdot62$, $P = 0\cdot0039$, $\alpha' = 0\cdot00625$ with Bonferroni correction for eight comparisons). Plants in bloom were scarce in the forest understorey plots, recorded in fewer than half of sites (see Table S1 in the supplementary material); there were no significant relationships between bee diversity or abundance and forest floral resources.

FOREST INTERIOR VS. EXTERIOR BEE COMMUNITIES

The tribal compositions of forest interior and exterior samples were strongly distinct (Fig. 8; $\chi_2^2 = 315\cdot6$, $P \ll 0\cdot0001$).
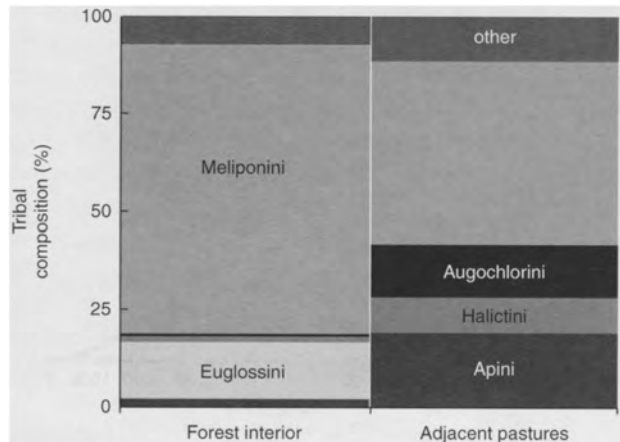
Fig. 8. Differences in bee tribal composition between forest interior and adjacent pastures ($\chi_2^2 = 315\cdot6$, $P \ll 0\cdot0001$).

Meliponine bees made up *c.* 75% of sampled individuals in forests, which dropped to *c.* 50% in pastures adjacent to forests. *Apis mellifera*, the introduced European honeybee, constituted only 2% of samples in forest but nearly 20% in pasture at forest edges. Halictid bees (primarily in tribes Augochlorini and Halictini) were rare in forest interior samples but together comprised nearly a quarter of bees sampled in pasture. The euglossine (orchid) bees comprised *c.* 15% of bees sampled in forest but not a single individual was caught in pasture.

Discussion

CORRELATES OF BEE COMMUNITY STRUCTURE

In the first study of the effects of tropical forest fragmentation on assemblages of ground-level foraging bees, we found no relationship between bee diversity or abundance and forest fragment size, shape or isolation. The tribal composition of bees collected in pastures adjacent to forests, however, changed significantly with forest area and shape (but not isolation), mostly because of an increasing proportion of tree cavity-nesting meliponine bees in larger fragments and those with a lower edge:area ratio. Meliponine bee abundance was also significantly related to the proportion of forest cover surrounding sample points at small scales (< 600 m radius).

In a parallel study of the effects of distance to forest on pasture bee communities in the same landscape, Brosi, Daily & Ehrlich (2007) found similar patterns: no change in bee diversity or abundance with distance from forest but strong changes in community composition, with meliponine bees comprising a much greater proportion of samples near forest.

Studies from other areas of the world also agree broadly with our findings. Klein *et al.* (2002), sampling bees in Indonesian agroforestry systems, detected a decrease in social bees (Meliponini and Apini) with increasing distance from forest, as well as an increase in solitary bee taxa with increasing light levels. Some solitary taxa, however, do respond positively to forest at a landscape scale (Brosi, Smith-Pardo & Gonzalez

2006; Klein, Steffan-Dewenter & Tscharntke 2006), probably because of their use of forests for nesting materials or substrate.

There are, to our knowledge, only three studies of whole bee communities and habitat fragmentation that have directly examined fragment size (Aizen & Feinsinger 1994; Donaldson *et al.* 2002; Cane *et al.* 2006). Of those, Donaldson *et al.* (2002) and Cane *et al.* (2006) found no overall relationships between habitat fragment size and bee diversity but did report differing responses by different groups of bees. For example, Cane *et al.* (2006) found an increase in the diversity and abundance of cavity-nesting bees in small fragments of desert surrounded by urbanized areas relative to continuous desert, probably because buildings, landscaped trees, etc., can provide increased nesting opportunities for such bees. In contrast, Aizen & Feinsinger (1994) found a decline in bee richness with declining habitat fragment size, but inference from their study is limited by their small sample size (eight study fragments), poor taxonomic resolution and potentially improper application of ANOVA (Cane 2001).

