Research

Contrasting bee foraging in response to resource scale and local habitat management

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It is hypothesized that two main factors drive the foraging patterns of native and exotic species: food resource availability and habitat composition. These factors are particularly relevant for native bees and exotic honeybees, essential crop pollinators that are sensitive to floral resources and habitat management, and that have recently exhibited alarming population declines. Mechanisms driving native and exotic bee foraging patterns may critically depend on floral resource availability and habitat composition, yet the impacts of these factors on bee foraging have never been simultaneously analyzed. In a coffee producing region in southern Mexico, we investigated the influence of coffee floral resource levels and habitat management on native and exotic bee foraging. We measured the amount of flowering coffee available at multiple spatial scales within two distinct agroforestry habitat types (high-shade and low-shade coffee) and recorded visits to coffee flowers, documenting bee species, visit duration and visit frequency. We observed a significantly greater number of visits in high-shade coffee habitats than in low-shade coffee habitats for both native and exotic bees. In high-shade coffee habitats, native solitary bee and native social bee visitation decreased significantly in response to increasing floral resource availability, exhibiting a 'dilution effect' at the smallest spatial scale. In contrast, in low-shade coffee habitats, Africanized honeybees exhibited a 'concentration effect', increasing visitation significantly in response to increasing floral resource availability at the largest spatial scale. This study is the first to show that foraging patterns of native bees and exotic honeybees contrast in response to floral resource level and scale and that this response is mediated by the vegetation management of the local habitat.

Foraging animals use a number of environmental cues in order to conserve energy and maximize resource acquisition. Because most habitats have resources that are distributed in a patchy manner, depending on scale, the ability to discern between low and high quality resource sites is an essential skill for many foraging communities (Schoener 1971, Mangel and Clark 1986, Fauchald and Tveraa 2006). Communities that are dependent on ephemeral resources may be particularly reliant on their foraging abilities, especially if there is an abundance of foragers and a limited number of resources. One such example is the native and exotic bee community, which is uniquely sensitive to food resource availability due to its dependence on pollen and nectar, the former of which is provisioned to offspring and the latter of which is mostly consumed by bees in order to sustain their high metabolic demands (Kunin 1993, Michener 2000, Potts et al. 2003).

Bee foraging is of great ecological and economic importance since the subsequent act of pollination provides an essential reproductive service, benefiting cultivated plants and their consumers (Daily 1997, Kremen et al. 2007, Klein et al. 2008). Approximately 35% of the global food supply relies on at least partially pollinator-dependent plants (reviewed by Klein et al. 2007). Most agricultural systems are frequented and serviced by native bees and exotic honeybees; however, recent worldwide declines in honeybee populations have drawn greater attention to the study of wild native bees as crop pollinators (Kremen et al. 2002, Steffan-Dewenter et al. 2005, Winfree et al. 2007). For many crops, native bees alone contribute substantially to increased fruit yields, highlighting the ecosystem service provided by native bees (Kremen et al. 2004, Klein et al. 2007, Winfree et al. 2007).

Bee foraging is especially critical to coffee agroforestry systems. Coffee agroforestry systems are ubiquitous across the tropics (Perfecto et al. 1996, Donald 2004) and many varieties of coffee are partially self-incompatible and exhibit greater fruit set when visited by diverse native bee communities (Klein et al. 2003a, Ricketts et al. 2004). Foraging bee diversity and coffee pollination are heavily influenced by the local agroforesty landscape (reviewed by Klein et al. 2007, Ricketts et al. 2008), yet it is unknown how local agroforestry management influences bee foraging responses. One previous study has revealed that the bee community exhibits complex and contrasting foraging responses to coffee flowering, depending on the spatial scale examined (Veddeler et al. 2006). At the largest spatial scale (field), bee foragers exhibit a 'dilution effect',

decreasing visitation with increasing floral resource availability; while at the smallest scale (bush), bee foragers exhibit a 'concentration effect', increasing visitation with increasing floral resource availability (Veddeler et al. 2006). These results were among the first to provide evidence that bee foraging communities could exhibit contrasting foraging responses depending on spatial scale. However, foraging responses may differ fundamentally between native and exotic species in a community and between habitat types, and understanding these differences may yield insight into the mechanisms driving contrasting foraging patterns.

