

Evaluating bee (Hymenoptera: Apoidea) diversity using Malaise traps in coffee landscapes of Costa Rica

H.T. Ngo,¹ J. Gibbs, T. Griswold, L. Packer

Abstract—Even though Arabica coffee (*Coffea arabica* Linnaeus, Rubiaceae) can self-pollinate, bees are important pollinators, without which there is lower fruit quality and yield. We studied bee diversity in coffee agroecosystems in Costa Rica during two coffee flowering seasons (2005 and 2006). Malaise traps were used as a passive sampling method to collect bees during coffee blooms. We collected 1012 bee individuals from three different site types: nonagricultural fields and shaded and unshaded coffee farms. Unshaded coffee farms had significantly higher species richness (S) and number of bee individuals (n) than did the shaded coffee farms and nonagricultural sites. Overall bee diversity did not differ among site types but evenness (J') was significantly lower in unshaded coffee farms. Using a more detailed community analysis, there was a significant association between functional groups and habitat type with more species and individuals of small-bodied ground-nesting bees (*Lasioglossum* (*Dialictus*) Robertson) associated with unshaded coffee farms. A large proportion (49%) of bees collected were of this subgenus, which was never before reported as common in coffee agroecosystems. Further studies should establish whether *Dialictus* is important in coffee pollination. We propose strategies involving conservation of native bees through simple habitat management for small-scale coffee farms that may improve crop quality and quantity.

Résumé—Bien que le caféier d'Arabie (*Coffea arabica* Linnaeus, Rubiaceae) puisse s'autopolliniser, les abeilles sont d'importants pollinisateurs sans lesquels la qualité et la production des fruits sont moindres. Nous avons étudié la diversité des abeilles dans les agroécosystèmes de caféier au Costa Rica durant deux saisons de floraison du caféier (2005 et 2006). Des pièges Malaise ont été utilisés comme méthode passive d'échantillonnage afin de récolter les abeilles durant la floraison du caféier. Nous avons récolté 1012 individus sur trois différents types de sites : des champs non-agricoles et des plantations de caféiers ombragées ou non. Les plantations de caféiers sans ombre possédaient une richesse d'espèces (S) et un nombre d'individus d'abeilles (n) significativement plus grands que les plantations de caféiers ombragées et les sites non-agricoles. La diversité globale des abeilles ne différaient pas entre les différents types de sites, mais l'équitabilité (J') était significativement plus basse dans les plantations de caféiers sans ombre. En utilisant des analyses de communauté plus détaillées, une association significative a été trouvée entre les groupes fonctionnels et le type d'habitat : plus d'espèces et d'individus de petites abeilles nichant au sol (*Lasioglossum* (*Dialictus*) Robertson) sont associés aux plantations de caféiers sans ombre. Une grande proportion (49%) des abeilles récoltées faisaient partie de ce sous-genre, qui n'a jamais été rapporté comme commun dans les agroécosystèmes de caféiers auparavant. Des études ultérieures devraient établir si *Dialictus* est important dans la pollinisation du caféier. Nous proposons une stratégie impliquant la conservation des abeilles natives par le biais d'une gestion de l'habitat simple qui pourrait améliorer la qualité et la quantité des récoltes pour des plantations de caféiers à petite échelle.

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Introduction

Bees (Hymenoptera: Apoidea) are, by far, the most important pollinators of wildflowers and agricultural crops (Free 1993; Kevan and Philips 2001; Aizen *et al.* 2009; Ollerton *et al.* 2011). Recent declines in managed honeybees (NRC 2007), native bumble bees (Goulson *et al.* 2005; Kosior *et al.* 2007; Colla and Packer 2008), and other pollinators (Biesmeijer *et al.* 2006) have led to increased interest in native bees (*e.g.*, Winfree *et al.* 2007, 2008; Tuell *et al.* 2008). Bee declines in America and Europe have been associated in part with habitat loss and agricultural practices including expansion (Goulson *et al.* 2008), intensification (Kremen *et al.* 2004), and increased pesticide use (Banaszak 1992; Steffan-Dewenter *et al.* 2002; Kremen *et al.* 2004; Biesmeijer *et al.* 2006).

Coffee production is ecologically significant in terms of land area and also economically important as the top earner of foreign capital in developing countries (Donald 2004). Coffee plantations cover ~11 million ha worldwide with Latin America producing ~34% of the world's supply (Perfecto and Armbrrecht 2003). Coffee-growing regions of Latin America and elsewhere are biodiversity hotspots known for their high species richness and endemism (Myers *et al.* 2000), making studies of their impacts on biodiversity particularly important.

There has been significant research focused on the impacts of agricultural expansion of or habitat conversion to coffee agroecosystems (Perfecto and Armbrrecht 2003). Such systems have been categorised based on criteria of floral diversity or complexity and pesticide use (Moguel and Toledo 1999). These categories, in order of increasing intensification are: (1) traditional rustic, (2) traditional polyculture, (3) commercial polyculture, (4) shaded monoculture, and (5) unshaded monoculture (Moguel and Toledo 1999). Previous studies have compared traditional polyculture, commercial polyculture, and shaded monoculture coffee farms to non-agricultural habitats, examining the differences in the diversity of birds (Wunderle and Latta 1994; Greenberg *et al.* 1997), mammals (Estrada *et al.* 1993; McCann *et al.* 2003; Pineda *et al.* 2005), frogs (Pineda *et al.* 2005), and various insect groups (Ibarra-Núñez *et al.* 1995;

Armbrrecht and Perfecto 2003; Horner-Devine *et al.* 2003; Ricketts 2004; Pineda *et al.* 2005). Responses to intensification differ among animal taxa and this prevents generalisations on the impact of the type of coffee production on biodiversity as a whole (Moguel and Toledo 1999; McCann *et al.* 2003; Perfecto *et al.* 2003; Tejeda-Cruz and Sutherland 2004; Pineda *et al.* 2005; Estrada *et al.* 2006).

Bee diversity and abundance can be important for successful coffee pollination (Roubik 2002; Klein *et al.* 2003a; Ricketts 2004; Vergara and Badano 2009). Pollinators can increase coffee yield by as much as 50% (Roubik 2002). Large forest fragments adjacent to coffee farms in Costa Rica are a source of bee pollinators (feral honeybees, stingless bees, and native wild bees) (Ricketts 2004; Brosi *et al.* 2007), and can result in higher visitation rates to coffee flowers and increased pollen deposition rates, at least within 100 m of a forest fragment (Ricketts 2004). In Indonesian coffee agroecosystems, solitary bees were more effective pollinators than social bees on a per visit basis but were much less abundant comprising only 33% of total flower visits (Klein *et al.* 2003a). Higher pollinator diversity and species richness has been related to increased coffee production (percentage fruit set) in Mexico (Vergara and Badano 2009).

Most studies of bee diversity in coffee agroecosystems have focused on coffee and pollination from the perspective of coffee yield (Florez *et al.* 2002; Roubik 2002; Klein *et al.* 2003a; Vergara and Badano 2009). The impact of different coffee management practices on bees has not been studied with one exception (Florez 2001). Our first objective was to quantify bee diversity and community composition in different levels of intensification in Costa Rican coffee farms using common diversity indices for samples obtained using Malaise traps. Bee functional groups are known to respond differently to landscape effects (Cane 2001; Grixti and Packer 2006; Williams *et al.* 2010), our second objective was to compare patterns among bees with different functional groups across our sites. Our final objective was to propose feasible management strategies for small-scale coffee farmers to increase bee diversity for improved pollination and coffee production.

