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Impacts of coffee agroforestry management on tropical bee communities

S. Jha [a,b,*], J.H. Vandermeer [a]

[a] Dept. of Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, MI 48109, USA
[b] Dept. of Environmental Science, Policy, and Management, University of California, Berkeley, 54 Mulford Hall, Berkeley, CA 94720, USA

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ABSTRACT

Though it is undoubted that tropical bees are influenced by habitat composition, few studies have investigated the relative importance of both local and landscape-level habitat parameters in supporting large and diverse bee communities. The conservation of native bee communities within agroforestry landscapes is particularly urgent given the importance of pollination services within these systems. In this study, we examined tropical bee communities within a largely deforested shade coffee-growing region in Chiapas, Mexico. We used regression tree modeling to examine the response of bee functional groups to local and landscape-level habitat management. Our models revealed that the most predictive factors for bee abundance and species richness were the number of tree species, the number of tree species in flower, and the canopy cover of the local agroforestry landscape. Solitary bees were most abundant in habitats with high canopy cover, while social bees were most abundant in habitats with greater tree species richness. Cavity-nesting and wood-nesting bee abundance was positively affected by the amount of canopy cover in the farm, while ground-nesting bees were most abundant in habitats with a large number of tree species in flower. Our results demonstrate that across bee sociality groups, nesting guilds, and tribes, the most critical factor impacting native bee communities was within-farm local vegetation management. These results reveal the important role that agroforestry managers can have on biodiversity conservation, and the potential contribution they can make by creating resource-rich agricultural matrices. Specifically, our findings highlight the importance of diverse overstory tree management in supporting native bee communities within tropical agroforestry systems.

1. Introduction

Bee communities are critically important for ecosystem function and the maintenance of the human agricultural enterprise through their pollinating activities. For example, an estimated 70% of world crops experience increased size, quality, or stability because of pollinator services (reviewed in Ricketts et al., 2008), benefitting 35% of the global food supply (reviewed in Klein et al., 2007). Animal pollination also contributes to the stability of food prices, food security, food diversity, and human nutrition (Steffan-Dewenter et al., 2005), and is estimated to be worth $200 billion worldwide (Kearns et al., 1998). Unfortunately, native pollinator populations face many threats, and evidence of a global pollination crisis is steadily growing (e.g., Kearns et al., 1998; Steffan-Dewenter et al., 2005; Biesmeijer et al., 2006). Acute declines in managed honeybee populations are cause for further concern (Johnson, 2007), with recent studies indicating that a reliance on managed honeybees for crop pollination is risky at best (Winfree et al., 2007).

Despite fears of pollinator shortages and strong ecological and agricultural dependencies on pollination, we are just beginning to understand how anthropogenic land-use impacts wild and managed pollinators. Though crop pollinators include a wide array of insects (e.g., beetles, butterflies, flies), bees are the most important and effective of these pollinators (Roubik, 1995; Klein et al., 2007). The bees (Hymenoptera: Apoidea) constitute an extremely species-rich fauna, with an estimated 20,000–30,000 species worldwide (Michener, 2000). Bees are ecologically and functionally diverse, foraging on a broad array of floral forms, nesting in a wide variety of substrates (Michener, 2000), and responding to both nesting and foraging resources at a wide range of spatial scales (e.g., Steffan-Dewenter et al., 2002; Tylianakis et al., 2006; Veddeler et al., 2006; Klein et al., 2008). Thus landscapes that offer heterogeneous nesting and floral resources, in both cultivated and non-crop areas, provide habitat for a diverse suite of bees (Kremen et al., 2002; Kim et al., 2006; Ockinger and Smith, 2007; Dover and Settele, 2009). Moreover, recent studies have revealed that crops experience higher or more stabilized fruit set in habitats with greater native bee diversity (Kremen et al., 2002; Klein et al., 2003a; reviewed in Klein

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[*] Corresponding author at: Dept. of Environmental Science, Policy, and Management, University of California, Berkeley, 54 Mulford Hall, Berkeley, CA 94720-3114, USA. Tel.: +1 248 719 0389; fax: +1 510 643 7428.
E-mail address: s.jha@berkeley.edu (S. Jha).