We found no effects of fragment isolation (distance to the nearest forest fragment) on bee communities. In some respects this is not surprising, given that there was not a great deal of variation in isolation distances in our study sites (which were selected along a gradient of fragment area). While we imposed a minimum isolation distance of 500 m when selecting sites, the median isolation distance was 760 m and more than three-quarters of the fragments we studied were isolated by 850 m or less. In a landscape with fewer patches of forest and more variation in the distances between them, isolation distance might have much stronger impacts on bee communities. This would probably be true for meliponine bees, whose colony behaviour limits reproductive dispersal to a range not much greater than their maximum foraging dispersal (Roubik 1988), i.e. possibly only 1–2 km in closed tropical forest (Roubik & Aluja 1983).

Meliponine abundance was significantly related to the proportion of forest surrounding sample points at small scales. Such a measure of landscape context is probably more relevant to tree-nesting meliponine bees than simple isolation. This mirrors the findings of Steffan-Dewenter *et al.* (2002) and Kremen *et al.* (2004). In particular, Steffan-Dewenter *et al.* (2002) found that increasing proportions of surrounding native calcareous grassland are coincident with increases in the richness and abundance of solitary bees, which are primarily ground-nesting, in accord with our findings of increases in tree-nesting meliponines with greater forest cover.

The bee fauna of forest fragments and adjacent pastures have substantially different tribal compositions. Forest bee communities were dominated by meliponine bees and had very low (*c.* 2%) representation of the exotic honeybee *Apis mellifera*, while in nearby pastures *Apis* increased to 15% of samples, with a decrease of social stingless bees from *c.* 75% to *c.* 50% of individuals. Brosi, Daily & Ehrlich (2007) documented a further shift in the social bee fauna at distances of > 500 m from forest, where *Apis* comprised *c.* 45% of samples and meliponines only *c.* 20%.

The orchid bees (tribe Euglossini) were unique, appearing only in the forest samples (of which they comprised *c.* 15% of specimens) and not in any samples taken in deforested habitats, in either this study, previous sampling (Brosi, Daily & Ehrlich 2007) or casual bee collecting in the same landscape, representing a combined total of > 4000 bee specimens. Orchid bees thus appear limited to forest habitats, at least for the bulk of their time. We found euglossine bees even in fragments < 1 ha in size, which suggests that orchid bee individuals may utilize several distinct forest patches; previous work has shown that euglossines are capable of crossing pastures between forests in Brazil (Tonhasca, Albuquerque & Blackmer 2003). The reasons underlying the forest habitat preferences of euglossine bees are unclear but may involve the availability of forage plants (e.g. Orchidaceae, Gesneraceae and Araceae), sites and construction materials for nests and/ or thermoregulation (Roubik & Hanson 2004).

We collected several other bee species from forests that did not appear in samples from deforested habitats (again considering previous work and casual collecting in this landscape). Among these was *Neocorynura tica*, a newly described augochlorine bee species known only from the interiors of three of the forest sites used in this study (Brosi, Smith-Pardo & Gonzalez 2006). In > 4000 specimens collected in this landscape, this was the only recognizable new species from any habitat. Although lack of taxonomic revisions in many genera prevents this from being a definitive statement, it is still striking that, with many fewer forest specimens than those from matrix habitats, our only new species came from forest habitats. This, plus the absence of an entire bee tribe (Euglossini), along with the lack of several species from other groups, from samples in deforested habitats, points to some degree of irreplaceability of native forest in this landscape for maintaining a diverse bee fauna.

FORESTS, MELIPONINES, AND APIS

As a group, the meliponine bees, important pollinators of many tropical crops (Heard 1999), had the strongest and most consistent responses to forests in our landscape. This is intuitive in some respects, as most meliponines nest in tree cavities and this group reaches its greatest diversity in lowland tropical rainforest (Roubik 1988, 2000). The statistical patterns we found with regard to meliponine bees and forests were not uniformly strong, however. For example, we did not find a significant decline in meliponine bee richness with decreasing forest size. Meliponines as a group are not limited to forest; on the contrary, we have seen nests of various species in isolated pasture trees and in anthropogenic structures (not every species is a cavity nester). Furthermore, we routinely observed and sampled meliponines foraging in deforested habitats. The general trends of forest association shown here may result from some meliponine species nesting only in forest; an increased susceptibility to disease, predation or parasitism in nests outside forests; or reliance on plant resources available only in forest for foraging (perhaps at certain times of year) or nest construction. Meliponine

colony dispersal, which involves hundreds or thousands of trips to the old nest to transfer provisions, etc. (Roubik 1988), may also limit colony resettlement in small or isolated forest patches. The direct impacts of people, who sometimes destroy meliponine nests to prevent nuisances from colony defence or to collect their locally valuable honey (B. Brosi, personal observation), may also make deforested habitats less hospitable to meliponines. Finally, different species and genera of Meliponini may have contrasting responses to deforestation (Brown & Albrecht 2001).