Methods

This study was conducted from January to April in both 2005 and 2006 in the southwestern region of Costa Rica at elevations ranging from 700 to 1200 m (Fig. 1). The three communities where sampling took place were Santa Elena, Quizarrá and Montecarlo, located ~14 km northeast of San Isidro in the El General Valley (Fig. 1); all are part of the Los Cusingos Las Nubes Biological corridor (Daugherty 2005). This region of Costa Rica is considered pre-montane/tropical moist forest according to the Holdridge Life Zones scheme (Janzen 1983). The landscape is composed of forest fragments and farms, primarily coffee farms and sugarcane fields (Daugherty 2005). Like the rest of Costa Rica, this area has two distinct seasons: dry (January–May) and rainy (June–December). The mean annual rainfall is ~4000 mm; the average maximum and minimum temperatures are 29.2°C and 18.7°C, respectively.

Each year there are three to four massive synchronous blooming events, or flushes, of coffee flowers, which typically lasts two to three days. At our study sites, all coffee flushes were separated by two to three weeks; the onset of a

coffee flush was dependent on rainfall. During each flush in 2005 and 2006 we sampled bees in three sites; each of a different treatment type: (1) shaded coffee farms, (2) unshaded coffee farms, and (3) nonagricultural sites. The fourth and final flush in 2005 was an exception in that only one shaded and one unshaded coffee farm could be sampled at that time. During the four flushes in 2005, we collected from 11 sites: four shaded coffee farms, four unshaded coffee farms, and three nonagricultural sites. Each collection lasted for the entire duration of the flush. There were three flushes in 2006 and nine of the previous year's 11 sites were sampled again: three shaded coffee farms, three unshaded coffee farms, and three nonagricultural sites (see Table 1).

All sites were separated by at least 600 m (mean distance >1 km) from each other. A majority of the coffee farms in this region are <10 ha with sun-tolerant strains of *Coffea arabica* Linnaeus (Rubiaceae) (Caturra, Catuai, and Catimor) (Hall 2001). In each shaded coffee farm, the main shade tree was Poró (*Erythrina poeppigiana* (Walpers) Cook; Fabaceae) (Merino *et al.*, personal communication) with the exception of one farm, which had Poró and Amarillon (*Terminalia amazonia* (Gmelin)

Fig. 1. Map of the study area near San Isidro, Costa Rica showing the three communities (Quizarrá, Montecarlo, and Santa Elena) where sampling took place. ★, Indicate shaded coffee farms; ■, Indicate unshaded coffee farms; ●, Indicate nonagricultural sites.

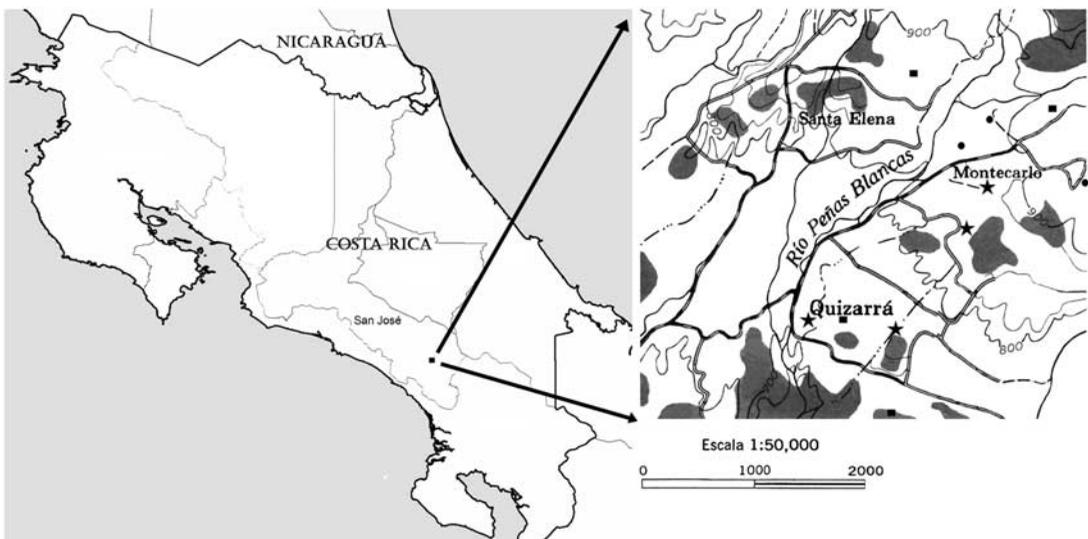


Table 1. Description of all the sites used in 2005 and 2006.

Community	Farm name	Coordinates	Site type	Description	Size (ha)
Montecarlo	Bonilla	N09°21.415' W083°36.235'	Unshaded coffee		5–10
	Monteverde/ Bernina	N09°20.858' W083°37.030'	Shaded coffee	Poró shade trees only	5–10
	Loma*	N09°20.800' W083°36.000'	Shaded coffee	Poró shade trees only	≤5
	Mora (1)	N09°20.516' W083°36.244'	Nonagricultural		5–10
	Mora (2)	N09°20.338' W083°36.604'	Nonagricultural		~5
	Quizarrá	Helga	N09°20.288' W083°36.235'	Unshaded coffee	
Quizarrá	Rojas Sr.*	N09°19.190' W083°36.235'	Unshaded coffee		~5
	Pancho	N09°20.124' W083°36.244'	Shaded coffee	Poró and Amarillón shade trees	≤5
	Ureñas	N09°19.193' W083°36.85'	Nonagricultural		≤5
	Vasquez	N09°20.235' W083°37.019'	Shaded coffee	Poró shade trees only	5–10
	Santa Elena	Gran Tico	N09°22.179' W083°36.713'	Unshaded coffee	

Note: *Approximation of coordinates.

Exell; Combretaceae). In unshaded coffee farms, rows of coffee plants were spaced 2 m apart and plants were separated by 1 m within rows. In the monospecific shaded coffee farms, Poró was arranged in a grid of either 4 m × 4 m, or 6 m × 6 m. The one site with both Poró and Amarillon trees had a similar planting scheme (*i.e.*, 6 m × 6 m) but alternating tree species; thus the density of shade trees did not vary among sites. Shade management practices consist of pruning the Poró trees twice a year (Hall 2001). Farms were chosen based on the cooperation of farm owners, farm size (>5 ha), synchronous blooming times and feasibility in terms of proximity to other farms sampled. Nonagriculture controls were selected in plots of land >5 ha which had been fallow for at least five years and were dominated by shrubs. Shrubs and plants from the family Asteraceae dominated these nonagricultural plots followed by some Rubiaceae (other than coffee). All nonagricultural sites were ~1 km from the closest shaded or unshaded coffee farm. Attempts were made to sample all site types on the same days.

For each site, one Townes' Style Malaise trap (Sante Traps, Lexington, Kentucky, United States of America) was set up for insect collection. They were placed along an insect flight path (Gressitt and Gressitt 1962) (*i.e.*, perpendicular to the rows of coffee) and each trap was positioned so that the collecting head faced in the direction that would receive the most sunlight throughout the day (Noyes 1989). The Malaise traps were set up in coffee fields the day before the first day of the coffee flush. The opening of ~2–5% of the flowers indicated the onset of a major flowering period. The Malaise traps were left up for three days, the length of the coffee flush, and replenished with propylene glycol as a collecting solution every day during the coffee flowering period. All bee specimens (Apoidea, excluding the four predatory wasp families) were pinned and identified for analyses.

Data analysis

The Shannon-Wiener (H') and Shannon Evenness (J') indices were used to quantify bee diversity at each site for each year ($n = 20$).

Hill's diversity index (N_1) was also calculated in order to confirm the pattern of diversity shown with the Shannon-Wiener values. SPSS 15.0 Statistical software (SPSS Inc., Chicago, Illinois, United States of America) was used to test for normality for the following dependent variables: species richness, number of individuals, biodiversity (H'), and evenness (J'). Consequently, evenness and number of individuals were subject to arcsin and square root transformations, respectively. All other data were normally distributed.