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et al., 2007; Vergara and Badano, 2009; Winfree and Kremen, 2009), a pattern explained by the greater niche complementarity between bee functional groups within diverse communities (Fenster et al., 2004; Hoehn et al., 2008).

The conservation of diverse pollinator communities is particularly essential in the tropics, where the majority of plant species are animal pollinated (Bawa et al., 1985). The tropics are home to immense faunal and floral diversity, and encompass much of the world's biodiversity hotspots (Myers et al., 2000). However, tropical regions also contribute substantially to global agriculture, producing crops like coffee, cacao, and rice, among many others. Much of the tropics exist as a mosaic of agricultural lands and forest patches, and these human-altered landscapes can have strong impacts on local biodiversity (e.g., Daily et al., 2001; Donald, 2004; Perfecto and Vandermeer, 2008). For bees, local forest patches can provide nesting and food resources within adjacent agricultural systems (e.g., Steffan-Dewenter et al., 2002; Kremen et al., 2004; Klein et al., 2008), potentially leading to increases in yields for crop species that are pollinated by insects, such as coffee (Klein et al., 2003b; Ricketts et al., 2004).

Coffee, which covers over 11 million ha of land (Donald, 2004), is traditionally grown under a canopy of shade trees that fix nitrogen (Perfecto et al., 1996; Moguel and Toledo, 1999), prevent soil erosion (Philpott et al., 2008b), and provide habitat for birds and bats, which can serve as coffee pest predators (reviewed in Van Bael et al., 2008). However, in recent years, with the increased availability of fertilizers, pesticides, and machines, many coffee farms have cut their shade trees, removed native understory vegetation, and intensified their farming practices, creating homogenous fields that lack vegetation structure or diversity (Perfecto et al., 1996; Donald, 2004). Among these practices, studies have shown that decreasing the availability of flowering understory plants can negatively impact bee diversity, and can differentially affect the abundance of distinct bee functional groups (e.g., Klein et al., 2008; Jha and Vandermeer, 2009). Though a broad range of local and landscape-level habitat variables may interact hierarchically to provide nesting and food resources, the complex relationship between these variables has rarely been examined across different members of the bee community.

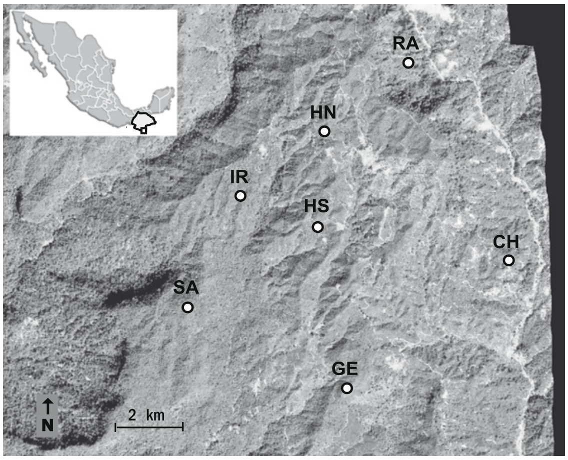

Fig. 1. Study sites in Nueva Alemania, a region in southern Chiapas, outlined in black within the inserted map of Mexico.

In this study, we use permutation tree modeling to investigate the effects of local and landscape-level habitat composition on bee communities within a coffee and forest landscape mosaic, in Chiapas, Mexico. Based on previous studies, we hypothesize that high levels of forest cover will be the most critical factor for wood-nesting and social bee abundance, while high herb density will be essential for solitary bee abundance within shade coffee systems (Klein et al., 2003b). We also hypothesize that ground-nesting bees will be negatively impacted by coffee bush density, while cavity-nesting bees will be primarily dependent on the availability of overstory trees for nesting resources. Utilizing conditional inference trees, we ask (1) How do bee communities change across landscapes with increasing forest availability? (2) How do bee communities respond to different agroforestry vegetation management styles? (3) Are local or landscape-level habitat factors more important for bee abundance and species richness? Specifically, we examine the responses of multiple functional groups within the bee community, based on sociality, evolutionary history, and nesting, in order to reveal functional group-specific answers to these critical questions.