Since the 1970's, fragmented neotropical landscapes have been dominated by exotic Africanized honeybees, and many studies have suggested that the success of these exotic bees lies in their recruitment-based foraging strategy and versatile nesting preferences (Roubik 1980, Aizen and Feinsinger 1994, Brosi et al. 2008). Native social bees also exhibit advanced foraging strategies which may have evolved specifically for the exploitation of mass-flowering patches (Dornhaus and Chittka 1999, 2004, Raine et al. 2006). However native social bees, native solitary bees and honeybees interpret the landscape at different scales (Steffan-Dewenter et al. 2002) and respond differently to local habitat conditions, such as light cover, floral density and distance to the nearest forest fragment (Klein et al. 2002, 2003c, Potts et al. 2003, Ricketts 2004). Thus, the foraging patterns exhibited by the bee community may depend critically on bee community composition and local habitat composition. In this study, we investigate the foraging responses of native bees and exotic Africanized honeybees within Mexican coffee agroforestry systems in order to assess the influence of resource availability, resource scale and local habitat composition on bee foraging patterns.

Material and methods

Study area

The study was conducted in Nueva Alemania, a coffee-growing region located in the southern highlands of Chiapas, Mexico ($92°18'55''$ to $92°20'24''$W, $15°09'38''$ to $15°10'48''$N) at an altitude ranging between 1125 and 1300 m. In the study region, *Coffea arabica* and *Coffea robusta* are planted in the understorey (approximately 4000 coffee bushes per hectare) under a canopy of overstorey trees that vary in density and diversity, based on the vegetation management style (Perfecto et al. 1996, Moguel and Toledo 1999, Soto-Pinto et al. 2001). The study site is composed of a low-shade coffee region, with a mean of 16.1 trees ha^{-1} (12.1 species ha^{-1}), resulting in 20–30% canopy cover, and a high-shade coffee region, with a mean of 42.3 trees ha^{-1} (18.4 species ha^{-1}), resulting in 55–65% canopy cover. Located between the two regions is a small (approximately 20 ha) uncut forest reserve, La Montañita. The two coffee regions investigated are extremely large; each is greater than 300 ha, and each equal in size to a dozen or more coffee farms typical of the Soconusco area. Also located between the two coffee regions is a managed Africanized honeybee apiary, which was constructed in November of 2004. The apiary contains an average of 70–100 colonies and had 83 domesticated colonies at the time of the study. All nests in the apiary were obtained by trapping for feral Africanized honeybees across the study region for three years before the study. Throughout the 2006 experimental season, nests found within the study site were continuously trapped and added to the apiary. Few feral nests (2) were found in the coffee fields after the intensive collection between 2002 and 2005.

Coffee plants were observed across coffee agroforestry habitat types between 20 and 23 April 2006, during the peak coffee bloom, which takes place shortly after the first major winter rainfall. Coffee bushes appear to flower almost uniformly at 2–3 km scales, but at smaller scales (bush, 5 m, 10 m and 100 m) flowering occurs in a patchy manner over the three day flowering period. This is likely due to microsite variations in soil moisture levels. Though coffee bushes were in full flower during the study season, the flowering of understorey herbs in both habitats was extremely low (less than 0.01% of the ground covering plants in flower) and was therefore not included in the study.