An initial three-factor analysis of variance (ANOVA) was used to determine the main effects and interactions of year, site type, and flush (nested within year) (PROC MIXED, SAS 1999) on bee species richness, number of individuals, biodiversity, and evenness. As the sites were not exactly the same in the two years, the "year" and "year" \times "site type" were included as random effects in the model. Neither "year" nor "year" \times "site type" were significant sources of variability. This initial analysis also showed no significant effect of flush on the response variables. ANOVA analyses were followed by Bonferroni's *post hoc* correction of multiple pair-wise comparisons on means. Higher-order interactions were used as the error term in testing these fixed main effects (Kirk 1982). Each effect was tested over the error term, and all the *F*-tests involve Type III sum of squares. All data analyses for ANOVA were performed using SAS Version 8 (1999) statistical software (SAS Institute, Cary, North Carolina, United States of America).

To compare observed species richness with unequal abundances across sites, individual-based rarefied estimates (\pm SE) were pooled by site type and used to calculate the number of expected species in each site (Magurran 1988). The number of individuals in the smallest sample determined the standardised sample size to allow a common sampling effort among three site types. All rarefaction estimates were obtained using Species Diversity and Richness IV (Pisces Conservation Ltd., Lymington, United Kingdom) with the default setting of 1000 iterations.

Four bee functional groups were defined: social versus solitary, ground versus above-ground nesters, small (<6 mm) versus medium

to large-bodied bees (≥ 6 mm), and nest makers versus cleptoparasites. We examined how the proportion of these observed bee functional groups was distributed among site types. Both species observed richness (S) and number of bee individuals (N) were compared for each of the four functional group categories. Certain taxa were excluded from these analyses either because their ecology was unknown or the number of individuals collected for that entire functional group was too small to generate meaningful values for comparison. Otherwise, each bee species was assigned to a specific group category for each analysis (Appendix A). χ^2 contingency tables (2×3) were used to investigate relationships between bee functional group and site type.

Last, we estimated the number of shared species or community similarity of bees using Jaccard and Morisita-Horn indices, respectively, for each pairwise site type comparison for each year. Both indices seek to measure the differences in diversity between two or more sites, also known as β diversity or complementarity (Magurran 2004). The Jaccard index is based on presence/absence of data, whereas the Morisita-Horn index is a quantitative method of comparing sites based on species abundance. Stepwise cluster analysis using unweighted pair group method with arithmetic mean (UPGMA) was then performed based on a matrix of the dissimilarity values.

Results

A total of 1012 bee individuals were caught in 20 sites over two years and 980 of them were used in the analyses: 32 males of the subgenus *Lasioglossum* (*Dialictus*) were excluded because we could not associate them with females. We identified all bees to 113 morphospecies belonging to 34 different genera. By far, the most abundant higher-level taxon collected was *Lasioglossum* (*Dialictus*), consisting of $\sim 49\%$ of all individuals. *Trigona* Jurine followed with $\sim 11.5\%$ and *Augochlora* Smith with 7% (Appendix B).

In the overall ANOVA model there were no significant effects due to year, coffee flush within year, or site type upon species diversity or abundance ($F_{2,14} = 1.72$, $P = 0.22$).

Table 2. Species diversity for each site type.

Site type	H'	J'	S	<i>n</i>	N ₁
Shaded coffee	2.4614	0.8776	17.143 (5.78)	39.286 (6.59)	12.4937
Unshaded coffee	2.6824	0.8090	28.286 (8.494)	85.143 (14.959)	16.4064
Nonagricultural	2.1974	0.9535	12.333 (8.519)	18.167 (1.566)	10.7858

Note: Shannon-Wiener (H'), Evenness (J') species richness (S and standard deviation), and abundance (*n* and standard deviation) data and Hill's diversity (N₁).

Biodiversity index data are summarised in Table 2. Average bee diversity was highest in unshaded coffee farms, followed by shaded coffee farms, and finally the nonagricultural sites. ANOVAs of diversity indices found no significant differences among site types ($F = 1.72$, $P = 0.2240$) (Table 2).

Again it was the unshaded coffee farms that had the highest average number of bee species followed by shaded coffee farms and then the nonagricultural sites. The results of the ANOVA analyses on observed species richness showed differences among sites were significant ($F_{5,14} = 3.24$, $P = 0.038$) with a highly significant effect of site type ($F_{2,14} = 7.46$, $P = 0.006$). The Bonferroni *post hoc* adjustment for multiple comparisons shows the significant difference to be primarily between unshaded and nonagricultural sites ($P = 0.007$), whereas that between coffee farm types was marginally non-significant ($P = 0.055$). Site type explained 54% of the variation in observed bee species richness among all sites in both years combined.

The rarefaction curves (Fig. 2) show that if sample size was standardised to 109 bees, the nonagricultural site would have the highest observed species richness, followed by the unshaded coffee farms and lastly the shaded coffee farms.

Average bee abundance over the two collecting seasons was highest in unshaded coffee farms, followed by the shaded coffee farms, and lastly the nonagricultural sites (Table 2). The overall ANOVA model was significant ($F_{2,14} = 15.52$, $P = 0.003$). The *post hoc* Bonferroni adjustment for multiple comparisons shows that unshaded coffee farms were significantly different from both nonagricultural sites and shaded coffee farms ($P = 0.0002$ and $P = 0.017$, respectively). Site type explained 71% of the variance in number of bee individuals collected among site types.

Average Shannon evenness (J') value was lowest for unshaded coffee farms, followed by shaded coffee farms, and then nonagricultural sites (Table 2). There was no significant overall model effect for evenness ($F_{5,14} = 1.96$, $P = 0.148$) but a marginally significant site effect ($F_{2,14} = 3.94$, $P = 0.044$). The *post hoc* Bonferroni correction for multiple comparisons shows that the only significant comparison was between unshaded coffee farms and non-agricultural sites ($P = 0.042$).

There were some significant associations among certain bee functional groups and site types (Table 3 and Fig. 4). The number of species (S) of aboveground versus ground-nesting bees was significantly associated with site type with more of the former found in unshaded coffee farms, whereas abundance (N) in these functional groups was not associated with site type. The number of social versus solitary bee individuals was associated with site type with a higher average of social bees individuals found in unshaded coffee farms, whereas the number of species was not associated with site type. Lastly, the number of small-bodied versus large-bodied bees was associated with site type but the number of species in these functional groups was not. There was no association between site type and the nester and cleptoparasitic bee functional group for either species richness or abundance. A closer examination of different bee functional groups and site types supports the idea that the distribution of bee functional groups is not random across site types and bees with different functional groups respond differently to environmental changes (Brosi *et al.* 2008).

Similarities among sites are shown graphically for number of individuals using the Jaccard and Morisita-Horn indices (Figs. 3A, 3B). Both show a similar pattern with a stronger association among agricultural sites.

Fig. 2. Rarefaction curves for each site type showing rates of species accumulations using BioDiversityPro software (McAleece *et al.* 1997). These curves were generated using randomised repeated sampling with the total number of individuals for each site (*n*).