2. Materials and methods

2.1. Study area

The study was conducted in the *Soconusco*, a coffee-growing region located in the southern foothills of Chiapas, Mexico (15°10′59″N, 92°20′44″W to 15°08′52″N, 92°18′33″W) at an altitude ranging between 825 and 1300 m (Fig. 1, Table 1). The study area covers approximately 51.8 km^2 and is comprised of numerous shade coffee farms and small forest fragments. We examined seven agroforestry systems which vary substantially in their overstory and understory vegetation management styles, ranging from shade monoculture to traditional/commercial polyculture (Moguel and Toledo, 1999; Philpott et al., 2008a) (Fig. 2). Within each farm, we established a 100 m × 100 m (1 ha) plot, and measured the fol-

Table 1
Mean local agroforestry habitat variables at each study site.

Site (map name)	Land use classification	% Canopy cover	Tree species richness (per/ha)	Tree density (per/ha)	Coffee density (per/m^2)	Basal area overstory trees (per/ha)
Irlanda (IR)	Traditional/commercial polyculture	60.5	18.0	164	3.58	8.15
Rancho Allegre (RA)	Traditional/commercial polyculture	58.2	14.5	210	3.18	5.42
Chiripa (CH)	Traditional/commercial polyculture	30.0	16.5	155	4.28	5.96
Santa Anita (SA)	Commercial polyculture	70.9	13.0	256	3.20	8.07
Genova (GE)	Commercial polyculture/shade monoculture	18.9	17.0	177	2.59	4.76
Hamburgo North (HN)	Shade monoculture	29.0	11.5	139	4.57	5.13
Hamburgo South (HS)	Shade monoculture	41.5	14.0	152	4.44	4.74

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lowing agroforestry habitat variables at the beginning and mid-point of the sampling season to account for mid-season pruning and replanting: (1) the density and species richness of overstory trees (trees), (2) the diameter at breast height (DBH) of shade trees (for basal area), (3) the density of understory coffee bushes, and (4) the plot elevation. We hand-counted all coffee plants and trees in the 1 ha plot. Elevation was measured with a GPS unit (Trimble GeoExplorer 3) at the SE corner of each plot.

2.2. Sampling design

Within each plot, bees were captured using a pan trap methodology, according to the Bee Inventory Plot (BIP) guidelines (LeBuhn et al., 2005). Pan traps are easy to standardize across sites, decrease the risk of collector's bias, and are extremely effective at trapping, thus they are considered the most practical and informative sampling methodology for bees (Westphal et al., 2008). Using the BIP pan trap methodology, we laid 30 pan traps made from 6 oz plastic bowls (SOLO model number: PB6-0099) across two intersecting 50 m transects located in the center of each plot. Before the experiment, 1/3 of the bowls were painted fluorescent blue, 1/3 painted fluorescent yellow and 1/3 left white, and the colors were alternated along the two transects. Bowls were then filled with a soapy water solution (1 tsp Dawn® blue soap per gallon water). To ensure pan trap visibility, coffee branches hanging above the pan traps were trimmed.

Pan traps were set out at all plots at 9 am and collected at 5 pm once every 2 weeks from 2 February to 13 April, 2006 (six sampling days). This period extends 6 weeks before and after the coffee bloom, from the middle of the dry season to the beginning of the wet season in southern Mexico. We processed the specimens on each sampling day by pinning and identifying them to the genus or subgenus level. All bees found in pan-traps in a single site were summed to provide a site-level count per sampling date (for a total of 42 samples). Bee pan traps were combined because they are not independent from one another and because the pan-trap colors do not differ significantly in the bees they attract (LeBuhn et al., 2005). We identified all individual bees trapped. For species-level identifications, we referred to local collections at *El Colegio de la Frontera Sur* in Tapachula, Mexico and the expertise of T. Griswold, at the USDA Bee Lab in Logan, Utah. For some individuals, we could not arrive at species-level classifications, thus we left their classification at the genus level (with a morphospecies label). Because many bee groups do not have adequate taxonomic treatments (Michener, 2000), especially in the tropics, identification to the morphospecies level was necessary. Previous work shows that morphospecies-level identifications can serve as a good proxy in the estimation of species richness (Oliver and Beattie, 1996).