Introduced *Apis*, a close relative of the meliponines and, like most of them, a tree-cavity nester, shows the opposite landscape patterns from the meliponines, representing decreasing proportions of our samples with increasing forest fragment area and decreasing edge:area ratio. Previous work has shown similar contrasting landscape patterns with *Apis* and meliponines with respect to distance to forest (Brosi, Daily & Ehrlich 2007). There are several possible explanations that could contribute to this pattern. *Apis* has a very different system of colony reproductive dispersal than meliponines, with the old queen and workers departing in a swarm that can travel tens of kilometres (Gould & Gould 1988), meaning *Apis* could potentially colonize isolated and small forest fragments, or isolated pasture trees, more easily than meliponines. Competitive interactions with the more robust meliponine populations in larger forest patches with less edge could potentially reduce the presence or abundance of *Apis*; Roubik (2000) observed that Napo, Ecuador, the area of greatest meliponine species density, has not been invaded by *Apis*. Finally, *Apis* could simply have habitat preferences for deforested areas and forest edges rather forest interior.

Meliponines are a particularly important group of native bees both ecologically and economically. Colony members recruit one another to floral resources, meaning they can successfully pollinate briefly blooming tropical plants and crops such as coffee (Heard 1999; Klein *et al.* 2002; Klein, Steffan-Dewenter & Tscharntke 2003; Ricketts 2004; Slaa *et al.* 2006), although they occasionally act as nectar robbers of crops and other plants (Roubik 2002). While *Apis* is also eusocial and recruits foragers, it is a single species that is, like many bee species, subject to substantial swings in population size between years. The diversity of meliponine bees in our study area buffers against such variance to allow for stable pollination services (Roubik 2000; Kremen, Williams & Thorp 2002; Ricketts 2004; Ricketts *et al.* 2004), and their range of behaviours and body sizes also allows for the pollination of a diverse component of native plants that *Apis* cannot successfully pollinate (Roubik 2000).

BEE COMMUNITIES IN THE FOREST UNDERSTOREY AND CANOPY

It is possible that we would have found stronger or even distinct results if sampling in the forest canopies of the study fragments had been possible. The one long-term canopy study of bees from Central America (Roubik 1993), however, suggests otherwise. Not only did our understorey sampling

record all but one of the same taxa, but Roubik (1993) also stated, 'Did bees prefer to forage in the canopy or specialize there? Except for the nocturnal genus *Megalopta* and one stingless bee, *Partamona*, the long-term data do not support this idea'. Despite even this statement, *Partamona orizabaensis* was the third-most abundant species in our inventory. Thus we believe that our understorey-based sampling is likely to have reflected the important trends in canopy bees as well. Developing practical, unbiased methods of sampling bees in forest canopies should be a priority for future research in this arena.

CONCLUSION

From this study and previous work showing declines in meliponine bees with distance to forest (Brosi, Daily & Ehrlich 2007), it is clear that preserving a diverse component of meliponine bees, the only eusocial bees native to our study area, requires conservation of native forest. Larger forests and those with a smaller edge:area ratio are associated with a more robust meliponine community adjacent to forest, as is a greater proportion of forest surrounding sample sites. At the same time, even very small forest fragments clearly provide habitat requirements for meliponine bees that are lacking in deforested habitats, and should be actively conserved. These small fragments also support other forest-related bee taxa, such as the euglossines, as well as a range of non-bee taxa, both in southern Costa Rica (Daily, Ehrlich & Sanchez-Azofeifa 2001; Ricketts *et al.* 2001; Hughes, Daily & Ehrlich 2002; Daily *et al.* 2003; Horner-Devine *et al.* 2003) and other tropical areas (Estrada, Coates-Estrada & Meritt 1997; Perfecto & Vandermeer 2002).