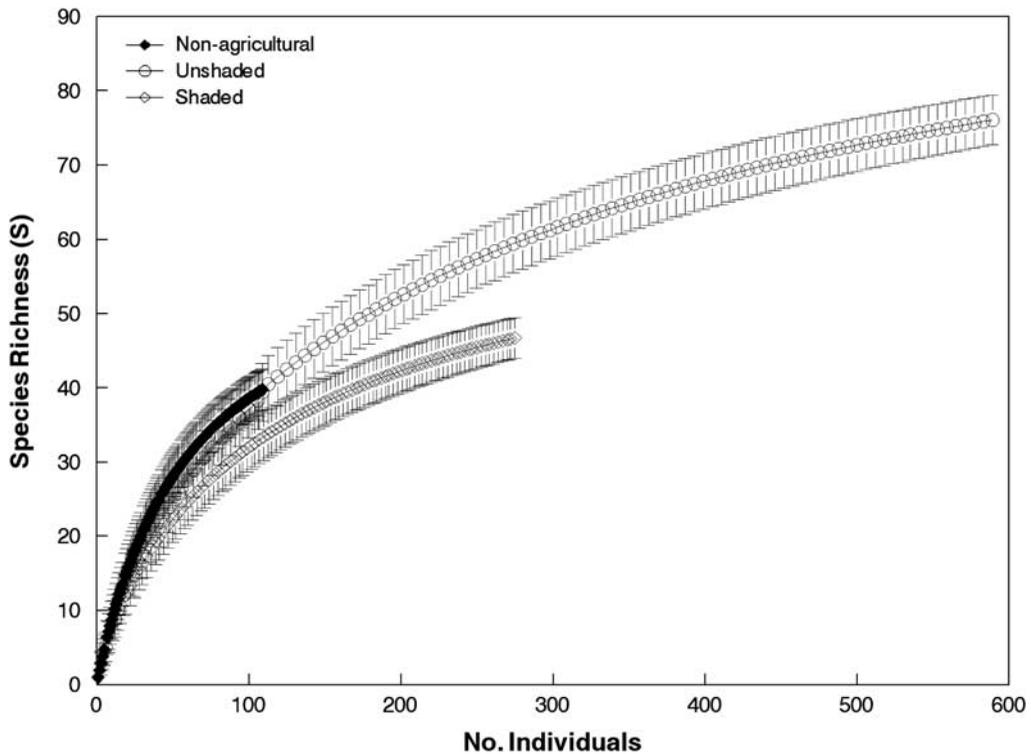


Table 3. Differences in bee functional groups and site type were determined using χ^2 -tests.

Functional group categories	Number of individuals (<i>n</i>)	Species richness (S)
Above/ground nesting bees	321/646 ($\chi^2=0.865$)	75/113 ($\chi^2=8.22^*$)
Nester/cleptoparasitic bees	963/17 ($\chi^2=0.800$)	192/13 ($\chi^2=0.344$)
Social/solitary bees	370/81 ($\chi^2=7.08^*$)	83/47 ($\chi^2=1.04$)
Small/large-bodied bees	709/270 ($\chi^2=14.0^*$)	119/83 ($\chi^2=2.85$)

Notes: This test shows whether the categorical variables (functional groups) are distributed equally across all site types (H_0). $df = 2$, $\alpha = 0.05$, and critical value = 5.99. At values >5.99 we reject the null hypothesis (H_0). Totals are reported with χ^2 -values in brackets.

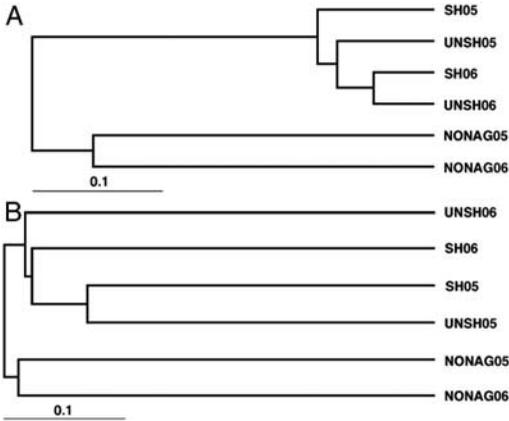
*Indicate that χ^2 values were statistically significant.

Discussion

Most previous studies of coffee agroecosystems and bees focused mainly on pollination and coffee production, not the impact of coffee agroecosystems on bees (Roubik 2002; Klein *et al.* 2003a, 2003b; Ricketts 2004; Vergara and Badano 2009) with one exception (Florez 2001). Florez (2001) studied both the effect of shade

conditions and surrounding forest fragments on bee abundance and richness in coffee farms. However, Malaise traps were not used in this study, instead, nets, aspirators, and chemical attractants were used to sample bees. He found honeybees and stingless bees (Hymenoptera: Apidae) to be the most abundant coffee flower visitors. In this study, Florez (2001) also collected halictid bees (Hymenoptera: Halictidae),

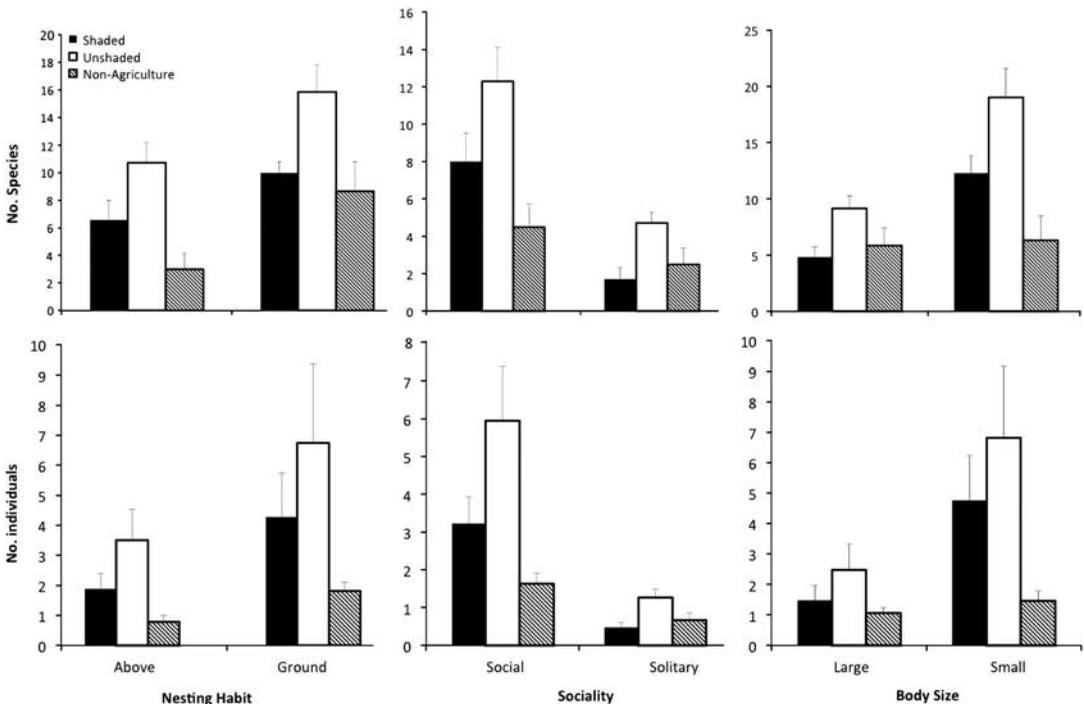
Fig. 3. (A) Clustering dendrogram for the Morisita-Horn (C_{MH}) community similarity index based on quantitative data. (B) Clustering dendrogram for the Jaccard (C_J) community similarity index based on presence/absence data. The numbers following site type refer to the collecting year. UNSH, unshaded coffee farms; SH, shaded coffee farms; NONAG, nonagricultural sites.



but the abundance of these bees was unrelated to distance from forest fragments or shade conditions. Instead, the extent of weedy plants was the strongest predictor of halictid bee abundance.

A large proportion of bee individuals (49%) collected in our study belong to the subgenus *Lasioglossum* (*Dialictus*). *Dialictus* is the largest subgenus in the family Halictidae (Moure and Hurd 1987) and are mostly ground-nesters (Moure and Hurd 1987; Cane 2001). The ground between rows of coffee plants in Costa Rican coffee farms is normally cleared of any other plants and grasses, exposing soil and thus providing a suitable habitat for many ground-nesting bees such as *Dialictus*, which seem to prefer sparsely vegetated or bare ground (Sakagami and Michener 1962; Michener 1974). *Dialictus* has never been reported as dominant in coffee agroecosystems. *Dialictus* may be potentially important in coffee pollination, as they have been observed visiting coffee flowers and are present in large numbers in coffee agroecosystems.