2.3. Local agroforestry management

Plots were sampled for additional agroforestry habitat variables once every 2 weeks, 1 day after bee sampling days. On each sampling day, we measured: (1) the density and species richness of understory plants in flower, (2) the percent of coffee bushes in flower, (3) the percent of canopy cover, (4) the percent ground cover, and (5) the density and species richness of trees in flower. To monitor the density and richness of understory plants in flower and the percent of coffee bushes in flower per plot, we established four 10 × 4 m transects, starting with a random starting point and continuing 10 m in the four cardinal directions. Transects did not overlap or extend outside of the plot. On each sampling day, we counted and identified to species all individual understory plants in flower within each transect. For each transect, we calculated the percent of coffee bushes in flower by dividing the number of branches in flower by the total number of branches for each bush and then averaging across all bushes in each transect. Canopy cover and ground cover were recorded along the diagonals of each 1 ha plot using a vertical tube densiometer (Geographic Resource Solutions, Arcata, CA), recording the vegetation cover overhead (canopy cover) and the vegetation cover on the ground (ground cover) every 3 m for a total of 46 sampling points for each index. This was then averaged per plot. We measured the density and species richness of trees in flower throughout the entire plot based on counts taken using binoculars.

2.4. Forest cover

Forest fragments were located both within and at the boundaries of coffee farms. For each farm, we measured the percent of primary forest cover within 100 m, 500 m, and 1 km radii of each plot, based on a panchromatic IKONOS® image with 1 m spatial resolution (Land Info Worldwide Mapping, 2007). The image was taken on 10 December 2005 and had negligible cloud cover. The image was orthorectified and ground-truthed using 20–30 points taken at all sampling sites within the region. Boundaries between coffee farms and forest fragments were measured using the visual aid of the panchromatic image and with the textural and reflectance patterns of a chlorophyll composite provided by the multispectral image (spectral bands 4-3-1, 4 m spatial resolution). Area of forest within each radius was calculated using the software ArcMap9.2 (ESRI, 1999–2006).

2.5. Statistical analyses

We used non-parametric analytical methods; therefore results presented are for untransformed data. However, transformation can decrease the variance around the mean (Sokal and Rohlf, 1995) potentially influencing splitting in permutation trees, thus we double-checked our findings with log + 1 transformed data and found no significant differences. We tested all variables for colinearity. Density of trees and basal area were collinear (pearson correlation coefficient = 0.501, $p = 0.0007$), so they were not tested simultaneously in the analyses. Species accumulation and estimation curves were generated using the Chao1 estimator (Chao, 1987), utilizing the EstimateS software (Colwell and Coddington, 1994).

To determine the most important factors predictive of bee abundance at the sociality, nesting guild, and tribe level, we used conditional inference trees (Strasser and Weber, 1999; Hothorn et al., 2006). Permutation trees, such as conditional inference trees, are commonly used to examine patterns in ecological data, and are especially useful for developing habitat models where factors may interact in a hierarchical fashion (reviewed in De'ath and Fabricius, 2000; Olden et al., 2008). The conditional inference tree estimates a regression relationship by utilizing a binary recursive data-partitioning algorithm. Conditional reference trees are non-parametric and do not assume linearities in response variables. We built conditional inference trees utilizing the 'party' package in the programming language R (R Development Core Team, 2005). Unlike the packages 'rpart' and 'randomforest', 'party' is not susceptible to 'variable selection bias' (Strobl et al., 2009). Variable selection bias is where the tree algorithm is biased in favor of variables that have many potential splitting points (e.g., continuous variables with large ranges). The package 'party' also offers many ways to evaluate the importance (conditional permutation-importance) and significance (p-value) of each variable.