Bee observations

Within each coffee system, observation sessions were made between the 8:00 and 14:00, when bee foraging activity was highest. The site of each observation session was randomly selected (>300 m away from any previously monitored site), and temperature, distance from the forest, and distance from the apiary were recorded at each site (distances ranged between 100–2000 m from both the forest and apiary). The closest bush to the randomly selected point was chosen for bee observations, and four fully flowering branches (minimum of 20 blossoms) were randomly chosen on the shrub. At each site, the four branches were observed for 15 min at a time, and observations of visiting bee species, duration of visit, and number of flowers visited were noted. In addition, resource levels for each observation site were measured at four scales; shrub, 5, 10 and 100 m scales. Given the large variation in branch number per bush, we measured the proportion of fully flowering branches per bush, while for the 5, 10 and 100 m scale, the proportion of coffee bushes with greater than ¼ of their branches fully flowering was measured within a 5, 10 and 100 m radius from the observation point, respectively.

Within the two agroforestry habitat types, 124 observation sessions were conducted, and 499 bee visits were recorded. When possible, bees were captured after the observation period for identification (96 specimens), and we referred to collections at El Colegio de la Frontera Sur in Tapachula, Mexico and T. Griswold, at the USDA Bee Lab in Logan, Utah, for guidance with identifications.

Statistical analyses

To meet conditions of normality, visit number and species number per observation period were square-root transformed and proportions of floral resource at all scales were arcsin-square-root-transformed for all regression analyses (Sokal 1995). Regression analyses using absolute floral

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Table 1. Pearson correlation coefficient matrix of floral resources at bush, 5, 10 and 100 m scales. ****p <0.0001.

	5 m scale	10 m scale	100 m scale
Bush scale	0.2874****	0.4711****	0.0160
5 m scale		0.7104****	0.3831****
10 m scale			0.3615****

resource values (not proportions) yielded the same results. All statistical analyses were conducted with the software R (R Development Core Team, URL <www.r-project. org>). Species accumulation and estimation curves were generated using the Chao1 estimator (Chao 1987), utilizing the software, EstimateS (Colwell and Coddington 1994). Variation in resources levels are correlated across a range of spatial scales (Table 1). Therefore, linear regressions for bee visitation and bee species richness were independently examined for each resource scale. For further analysis, all bee visits were classified into bee groups based on foraging strategy (social vs solitary) and origin (native vs exotic Africanized honeybee), so that three bee functional groups remained: 1) native solitary bees, 2) native social bees, and 3) exotic Africanized honeybees. To examine the influence of all factors on the number of visiting bees within each functional group, we utilized an analysis of covariance, ANCOVA, using a non-sequential test for examining individual coefficients (also known as a type III sum of squares test). The covariates include (1) floral resource levels, (2) cloud cover, (3) temperature, (4) distance from the forest, and (5) distance from the apiary. The fixed factors include (1) vegetation management, and (2) bee functional group. We utilized an ANCOVA because it provides a descriptive comparison between the visitation levels across different habitats and between functional groups, and can thus test hypotheses concerning the significant differences between these two categorical variables. Also, the ANCOVA, unlike the analysis of variance (ANOVA), disentangles differences in the effects of the covariates, which range in value, from the fixed factors. The ANCOVA is based on exact F and t distributions for testing the significance of factors and covariates, yielding measures of R^2 that can be interpreted as the percentage of variance explained (Faraway 2005). The model error was independent and normally distributed.

Results

Visitation and species richness

Across both habitat types, bee visitation per observation period did not correlate with any measures of temperature (mean = 29.1°C, SE = 0.33), distance from the forest (mean = 497 m, SE = 20.2), or distance from the apiary (mean = 1067 m, SE = 24.9 m). Visitation was significantly influenced by bee foraging group, habitat quality, and resource levels at all scales, and the model of bee visitation in both habitat types was best fit for the 10 m resource scale (ANCOVA, Table 2).