Fig. 4. The effect of site type on bee species richness and abundance (mean + SE) for the following functional traits: nesting habitat, sociality, and body size.



Alternatively, *Dialictus* may only be a minor coffee pollinator, primarily visiting the weeds among the coffee plants or at farm edges. Further studies may help shed light on the true role of *Dialictus* as a coffee pollinator.

Previous studies, mainly based on visual observations, have found honeybees (*Apis* species) to be dominant visitors of coffee in Brazil (Nogueira-Neto *et al.* 1959; Amaral 1972; Malerbo-Souza and Nogueira-Couto 1997), Costa Rica (Ricketts 2004), Ecuador (Veddeler *et al.* 2006, 2008), Indonesia (Klein *et al.* 2003a), Jamaica (Raw and Free 1977), Mexico (Vergara and Badano 2009), Panama (Roubik 2002), and Papua New Guinea (Willmer and Stone 1989; Martins 2007; Karanja *et al.* 2010). In almost every case, stingless bees (Hymenoptera: Apidae: Apinae: Meliponini) were also found to be major coffee visitors, second only to *Apis*. These social bees are generalist foragers that display floral constancy, a temporary preference to one single floral source, when foraging (Linsley and MacSwain 1958; Wilson and Stine 1996). This floral constancy may explain the large number of social bees found on coffee flowers during mass blooms (Free 1963; Waser 1986; Grüter *et al.* 2010). Our data showed *Dialictus* to be most abundant in coffee farms followed by stingless bees (*Trigona*). The visual observation method used in the earlier studies is potentially biased towards bees that are easier to see due to their size and foraging behaviour. *Dialictus* can be relatively difficult to see on flowers; however, passive sweep netting can yield large numbers even when visual observations fail to detect them in abundance. The limitations of visual observation could explain the relatively low number of small halictids found in previous studies. *Dialictus* are broadly polylectic (*sensu* Cane and Sipes 2006) and are known to visit various genera in the Rubiaceae among others (Moure and Hurd 1987). For this reason it would be unexpected for *Dialictus* not to visit coffee unless there was a significantly more attractive resource in the vicinity. It is worth noting that the short duration of coffee flushes would provide insufficient resources for bees to specialise upon coffee pollen, especially for social bees that are generally active for a longer proportion of the year than are solitary bees (Minckley and Roulston 2006).

Some of the differences between bee communities as recorded in this study compared to other studies may be attributed to our sampling method; ours is the first to use Malaise traps to survey bees, despite them being a commonly employed passive insect sampling method (*e.g.*, Matthews and Matthews 1971; Kerr *et al.* 2000). Some argue that it is the best method of trapping insects in tropical biodiversity surveys (Brown 2005; Missa *et al.* 2009). Compared to the sampling biases of visual observations, the Malaise trap is more likely to catch smaller bees such as *Dialictus*. Several other studies that compare insect traps confirm that the Malaise trap is relatively efficient at catching a diverse and representative array of arthropods (Oxbrough *et al.* 2010) including Hymenoptera (Noyes 1989; Bartholomew and Prowell 2005; Smith-Pardo and Gonzalez 2007).

Integrating multiple surveying methods (*e.g.*, sweep netting, Malaise trapping and pan-trapping) in diversity studies is recommended (Leong and Thorp 1999; Bartholomew and Prowell 2005; Campbell and Hanula 2007; Westphal *et al.* 2008; Missa *et al.* 2009) in order to counteract the various biases present in sampling methods (Cane 2001; Wilson *et al.* 2008). In this study, the short flowering flush of coffee plants precluded the use of more labour intensive survey methods that would have been necessary to sample so many sites simultaneously. Nonetheless, the bee community compositions we found are strikingly different from those obtained through visual observations (Nogueira-Neto *et al.* 1959; Amaral 1972; Raw and Free 1977; Willmer and Stone 1989; Malerbo-Souza and Nogueira-Couto 1997; Roubik 2002; Klein *et al.* 2003a; Ricketts 2004; Veddeler *et al.* 2006, 2008; Vergara and Badano 2009).

We found that land-use activities (agriculture) and shade trees in agroecosystems were important in shaping bee communities. Unshaded coffee sites had significantly higher observed bee species richness and a greater number of bee individuals compared to shaded coffee farms and nonagricultural sites. However, bee evenness was significantly lower for unshaded sites. This suggests that the absence of shade trees benefited only a small proportion of the regional bee fauna and the functional group analysis showed that the affected group was primarily ground nesting

bees of the subgenus *Dialictus*. The only dependent variable that did not show a significant difference between the unshaded coffee farms and the nonagricultural sites was the Shannon-Wiener biodiversity index (H'). However, the small range of Shannon-Wiener values (normally between 1.5 and 3.5 based on empirical data), often makes significant differences difficult to detect with this index (Margalef 1972; Magurran 2004).

Bee functional group analyses showed unshaded coffee farms had the highest observed species richness and abundance in every functional group category compared to shaded coffee farms and nonagricultural sites (Fig. 4). The distribution of number of species of aboveground versus ground-nesting bees was significantly associated with site type with more species (above and below ground) in the unshaded coffee farms, whereas the distribution of the individuals in these functional group categories was not. The stronger presence of ground nesting bee species in unshaded coffee farms is expected given that availability of nesting sites is higher. The presence of higher aboveground bee species in coffee farms may be due to the synchronous bloom of coffee creating a sudden abundance of nectar. Aboveground nesting bee species may not necessarily have their nests within the coffee farms but may be flying from adjacent areas to obtain floral resources.

The observed abundance of social bees was higher than expected in both the shaded and unshaded coffee farms. This is likely a result of social bee foraging behaviour. Highly social bees, such as honeybees and stingless bees, have advanced recruitment behaviours that improve their foraging efficiency (Nieh 2004). This could explain our observation of higher abundance of highly social bees without a concomitant increase in their observed species richness.

Last, the observed abundance of small and large-bodied bees was significantly different from expected values; both shaded and unshaded coffee farms had a larger number of small-bodied bees, mostly attributable to *Dialictus*. A few species clearly dominate in abundance followed by many with only a few individuals. The abundance of *Dialictus* in our samples is likely related to sociality and the availability of nesting sites. The nesting biology of *Dialictus* has not been studied for many species but most

are expected to be primitively eusocial (Danforth *et al.* 2003; Gibbs *et al.*, 2012). Social bees usually have more foraging individuals per nest than solitary ones (Michener 1974); therefore, the presence of suitable nesting sites for *Dialictus* may have led to a disproportionately large increase in *Dialictus* foragers. Although the observed species-richness distribution of small and large-bodied bees was higher in unshaded coffee farms, it was not significantly different from the expected species richness calculated based on our control sites.

If further research can link the diversity of non-*Apis* species, especially *Dialictus*, to coffee crop yield we would recommend a shift towards more bee-diverse, sustainable shade coffee farming strategies. We recommend integrating nesting habitats for native bees in coffee plantations. A diverse assemblage of shade trees could provide nesting sites for both cavity-nesting and twig-nesting bees. Bees with these nest site preferences are relatively abundant in tropical areas (Michener 1979) where coffee is grown and includes taxa important for pollination (Heard 1999; Bosch and Kemp 2002). Shade trees are also beneficial for other animal taxa (Moguel and Toledo 1999) and their use improves coffee quality (Muschler 2001). We agree with Klein *et al.* (2003a) that integrating areas of open soil into the farm matrix in a shaded system will encourage ground-nesting bees to occupy coffee farms. Specifically, *Dialictus* are known not to have very specific edaphic requirements (Kim *et al.* 2006); therefore, providing suitable nesting areas for them in agricultural settings could be an easy strategy for increasing their numbers (Williams *et al.* 2010). The majority of bee species are ground nesters but this is less so in tropical areas (Michener 1979). High humidity and heavy rainfall can waterlog soils, leading to brood mortality (Packer and Knerer 1986). High intensity land use and tree removal on coffee farms may decrease ground-level humidity (Klein *et al.* 2002) and improve conditions for ground-nesting bees. A combination of open space and shaded areas would provide nesting habitats for both bee functional groups and increase habitat complexity to benefit overall biodiversity.