Conditional inference trees function by first testing whether input variables are independent of one another and independent of the response variable. If this hypothesis is rejected, then it selects the input variable with the greatest association to the response variable, as measured by a p-value for the test of the partial null

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Fig. 2. Photo of a shaded coffee agroforestry system, Finca Irlanda, where coffee bushes line the understory and shade trees fill the canopy. For scale, the author stands in the bottom center of the photo.

hypothesis of the single input variable and the response variable. It then splits the data into two sections (nodes) based on the variable and repeats the search for the input variable with the greatest association to the response variable. This continues until the criterion (1 − *p*-value) does not exceed the minimum criterion established in the analysis. This approach ensures that the appropriate sized tree is grown. In this analysis, the stop criterion was based on univariate *p*-values and a minimum criterion of 0.95. For cavity-nesting and ground-nesting bees, we reduced this minimum criterion to 0.65 for the purpose of visualizing the relationship between input and response variables, despite their lack of significance. Each conditional inference tree model began by including all agroforestry habitat variables and forest cover at each of the three radii as input variables.

Because agroforestry habitat variables exhibited substantial variation over time, we treated the six sampling periods as separate replicates for each site. However, repeated sampling may potentially bias tree building (De'ath and Fabricius, 2000) therefore we used the package 'coin' (Hothorn et al., 2008) to examine the independence of the response variable and the primary explanatory variable, given site-level stratification. The null distribution of the test statistic was calculated using Monte-Carlo resampling and these 'site-stratified' *p*-values were calculated for the first node of each tree and presented in the text as the 'site-stratified *p*-values'.

3. Results

3.1. Local and landscape-level agroforestry management

Sites exhibited a wide range of agroforestry management styles, varying between 13.2% and 69.4% canopy cover and 162–258 trees per/ha (Table 1). Across all sites and sampling periods, we documented 25 tree species (six flowered during the season) and 16 understory flowering plant species (Supplementary material, Appendix S1). Coffee flowering began in the 6th week of the survey and lasted 9 days across the entire region. Coffee cultivation accounted for approximately 93.7% of the entire study area and forest for the remaining 6.3%. For each plot, local forest cover within a 100 m–1 km radius ranged between 0.0% and 14.2%.

3.2. Bee communities

We trapped a total of 648 bees, including 46 different species representing two families, the Halictidae (72.2%) and Apidae (27.8%) (Supplementary material, Appendix S2). The observed species accumulation curve (Fig. 3) approached but did not reach a plateau, and the estimated species richness in the region was 59 species. For the entire bee community, the most critical habitat variables for predicting abundance were tree species richness (site-stratified *p*-value = 0.020) and percent canopy cover (Fig. 4a). Overall bee species richness was most impacted by coffee bush density (site-stratified *p*-value = 0.045) and flowering tree species richness (Fig. 4b). Overall bee community composition (tribe level) did not vary substantially based on a gradient of forest cover or tree species richness, but did show a weak trend of increasing tribe richness with increasing tree species richness (Fig. 5). Given the diverse composition of the sampled bee community, and the likely divergence in responses to agroforestry management depending on (1) sociality, (2) evolutionary history (tribe), and (3) nesting guild, we separately examined bee abundance in response to habitat variables within these three groups. While these analyses are not completely independent of one another (e.g., many social bees are wood-nesting), we feel that it is valuable to examine the responses of conventionally defined groups in order to compare the findings with those of previous studies. Given that grouping based on tribes by definition clusters individuals that share an evolutionary history, we expect that this grouping will have the most predictive power.

3.3. Sociality, tribes, and nesting guilds

The most predictive factors for solitary bee abundance were percent canopy cover (site-stratified *p*-value = 0.039) and the number of flowering herb species, while the most predictive factors for social bee abundance were the number of tree species (site-stratified *p*-value = 0.012), followed by the number of flowering tree species (Fig. 6). For the tribe Halictini, the factors with the greatest effect on bee abundance were the number of tree species in flower (site-stratified *p*-value = 0.002) and the number of tree species. For the tribe Augochlorini, the factors showing the greatest effect on bee abundance were the number of tree species (site-stratified *p*-value = 0.021), followed by the percent canopy cover. For the tribe Ceratinini, the traits that showed the greatest effect on bee abundance were percent canopy cover (site-stratified *p*-value = 0.050) and the number of herb species in flower (Fig. 7). The most predic-

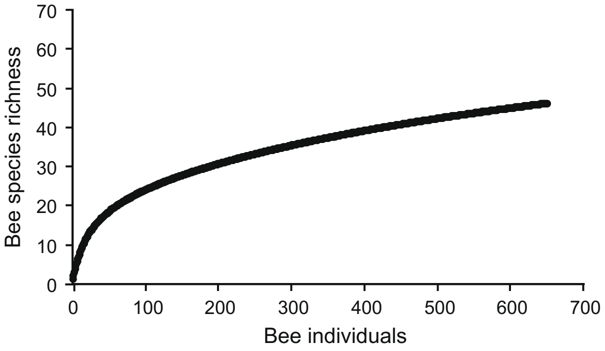

Fig. 3. Observed species accumulation curve reaching 46 species.