On average there were 22.3 (SE = 13.8) branches in flower per bush across both habitats, and the average

Table 2. Results of repeated-measures ANCOVA, testing the effects of floral resource levels (at 10 m scale), cloud cover, temperature, distance to the forest, vegetation management (high or low-shade coffee), and bee group (honeybees, native social bees, native solitary bees) on the number of bee visits per observation period. The variables floral resource levels, cloud cover, temperature, distance to forest, and distance to apiary were treated as covariates, while vegetation management and bee group were treated as main effects. Though all interaction terms were originally tested, for simplicity, only the significant interaction term is included in this model. All data were arcsin(sqrt(x)) transformed prior to analysis. n = 375 observation periods, R^2 = 0.5753.

Source	DF	F	p
Covariates			
floral resource levels	1	7.39	0.006
cloud cover	1	0.37	0.541
temperature	1	2.14	0.144
forest distance	1	3.12	0.088
apiary distance	1	5.09	0.558
Main effects			
vegetation management	1	147.66	<0.0001
bee foraging group	2	46.42	<0.0001
Significant interaction terms			
floral resource levels × bee foraging group	2	73.67	<0.0001
Error	364	–	–

number of branches in flower per bush was not significantly different between habitat types (t-test, p = 0.23, n = 67 and 57). We did not observe any aggressive physical interactions between bee visitors. Bee visitation at coffee bushes was significantly higher in high-shade coffee habitats, with a mean of 4.61 visits per observation period (SE = 0.46), compared to a mean of 1.56 visits per observation period (SE = 0.27) in low-shade coffee habitats (t-test, p < 0.0001, n = 67 and 57). The overall species richness of bee visitors was also greater in high-shade habitats (Table 3, Fig. 1). Estimated species richness converged on observed species richness curves, with an estimated number of 17.5 species in high-shade habitats and an estimated number of 8.17 species in low-shade coffee habitats. Shannon–Wiener diversity indices reflected the same patterns, with a value of 1.54 in high-shade habitats and 0.62 in low-shade habitats.

Visit duration was not significantly different between high-shade and low-shade habitats for native solitary bees (t-test, p = 0.61, n = 12 and 3), native social bees (t-test, p = 0.49, n = 75 and 12), or Africanized honeybees, t-test, (p = 0.70, n = 270 and 119). However, the number of visits was significantly greater in high-shade habitats than low-shade habitats, for native solitary bees (t-test, p = 0.048, n = 67 and 57), native social bees (t-test, p < 0.0001, n = 67 and 57), and Africanized honeybees (t-test, p = 0.002, n = 67 and 57) (Fig. 2A–C). The proportion of visits conducted by solitary bees was not significantly different between the two habitat types (t-test, p = 0.911, n = 67 and 57, Fig. 2D). The proportion of visits conducted by social native bees was significantly higher in high-shade habitats (t-test, p = 0.048, n = 67 and 57, Fig. 2E), while the proportion of Africanized honeybee visits was slightly higher in low-shade habitats (t-test, p = 0.204, n = 67 and 57, Fig. 2F).

Table 3. Species present in high-shade coffee (HSC) and low-shade coffee (LSC) agroforestry habitats and their functional group (FG), classified as an Africanized honeybee (AHB), native solitary bee (NSOL), or native social bee (NSOC).

Species	Family	LSC	HSC	FG
Apis mellifera, scutellata	Apidae	x	X	AHB
Ceratina eximia	Apidae		X	NSOL
Ceratina ignara	Apidae		X	NSOL
Ceratina sp. 1	Apidae		X	NSOL
Eulaema cingulata	Apidae	x	x	NSOC
Melipona beecheii	Apidae		x	NSOC
Nanotrigona testaceicornis	Apidae	x	x	NSOC
Plebia sp. 1	Apidae	x	x	NSOC
Scaptotrigona mexicana	Apidae		x	NSOC
Trigona fulviventris	Apidae	x	x	NSOC
Xylocopa tabaniformis, tabaniformis	Apidae	x	x	NSOL
Augochlora aurifera	Halictidae		x	NSOC
Augochlora nigrocyanea	Halictidae		x	NSOC
Dialictus sp. 1	Halictidae	x		NSOC
Dialictus sp. 2	Halictidae		x	NSOC
Halictus hesperus	Halictidae		x	NSOC
Halictus sp. 1	Halictidae	x		NSOC

Foraging in response to resource scale

Bee functional groups displayed marked differences in visitation based on resource levels at multiple scales. In addition, bee functional groups exhibited contrasting foraging responses between the two habitat types.