To attract more bees to coffee farms, there should be minimal weed control to that other

flowers can grow alongside the coffee plants providing additional resources for bees outside the restricted periods of coffee flushes. Noncrop food plants can be essential in building and maintaining sustainable pollinator populations in agroecosystems. For example, Sheffield *et al.* (2008) found that lupine, *Lupinus polyphyllus* Lindley (Fabaceae), was an important alternative food source for pollinators in Nova Scotia, Canada apple orchards because apple trees flower for such a short period of time that pollinator populations dwindled without the alternative food source. Similar strategies might be beneficially applied to sustain pollinator populations for coffee production.

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Appendix A. List of the bees (Hymenoptera: Apoidea) found across all sites and their guild categories

	Genus and species	Aboveground/ ground-nesting	Nester/ cleptoparasite	Social/ solitary	Large/small- bodied
1	<i>Apis mellifera</i> Linnaeus (Apidae)	A	N	Soc	Lg
2	<i>Augochlora antonita</i> Michener (Halictidae)	G	N	Soc	Lg
3	<i>Augochlora aurifera</i> Cockerell (Halictidae)	G	N	Soc	Lg
4	<i>Augochlora clarki</i> Michener (Halictidae)	G	N	Soc	Lg
5	<i>Augochlora cordiaefloris</i> Cockerell (Halictidae)	G	N	Soc	Sm
6	<i>Augochlora nominata</i> Michener (Halictidae)	G	N	Soc	Lg
7	<i>Augochlora sidaefoliae</i> Cockerell (Halictidae)	A	N	Sol	Lg
8	<i>Augochlora smaragdina</i> Friese (Halictidae)	A	N	Sol	Lg
9	<i>Augochlora</i> sp. 1 (Halictidae)	A	N	Soc	Lg
10	<i>Augochlora</i> sp. 5 (Halictidae)	A	N	Soc	Lg
11	<i>Augochlora</i> sp. 8 (Halictidae)	A	N	Soc	Lg
12	<i>Augochlora</i> sp. 10 (Halictidae)	A	N	Sol	Lg
13	<i>Augochlora</i> sp. A (Halictidae)	A	N	Sol	Lg
14	<i>Augochlorella comis</i> Vachal (Halictidae)	G	N	Soc	Sm
15	<i>Augochlorella pomoniella</i> Cockerell (Halictidae)	G	N	Soc	Sm
16	<i>Augochloropsis ignita</i> Smith (Halictidae)	G	N	Sol	Lg
17	<i>Augochloropsis</i> sp. 10 (Halictidae)	G	N	Sol	Lg
18	<i>Augochloropsis</i> sp. 12 (Halictidae)	G	N	Sol	Lg
19	<i>Augochloropsis</i> sp. 5 (Halictidae)	G	N	Sol	Lg
20	<i>Augochloropsis</i> sp. 7 (Halictidae)	G	N	Sol	Lg
21	<i>Augochloropsis vesta</i> Smith (Halictidae)	G	N	Sol	Lg
22	<i>Bombus pullatus</i> Franklin (Apidae)		N	Soc	Lg
23	<i>Caenaugochlora</i> sp. 1 (Halictidae)	G	N		Lg
24	<i>Caenaugochlora</i> sp. 2 (Halictidae)	G	N		Lg
25	<i>Caenaugochlora</i> sp. 3 (Halictidae)	G	N		Lg
26	<i>Calliopsis hondurasica</i> Cockerell (Andrenidae)	G	N	Sol	Lg
27	<i>Ceratina buscki</i> Cockerell (Apidae)	A	N	Sol	Sm
28	<i>Ceratina eximia</i> Smith (Apidae)	A	N	Sol	Sm
29	<i>Ceratina</i> sp. AB (Apidae)	A	N	Sol	Sm
30	<i>Ceratina</i> sp. X (Apidae)	A	N	Sol	Sm
31	<i>Ceratina</i> sp. 9 (Apidae)	A	N	Sol	Sm
32	<i>Ceratina</i> sp. 12 (Apidae)	A	N	Sol	Sm
33	<i>Ceratina</i> sp. 2 (Apidae)	A	N	Sol	Sm
34	<i>Ceratina</i> sp. 3 (Apidae)	A	N	Sol	Sm
35	<i>Ceratina</i> sp. 4 (Apidae)	A	N	Sol	Sm
36	<i>Chilicola</i> sp. (Colletidae)	A	N	Sol	Sm
37	<i>Exomalopsis mexicana</i> Cresson (Apidae)	G	N	Soc	Lg
38	<i>Exomalopsis similis</i> Cresson (Apidae)	G	N	Soc	Sm
39	<i>Exomalopsis analis</i> Spinola (Apidae)	G	N	Soc	Lg
40	<i>Habralictus</i> sp. (Halictidae)	G	N	Sol	Sm
41	<i>Halictus hesperus</i> Smith (Halictidae)	G	N	Soc	Lg
42	<i>Halictus ligatus</i> Say (Halictidae)	G	N	Soc	Lg
43	<i>Hylaeus</i> sp. (Colletidae)	A	N	Sol	Sm
44	<i>Lasioglossum</i> sp. 1 (Halictidae)	G	N		Sm
45	<i>Lasioglossum (Dialictus) cupreicolle</i> Friese (Halictidae)	G	N		Sm
46	<i>Lasioglossum (Dialictus) picadense</i> Strand (Halictidae)	G	N		Sm
47	<i>Lasioglossum (Dialictus)</i> sp. 16 (Halictidae)	G	N		Sm
48	<i>Lasioglossum (Dialictus)</i> sp. 19 (Halictidae)	G	N		Sm