The rustically managed deforested habitats in our study area, however, provide habitat value for a range of other bee taxa, notably soil-nesting halictid bees, echoing the findings of Tylianakis, Klein & Tscharntke (2005) for trap-nesting bees and wasps in a similarly heterogeneous and low-intensity landscape in Ecuador. Indeed, in a mosaic landscape in southern New Jersey, USA, Winfree, Griswold & Kremen (2007) found increases in overall bee diversity and abundance with increasing anthropogenic activity (primarily small agricultural fields and low-intensity suburban development). This is in contrast to very intensively managed landscapes, such as industrial agricultural areas in the Central Valley of California, USA (Kremen, Williams & Thorp 2002; Kremen *et al.* 2004), which apparently have little habitat value for bees. Activities associated with such high-intensity land uses, such as pesticide application, tilling and other soil disturbance, and the clearing of native habitat, may make it difficult for bees of nearly any guild to persist in such areas. When at least some elements of native habitat are left intact, however, bee communities appear to have some degree of resilience to land-use change, as diverse bee faunas have persisted over decadal time scales in agricultural landscapes in Poland (Banaszak 1992) and Illinois, USA (Marlin & LaBerge 2001), despite some ongoing agricultural intensification in both of those locales. A critical point for future research will be to determine whether land-use change affects plant–pollinator interaction webs despite resilience with regard to bee diversity, as has been shown with hymenopteran parasitoid networks in Ecuador (Tylianakis, Tscharntke & Lewis 2007).

The work presented here adds to a growing body of evidence that different groups of bees show contrasting responses to land-use change, probably driven by differences in their foraging and nesting biology. While bees as a whole show some degree of resilience to land-use change, there is clear value to conserving native habitat, particularly in our study area, for the ecologically and economically important meliponine and euglossine bees. This study also echoes the findings of previous work of the value of even very small parcels of native habitat for maintaining biodiversity in agricultural landscapes. Given the importance of bees for the maintenance of native plant populations and the human agricultural enterprise, it is vital that we continue to unravel their complex responses to ongoing global changes, particularly in the tropics.

References

Aizen, M.A. & Feinsinger, P. (1994) Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine Chaco Serrano. *Ecological Applications*, **4**, 378–392.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane. J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**, 8–17.

Banaszak, J. (1992) Strategy for conservation of wild bees in an agricultural landscape. *Agriculture Ecosystems and Environment*, **40**, 179–192.

Bawa, K. (1990) Plant–pollinator interactions in tropical rain-forests. *Annual Review of Ecology and Systematics*, **21**, 399–422.

Becker, P., Moure, J.S. & Peralta, F.J.A. (1991) More about euglossine bees in Amazonian forest fragments. *Biotropica*, **23**, 586–591.

Brosi, B.J., Daily, G.C. & Ehrlich, P.R. (2007) Bee community shifts with landscape context in a tropical countryside. *Ecological Applications*, **17**, 418–430.

Brosi, B.J., Smith-Pardo, A. & Gonzalez, V.H. (2006) A new wood-nesting *Neocorynura* (Hymenoptera: Halictidae: Augochlorini) from Costa Rica, with notes on its biology. *Zootaxa*, **1189**, 55–68.

Brown, J.C. & Albrecht, C. (2001) The effect of tropical deforestation on sting-less bees of the genus *Melipona* (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography*, **28**, 623–634.

Cane, J.H. (2001) Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology*, **5**, article 3.

Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H. & Williams, N.M. (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*, **16**, 632–644.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies* (eds F. Dallmeier & J.A. Comiskey), pp. 285–309. UNESCO, Parthenon Publishing Group, Paris, France.

Clement, R. & Horn, S. (2001) Pre-Columbian land-use history in Costa Rica: a 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. *Holocene*, **11**, 419–426.

Colwell, R.K. (2005) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 7·5. User's Guide and Application.* http://purl.oclc.org/estimates, accessed August 2007.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **345**, 101–118.

Daily, G., Ceballos, G., Pacheco, J., Suzan, G. & Sanchez-Azofeifa, A. (2003) Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology*, **17**, 1814–1826.

Daily, G., Ehrlich, P. & Sanchez-Azofeifa, G. (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications*, **11**, 1–13.

Donaldson, J., Nanni, I., Zachariades, C., Kemper, J. & Thompson, J.D. (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology*, **16**, 1267–1276.

Estrada, A., Coates-Estrada, R. & Meritt, D. (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, **6**, 19–43.

Ghazoul, J. (2005) Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution*, **20**, 367–373.

Gould, J.L. & Gould, C.G. (1988) *The Honey Bee.* Scientific American Library. W. H. Freeman, New York, NY.

Heard, T. (1999) The role of stingless bees in crop pollination. *Annual Review of Entomology*, **44**, 183–206.