Native solitary bees
In low-shade coffee habitats, native solitary bees did not increase or decrease visitation levels in response to floral resources at any scale. In contrast, within high-shade habitats native solitary bees showed a significant decrease in visitation with increasing floral resources at the 5 and 10 m resource scale, with strongest effects at the 10 m scale ($F_{1,65} = 8.454$, $r^2 = 0.112$, $p = 0.005$, $y = -0.601x + 0.539$, Fig. 3A).

Native social bees
In low-shade coffee habitats, native social bees did not increase or decrease visitation levels in response to floral resources at any scale. In contrast, within the high-shade habitats, native social bees showed a significant decrease in visitation with increasing floral resources only at the 5 and

Figure 1. Species richness of bee visitors in high-shade coffee (HSC) and low-shade coffee (LSC) habitats. Error bars represent observed SD (Colwell and Coddington 1994).

10 m resource scale, with strongest effects at the 10 m scale ($F_{1,65} = 6.756$, $r^2 = 0.093$, $p = 0.012$, $y = -1.476x + 1.766$, Fig. 3A).

Africanized honeybees
Unlike the native bees, in the low-shade habitats exotic Africanized honeybees exhibited a strong significant increase in visitation only at the 100 m scale ($F_{1,55} = 8.792$, $r^2 = 0.122$, $p = 0.004$, $y = 1.586x + 0.200$, Fig. 3B). In contrast, within the high-shade habitats Africanized honeybees did not increase or decrease visitation levels in response to floral resources at any scale.