Appendix A. Continued

Genus and species		Aboveground/ ground-nesting	Nester/ cleptoparasite	Social/ solitary	Large/small- bodied
49	<i>Lasioglossum (Dialictus)</i> sp. 27 (Halictidae)	G	N		Sm
50	<i>Lasioglossum (Dialictus)</i> sp. 28 (Halictidae)	G	N		Sm
51	<i>Lasioglossum (Dialictus)</i> sp. 29 (Halictidae)	G	N		Sm
52	<i>Lasioglossum (Dialictus)</i> sp. 3 (Halictidae)	G	N		Sm
53	<i>Lasioglossum (Dialictus)</i> sp. 3 nr (Halictidae)	G	N		Sm
54	<i>Lasioglossum (Dialictus)</i> sp. 36 nr (Halictidae)	G	N		Sm
55	<i>Lasioglossum (Dialictus)</i> sp. 38 (Halictidae)	G	N		Sm
56	<i>Lasioglossum (Dialictus)</i> sp. 39 (Halictidae)	G	N		Sm
57	<i>Lasioglossum (Dialictus)</i> sp. 4 (Halictidae)	G	N		Sm
58	<i>Lasioglossum (Dialictus)</i> sp. 45 nr (Halictidae)	G	N		Sm
59	<i>Lasioglossum (Dialictus)</i> sp. 46 (Halictidae)	G	N		Sm
60	<i>Lasioglossum (Dialictus)</i> sp. 51 (Halictidae)	G	N		Sm
61	<i>Lasioglossum (Dialictus)</i> sp. A (Halictidae)	G	N		Sm
62	<i>Lasioglossum (Dialictus)</i> sp. AAA (Halictidae)	G	N		Sm
63	<i>Lasioglossum (Dialictus) strigosigena</i> Michener (Halictidae)	G	N		Sm
64	<i>Lasioglossum (Dialictus)</i> sp. unknown (Halictidae)	G	N		Sm
65	<i>Lasioglossum (Evylaeus)</i> sp. B (Halictidae)	G	N		Lg
66	<i>Lasioglossum (Evylaeus)</i> sp. 1 (Halictidae)	G	N		Lg
67	<i>Lasioglossum (Evylaeus)</i> sp. 11 (Halictidae)	G	N		Sm
68	<i>Lasioglossum (Evylaeus)</i> sp. 3 (Halictidae)	G	N		Sm
69	<i>Lasioglossum (Evylaeus)</i> sp. 8 (Halictidae)	G	N		Lg
70	<i>Megachile</i> sp. 3 (Megachilidae)	A	N	Sol	Lg
71	<i>Megammaton</i> sp. (Halictidae)	G	N		Lg
72	<i>Melipona fasciata</i> Latreille (Apidae)	A	N	Soc	Lg
73	<i>Melissodes</i> sp. A (Apidae)	G	N	Sol	Lg
74	<i>Melissodes</i> sp. B (Apidae)	G	N	Sol	Lg
75	<i>Melissodes</i> sp. C (Apidae)	G	N	Sol	Lg
76	<i>Melissodes</i> sp. D (Apidae)	G	N	Sol	Lg
77	<i>Melissodes tepaneca</i> Cresson (Apidae)	G	N	Sol	Lg
78	<i>Nannotrigona mellaria</i> Smith (Apidae)	A	N	Soc	Sm
79	<i>Neocorynura</i> sp. (Halictidae)	G	N		Sm
80	<i>Osiris panamensis</i> Cockerell (Apidae)		C		Sm
81	<i>Paratetrapedia calcarata</i> Cresson (Apidae)	G	N	Sol	Lg
82	<i>Paratetrapedia</i> sp. A (Apidae)	G	N	Sol	Lg
83	<i>Paratrigona opaca</i> Cockerell (Apidae)	A	N	Soc	Sm
84	<i>Paratrigona</i> sp. B (Apidae)	A	N	Soc	Sm
85	<i>Partamona cupira</i> Smith (Apidae)	A	N	Soc	Sm
86	<i>Pereirapis</i> sp. (Halictidae)	A	N	Soc	Sm
87	<i>Plebeia frontalis</i> Friese (Apidae)	A	N	Soc	Sm
88	<i>Plebeia jatiformis</i> Cockerell (Apidae)	A	N	Soc	Sm
89	<i>Plebeia</i> sp. A (Apidae)	A	N	Soc	Sm
90	<i>Plebeia</i> sp. B (Apidae)	A	N	Soc	Sm
91	<i>Plebeia tica</i> Wille (Apidae)	A	N	Soc	Sm
92	<i>Pseudoaugochlora graminea</i> Fabricius (Halictidae)	G	N	Soc	Lg
93	<i>Ptiloglossa</i> sp. (Colletidae)	G	N	Sol	Lg
94	<i>Scaptotrigona pectoralis</i> Dalla Torre (Apidae)	A	N	Soc	Sm
95	<i>Scaptotrigona subobscuripennis</i> Schwarz (Apidae)	A	N	Soc	Lg

Appendix A. *Continued*

Genus and species		Aboveground/ ground-nesting	Nester/ cleptoparasite	Social/ solitary	Large/small- bodied
96	<i>Scaura latitarsis</i> Friese (Apidae)	A	N	Soc	Sm
97	<i>Sphecodes</i> sp. unknown (Halictidae)		C		Sm
98	<i>Sphecodes</i> sp. 1 (Halictidae)		C		Sm
99	<i>Sphecodes</i> sp. 2 (Halictidae)		C		Sm
100	<i>Sphecodes</i> sp. 3 (Halictidae)		C		Sm
101	<i>Sphecodes</i> sp. A (Halictidae)		C		Sm
102	<i>Sphecodes</i> sp. B (Halictidae)		C		Sm
103	<i>Temnosoma smaragdinum</i> Smith (Halictidae)		C		Lg
104	<i>Thygater analis</i> LePeletier (Apidae)	G	N	Sol	Lg
105	<i>Tetragonisca angustula</i> Latreille (Apidae)	A	N	Soc	Sm
106	<i>Tetragonisca buchwaldi</i> Friese (Apidae)	A	N	Soc	Sm
107	<i>Trigona corvina</i> Cockerell (Apidae)	A	N	Soc	Sm
108	<i>Trigona fulviventris</i> Guérin-Méneville (Apidae)	A	N	Soc	Lg
109	<i>Trigona fuscipennis</i> Friese (Apidae)	A	N	Soc	Sm
110	<i>Trigona silvestriana</i> Vachal (Apidae)	A	N	Soc	Lg
111	<i>Trigona amalthea</i> Olivier (Apidae)	A	N	Soc	Sm
112	<i>Geotrigona</i> sp. (Apidae)	G	N	Soc	Sm
113	<i>Trigonisca schulthessi</i> Friese (Apidae)	A	N	Soc	Sm

Note: Unknown bee species guild categories were left blank and excluded from the guild analyses.

Appendix B. List of the bee abundances found among all sites in decreasing order.

Genus	Species	Total	Total (%)	Site type		
				Shaded coffee	Unshaded coffee	Nonagricultural
<i>Lasioglossum (Dialictus)</i>	sp. 3	201	20.51	52	145	4
<i>Lasioglossum (Dialictus)</i>	<i>cupreicolle</i>	74	7.55	35	39	0
<i>Trigona</i>	<i>fulviventris</i>	74	7.55	20	49	5
<i>Lasioglossum (Dialictus)</i>	sp. 27	56	5.71	25	24	7
<i>Lasioglossum (Dialictus)</i>	sp. 28	33	3.37	7	22	4
<i>Lasioglossum (Dialictus)</i>	sp. 39	30	3.06	5	15	10
<i>Apis</i>	<i>mellifera</i>	29	2.96	6	22	1
<i>Pereirapis</i>	sp.	25	2.55	9	13	3
<i>Plebeia</i>	<i>frontalis</i>	22	2.24	8	13	1
<i>Lasioglossum (Dialictus)</i>	sp. 29	21	2.14	8	11	2
<i>Paratrigona</i>	<i>opaca</i>	18	1.84	4	11	3
<i>Augochlora</i>	<i>aurifera</i>	16	1.63	6	8	2
<i>Augochlora</i>	<i>cordiaefloris</i>	16	1.63	7	7	2
<i>Augochlorella</i>	<i>comis</i>	16	1.63	5	7	4
<i>Lasioglossum (Dialictus)</i>	sp. 19	16	1.63	7	8	1
<i>Partamona</i>	<i>cupira</i>	16	1.63	4	11	1
<i>Trigona</i>	<i>amalthea</i>	15	1.53	0	15	0
<i>Melipona</i>	<i>fasciata</i>	14	1.43	4	10	0
<i>Augochlora</i>	<i>nominata</i>	13	1.33	3	8	2
<i>Lasioglossum (Evylaeus)</i>	sp. 8	13	1.33	5	8	0
<i>Lasioglossum (Dialictus)</i>	sp. 4	11	1.12	3	6	2
<i>Trigona</i>	<i>fuscipennis</i>	10	1.02	0	10	0
<i>Augochloropsis</i>	sp. 12	6	0.61	1	5	0