Horner-Devine, M., Daily, G., Ehrlich, P. & Boggs, C. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**, 168–177.

Hughes, J., Daily, G. & Ehrlich, P. (2002) Conservation of tropical forest birds in countryside habitats. *Ecology Letters*, **5**, 121–129.

Jenness, J. (2004) *Nearest Features Extension for ArcView 3·2, v.3·8a.* Jenness Enterprises, Flagstaff, AZ. http://www.jennessent.com/arcview/nearest_features.htm (accessed August 2006).

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998) Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83–112.

Klein, A., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, **16**, 1003–1014.

Klein, A., Steffan-Dewenter, I. & Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **270**, 955–961.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2006) Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *Journal of Animal Ecology*, **75**, 315–323.

Klein, A., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **274**, 303–313.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J. & Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, **7**, 1109–1119.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 16812–16816.

Marlin, J.C. & LaBerge, W.E. (2001) The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conservation Ecology*, **5**, 1–24.

Michener, C.D. (2000) *The Bees of the World.* Johns Hopkins University Press, Baltimore, MD.

Oksanen, J., Kindt, R., Legendre, P. & O'Hara, R. (2006) *Vegan: Community Ecology Package. Ordination Methods and Other Useful Functions for Community and Vegetation Ecologists.* http://cc.oulu.fi/ ~jarioksa/ (accessed August 2006).

Perfecto, I. & Vandermeer, J. (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology*, **16**, 174–182.

Powell, A.H. & Powell, G.V.N. (1987) Population-dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica*, **19**, 176–179.

Ricketts, T.H. (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, **18**, 1262–1271.

Ricketts, T., Daily, G., Ehrlich, P. & Fay, J. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378–388.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Michener, C.D. (2004) Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 12579–12582.

Roubik, D.W. (1988) *Ecology and Natural History of Tropical Bees.* Cambridge University Press, Cambridge, UK.

Roubik, D.W. (1993) Tropical pollinators in the canopy and understorey: field data and theory for stratum 'preferences'. *Journal of Insect Behavior*, **6**, 659–673.

Roubik, D.W. (2000) Pollination system stability in tropical America. *Conservation Biology*, **14**, 1235–1236.

Roubik, D.W. (2002) Feral African bees augment neotropical coffee yield. *Pollinating Bees: The Conservation Link Between Agriculture and Nature* (eds P. Kevan & V.L. Imperatriz-Fonseca), pp. 255–266. Ministry of Environment, Brasília, Brazil.

Roubik, D.W. & Aluja, M. (1983) Flight ranges of *Melipona* and *Trigona* in tropical forest. *Journal of the Kansas Entomological Society*, **56**, 217–222.

Roubik, D.W. & Hanson, P.E. (2004) *Orchid Bees of Tropical America: Biology and Field Guide.* Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Slaa, E.J., Sánchez Chaves, L.A., Malagodi-Braga, K.S. & Hofstede, F.E. (2006) Stingless bees in applied pollination: practice and perspectives. *Apidologie*, **37**, 293–315.

Smith-Pardo, A. (1999) Evaluación de cuatro diferentes métodos de captura de abejas silvestres en el área de influencia del Embalse Porce II. *Revista Facultad de Ciencias Agropecuarias, Medellin, Colombia*, **52**, 435–450.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432.

Steffan-Dewenter, I., Potts, S.G. & Packer, L. (2005) Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution*, **20**, 651–652.

Tonhasca, A., Albuquerque, G.S. & Blackmer, J.L. (2003) Dispersal of euglossine bees between fragments of the Brazilian Atlantic Forest. *Journal of Tropical Ecology*, **19**, 99–102.

Tonhasca, A., Blackmer, J.L. & Albuquerque, G.S. (2002) Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic forest. *Biotropica*, **34**, 416–422.

Tylianakis, J.M., Klein, A.M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*, **86**, 3296–3302.

Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, **445**, 202–205.

Vamosi, J.C., Knight, T.M., Steets, J.A., Mazer, S.J., Burd, M. & Ashman, T.L. (2006) Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 956–961.

Winfree, R., Griswold, T. & Kremen, C. (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, **21**, 213–223.

Supplementary material

The following supplementary material is available for this article.

Table S1. Summary data of bee sampling by site

Fig. S1. Relationships between plant and bee diversity and abundance, 2004 forest exterior data.

Fig. S2. Relationships between plant and bee diversity and abundance, 2005 forest exterior data.

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