Discussion

Forager visitation

Large floral resource bursts, such as the mass-flowering of tropical trees or the annual coffee bloom, are common in the tropics and can have major implications on the foraging behaviour of bees. As seen in previous studies, our results indicate that habitat composition and coffee floral resource availability have stronger effects on visitation levels than distance to the nearest forest fragment (Klein et al. 2003b, 2006). Past studies document that social bees often increase in density and diversity with increasing proximity to tropical forest, suggesting that bees prefer to forage near their nesting sites (Klein et al. 2003b, 2004, Ricketts 2004). In this study, greater native bee visitation in high-shade agroforestry habitats is also likely driven by nest site preferences and availability, since most native social bees in the study (e.g. *Melipona beecheii, Nanotrigona testaceicornis, Plebia* sp., *Scaptotrigona mexicana*) prefer to nest in old trees or rotting wood, most solitary bees in the study (e.g. *Ceratina eximia, Ceratina ignara, Ceratina* sp. 1) are small-bodied and nest in hollow woody stems (Michener 2000), and both substrates are more abundant in high-shade coffee habitats. The fact that local forest patches are small, and that overstorey trees managed in high-shade coffee habitats are especially diverse and dense (Moguel and Toledo 1999) could explain why regional preferences for
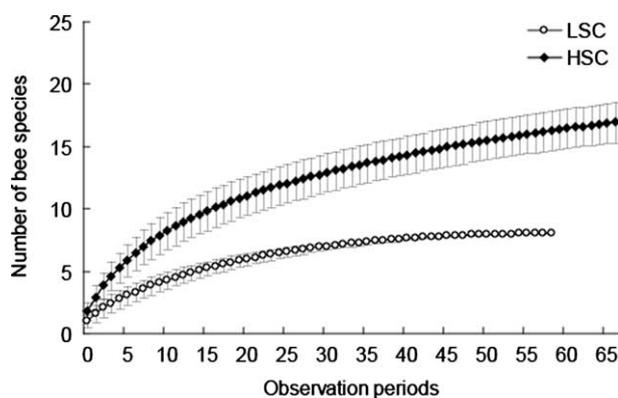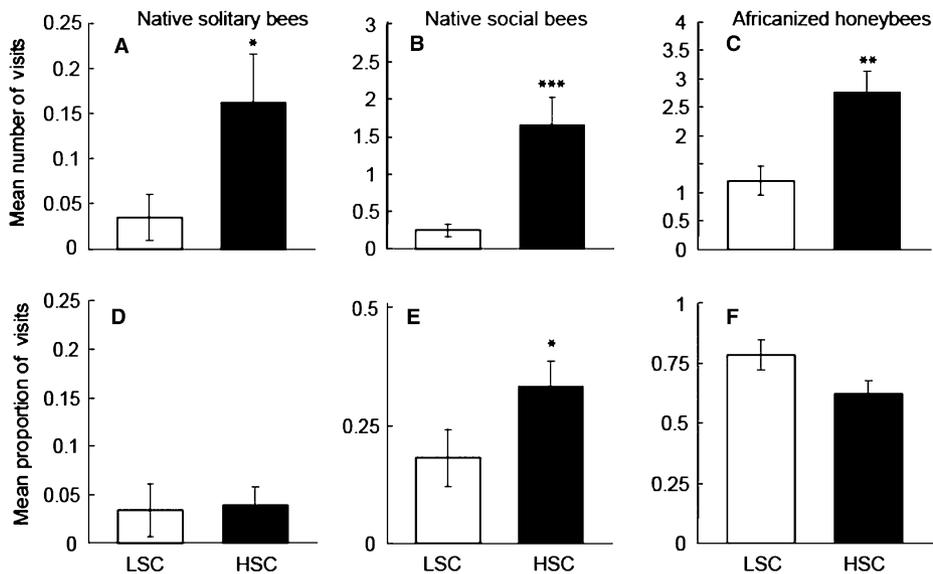
Figure 2. Visitation was significantly higher in high-shade coffee habitats (HSC) than low-shade habitats (LSC) for (A) native solitary bees, (B) native social bees, and (C) Africanized honeybees. The proportion of visits conducted by (D) native solitary bees was not significantly different between habitat types, (E) social native bees was significantly higher in high-shade coffee habitats, and (F) Africanized honeybees was slightly higher in low-shade coffee habitats. Error bars represent SE. Codes for significant differences in between habitats: *p <0.05, **p <0.01, ***p <0.001.
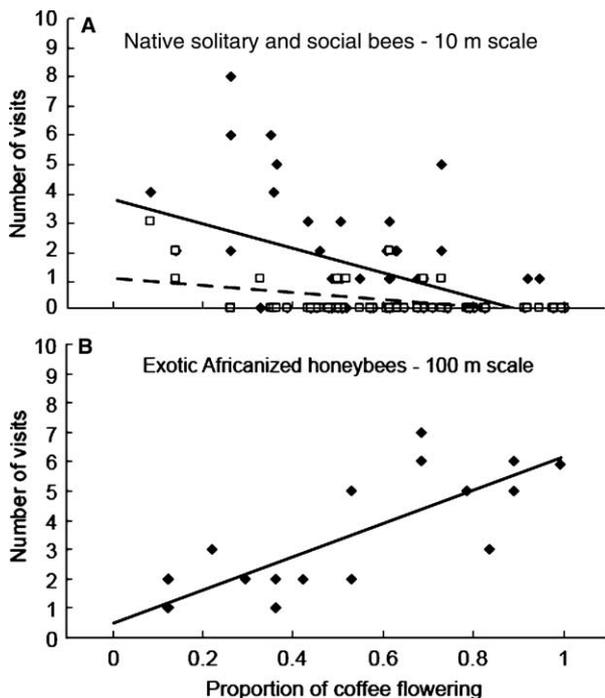
Figure 3. Contrasting responses of native and exotic bees under differing habitat management styles. (A) In high-shade coffee habitats, native solitary bee visitation (open squares, dashed line) and native social bee visitation (closed diamonds, solid line) decreased significantly as the floral resources decreased at the 10 m resource scale. (B) In low-shade coffee habitats, Africanized honeybee visitation (closed diamonds, solid line) increased significantly as floral resources increased at the 100 m resource scale.