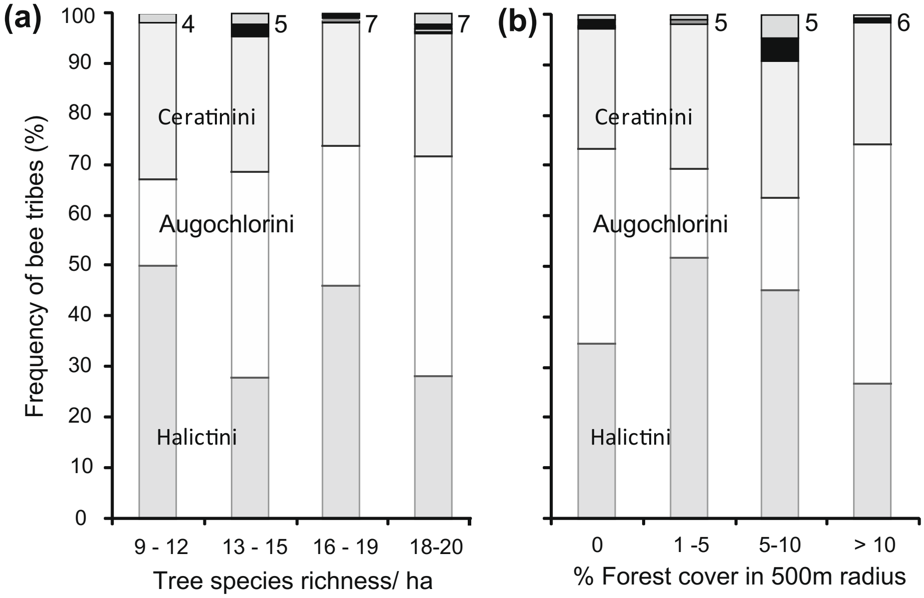

Fig. 4. Bee community composition across a gradient of: (a) tree species richness and (b) local forest cover. The three most dominant tribes are labeled, while the total number of tribes in each group is noted at the top right of each column.