Appendix B. Continued

Genus	Species	Total	Total (%)	Site type		
				Shaded coffee	Unshaded coffee	Nonagricultural
<i>Lasioglossum (Dialictus)</i>	sp. 36 near	6	0.61	1	5	0
<i>Paratrigona</i>	sp. B	6	0.61	0	3	3
<i>Plebeia</i>	<i>jatiformis</i>	6	0.61	2	4	0
<i>Augochlora</i>	<i>antonita</i>	5	0.51	0	2	3
<i>Augochlora</i>	<i>clarki</i>	5	0.51	2	1	2
<i>Augochlora</i>	sp. 1	5	0.51	2	1	2
<i>Caenaugochlora</i>	sp. 1	5	0.51	0	2	3
<i>Halictus</i>	<i>hesperus</i>	5	0.51	1	4	0
<i>Lasioglossum (Dialictus)</i>	<i>unknown</i>	5	0.51	3	2	0
<i>Lasioglossum (Evylaeus)</i>	sp. 1	5	0.51	1	3	1
<i>Sphecodes</i>	sp. B	5	0.51	2	2	1
<i>Augochlora</i>	<i>sidaefoliae</i>	4	0.41	0	2	2
<i>Augochloropsis</i>	<i>ignita</i>	4	0.41	0	2	2
<i>Calliopsis</i>	<i>hondurasica</i>	4	0.41	0	4	0
<i>Habralictus</i>	sp.	4	0.41	0	4	0
<i>Melissodes</i>	sp. D	4	0.41	0	3	1
<i>Nannotrigona</i>	<i>mellaria</i>	4	0.41	3	1	0
<i>Paratetrapedia</i>	<i>calcarata</i>	4	0.41	2	1	1
<i>Tetragonisca</i>	<i>angustula</i>	4	0.41	1	3	0
<i>Augochloropsis</i>	sp. 7	3	0.31	0	2	1
<i>Lasioglossum (Dialictus)</i>	sp. 46	3	0.31	1	2	0
<i>Lasioglossum (Dialictus)</i>	sp. AAA	3	0.31	0	2	1
<i>Sphecodes</i>	sp. A	3	0.31	0	3	0
<i>Tetragonisca</i>	<i>buchwaldi</i>	3	0.31	0	2	0
<i>Thygater</i>	<i>analisis</i>	3	0.31	0	2	1
<i>Trigona</i>	<i>corvina</i>	3	0.31	2	1	0
<i>Trigona</i>	<i>silvestriana</i>	3	0.31	1	2	0
<i>Ceratina</i>	<i>eximia</i>	2	0.20	0	2	0
<i>Ceratina</i>	sp. AB	2	0.20	1	1	0
<i>Ceratina</i>	sp. X	2	0.20	1	1	0
<i>Exomalopsis</i>	<i>analisis</i>	2	0.20	0	1	1
<i>Lasioglossum (Dialictus)</i>	<i>picadense</i>	2	0.20	0	1	1
<i>Lasioglossum (Dialictus)</i>	sp. 3 near	2	0.20	0	2	0
<i>Lasioglossum (Dialictus)</i>	sp. 51	2	0.20	0	1	1
<i>Lasioglossum (Dialictus)</i>	<i>strigosigena</i>	2	0.20	0	2	0
<i>Lasioglossum (Evylaeus)</i>	sp. B	2	0.20	0	1	1
<i>Megammaton</i>	sp.	2	0.20	0	0	2
<i>Melissodes</i>	sp. A	2	0.20	0	2	0
<i>Melissodes</i>	<i>tepaneca</i>	2	0.20	1	1	0
<i>Neocorynura</i>	sp.	2	0.20	0	1	1
<i>Plebeia</i>	sp. A	2	0.20	1	1	0
<i>Plebeia</i>	sp. B	2	0.20	1	1	0
<i>Scaptotrigona</i>	<i>pectoralis</i>	2	0.20	1	1	0
<i>Scaptotrigona</i>	<i>subobscuripennis</i>	2	0.20	0	2	0
<i>Sphecodes</i>	sp. unknown	2	0.20	1	1	0
<i>Sphecodes</i>	sp. 1	2	0.20	0	1	1
<i>Temnosoma</i>	<i>smaragdinum</i>	2	0.20	0	1	1
<i>Augochlora</i>	<i>smaragdina</i>	1	0.10	0	1	0
<i>Augochlora</i>	sp. 5	1	0.10	1	0	0

Appendix B. Continued

Genus	Species	Total	Total (%)	Site type		
				Shaded coffee	Unshaded coffee	Nonagricultural
<i>Augochlora</i>	sp. 8	1	0.10	1	0	0
<i>Augochlora</i> (<i>Augochlora</i>)	sp. 10	1	0.10	1	0	0
<i>Augochlora</i> (<i>Mycterochlora</i>)	sp. A	1	0.10	0	1	0
<i>Augochlorella</i>	<i>Pomoniella</i>	1	0.10	0	0	1
<i>Augochloropsis</i>	sp. 10	1	0.10	0	1	0
<i>Augochloropsis</i>	sp. 5	1	0.10	0	0	1
<i>Bombus</i>	<i>pullatus</i>	1	0.10	0	1	0
<i>Caenaugochlora</i>	sp. 2	1	0.10	0	1	0
<i>Caenaugochlora</i>	sp. 3	1	0.10	0	0	1
<i>Ceratina</i> (<i>Calloceratina</i>)	sp. 9	1	0.10	1	0	0
<i>Ceratina</i> (<i>Ceratina</i>)	sp. 12	1	0.10	1	0	0
<i>Ceratina</i> (<i>Ceratina</i>)	sp. 2	1	0.10	1	0	0
<i>Ceratina</i> (<i>Ceratina</i>)	sp. 3	1	0.10	0	1	0
<i>Ceratina</i> (<i>Zadontomerus</i>)	sp. 4	1	0.10	1	0	0
<i>Chilicola</i>	sp.	1	0.10	0	1	0
<i>Exomalopsis</i>	<i>mexicana</i>	1	0.10	0	0	1
<i>Exomalopsis</i>	<i>similis</i>	1	0.10	0	1	0
<i>Geotrigona</i>	sp.	1	0.10	0	1	0
<i>Halictus</i>	<i>ligatus</i>	1	0.10	1	0	0
<i>Hylaeus</i> (<i>Hylaeopsis</i>)	sp.	1	0.10	0	1	0
<i>Lasioglossum</i>	sp. 1	1	0.10	0	1	0
<i>Lasioglossum</i> (<i>Dialictus</i>)	sp. 16	1	0.10	1	0	0
<i>Lasioglossum</i> (<i>Dialictus</i>)	sp. 38	1	0.10	0	0	1
<i>Lasioglossum</i> (<i>Dialictus</i>)	sp. 45 near	1	0.10	0	1	0
<i>Lasioglossum</i> (<i>Dialictus</i>)	sp. A	1	0.10	0	1	0
<i>Lasioglossum</i> (<i>Evylaeus</i>)	sp. 11	1	0.10	0	1	0
<i>Lasioglossum</i> (<i>Evylaeus</i>)	sp. 3	1	0.10	0	0	1
<i>Megachile</i>	sp. 3	1	0.10	1	0	0
<i>Melissodes</i>	sp. B	1	0.10	0	0	1
<i>Melissodes</i>	sp. C	1	0.10	0	1	0
<i>Osiris</i>	<i>panamensis</i>	1	0.10	0	1	0
<i>Paratetrapedia</i>	sp. A	1	0.10	0	1	0
<i>Scaura</i>	<i>latitarsis</i>	1	0.10	0	1	0
<i>Plebeia</i>	<i>tica</i>	1	0.10	1	0	0
<i>Pseudoaugochlora</i>	<i>graminea</i>	1	0.10	0	1	0
<i>Ptilglossa</i>	sp.	1	0.10	0	0	1
<i>Sphecodes</i>	sp. 2	1	0.10	1	0	0
<i>Sphecodes</i>	sp. 3	1	0.10	0	1	0
<i>Trigonisca</i>	<i>schulthessi</i>	1	0.10	1	0	0
Total		980	100	275	596	109