forest proximity are particularly weak, and why local preferences for high-shade agroforestry habitats are stronger.

Though we found higher numbers of Africanized honeybee visitors in high-shade coffee habitats, we documented a greater proportion of visits conducted by Africanized honeybees in low-shade coffee habitats. This may be due to the honeybee's ability to navigate in open habitats (Barron et al. 2005), to fly greater distances from their nesting sites (Schneider and Hall 1997), or to tolerate higher temperatures (Heinrich 1979) than native solitary and social bees. Previous studies have documented greater abundances of Africanized honeybees in more disturbed, less forested landscapes (Aizen and Feinsinger 1994, Brosi et al. 2008). Our findings suggest that Africanized honeybees forage well in forested habitats, but are capable of exploiting high resources more easily than native bees in less forested habitats, likely due to their advanced foraging capabilities and high colony needs.

Foraging response to resource scale

Most importantly, this study reveals that bee functional groups respond to resources in significantly different ways across different spatial scales and habitats. While native solitary and social bees showed no foraging response to floral resources within low-shade coffee habitats, they exhibited a significant decrease in visitation with increasing floral resources at the 10 m resource scale in high-shade coffee habitats. These results suggest that native social and solitary bees perceive and respond to resources at small spatial scales, a pattern that has been documented for a number of small-bodied bee species (reviewed by Greenleaf et al. 2007). The significant negative foraging response exhibited by native solitary and social bees in our study suggests that they respond to floral resource levels by

spreading out between high resource patches, a pattern known as the 'dilution effect' (Root and Kareiva 1984, Yamamura 1999, Veddeler et al. 2006). This pattern has been observed a number of times for bees, especially in landscapes where their numbers are assumed to be limited in relation to floral resource availability (Totland and Matthews 1998, Sargent 2003, Veddeler et al. 2006).

In contrast, in our study, only Africanized honeybees exhibited a positive foraging response to increasing coffee resource availability, and only within low-shade coffee habitats. This foraging pattern, known as the 'concentration effect', is usually the result of an abundance of foragers that exhibit strong preferences for high-resource sites, leading to massive recruitment (Sih and Baltus 1987, Kunin 1993, Totland and Matthews 1998). While native solitary and social bees exhibit small foraging scales, honeybees exhibit relatively large foraging scales, as seen in previous studies (Steffan-Dewenter et al. 2002). Honeybees are capable of foraging outside of their usual foraging ranges in search of high-resource sites (Schneider and Hall 1997), making themselves available foragers at large spatial scales, especially when foraging for high-productive, mass-flowering sites (Schaffer et al. 1979, 1983). Because honeybees are also known to fly through more open habitats with greater speed and directness (Tautz et al. 2004, Barron et al. 2005) the forager concentration effect best describes the foraging response for honeybees within low-shade agroforestry habitats. While both the dilution and concentration effect can be observed for foraging bee communities depending on the spatial scale examined (Veddeler et al. 2006), our study indicates that bee functional group can explain contrasting foraging responses for bee communities across spatial scales.

We conclude that that coffee vegetation management distinctly impacts bee community composition and foraging response. Our study reveals that both vegetation management and bee functional group are critical factors driving contrasting bee foraging patterns. From a conservation perspective, we demonstrate that land management not only impacts bee abundance, but also impacts bee foraging patterns on ephemeral mass-flowering crops.

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