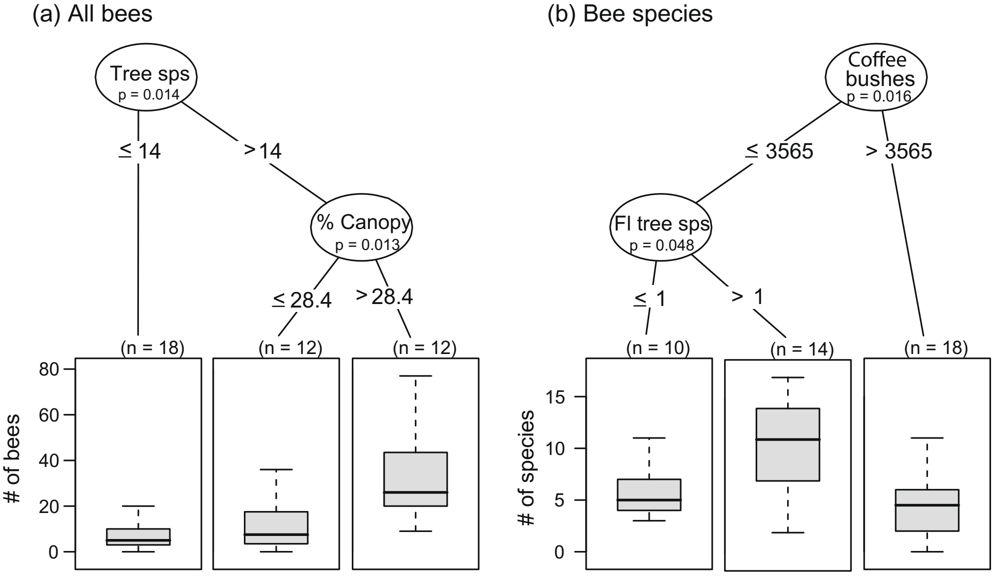

Fig. 5. Conditional inference tree for (a) total bee abundance and (b) total bee species richness. The encircled variables are those showing the strongest association to the response variable (total bee abundance or bee species richness, respectively). The *p*-values listed at each node represent the test of independence between the listed variable and the response variable. Box plots at the terminal nodes show the distribution of the abundance data within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median, while whiskers represent the extent of data within the 1.5× inner-quartile range. Circles above and below the whiskers represent data points outside of this range. The number of sites that fall within each branch (*n*) are listed above the box plots.

tive factors for cavity-nesting bee abundance were the percent canopy cover (site-stratified *p*-value = 0.901) and the number of herb species; however both factors were not significant, likely due to small sample size. The factors that showed the greatest effect on wood-nesting bee abundance were the percent canopy cover (site-stratified *p*-value = 0.038), followed by the number of herb species in flower. The most predictive factors for ground-nesting bee abundance were the number of tree species in flower (site-stratified *p*-value = 0.003), followed by the number of tree species, though this second factor was only marginally significant (Fig. 8).

4. Discussion

4.1. Bee communities

In contrast to our hypotheses, we found that within-farm habitat management was more predictive of bee abundance than landscape-level forest cover at all spatial scales. While a handful of studies have similarly found that bee richness does not increase with increasing semi-natural habitat size or availability (Donaldson et al., 2002; Cane et al., 2006; Brosi et al., 2008), the majority

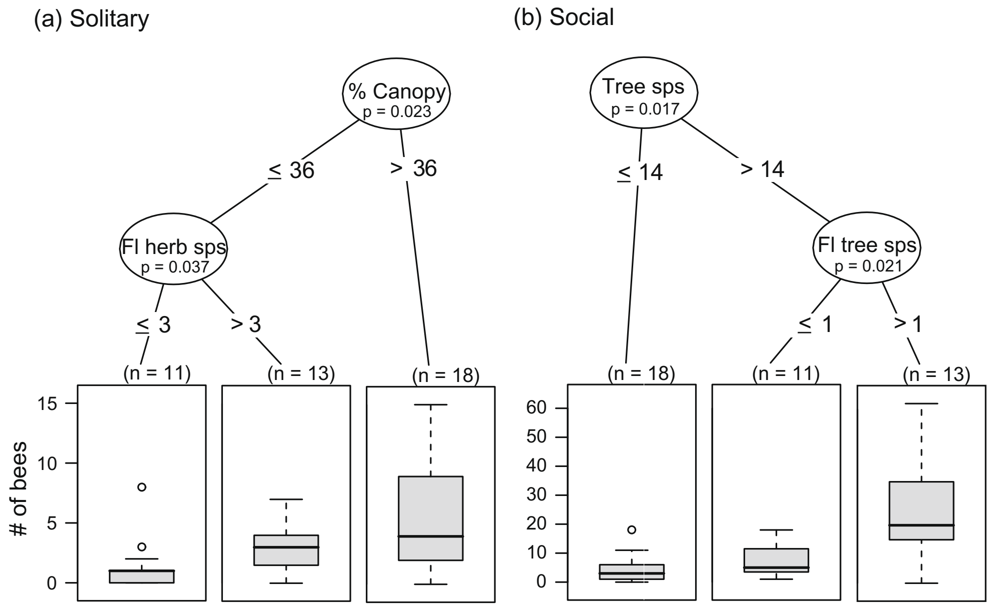

Fig. 6. Conditional inference tree for (a) solitary bee abundance and (b) social bee abundance. The encircled variables are those showing the strongest association to the response variable (solitary or social bee abundance, respectively). The *p*-values listed at each node represent the test of independence between the listed variable and the response variable. Box plots at the terminal nodes show the distribution of the abundance data within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median, while whiskers represent the extent of data within the 1.5× inner-quartile range. Circles above and below the whiskers represent data points outside of this range. The number of sites that fall within each branch (*n*) are listed above the box plots.

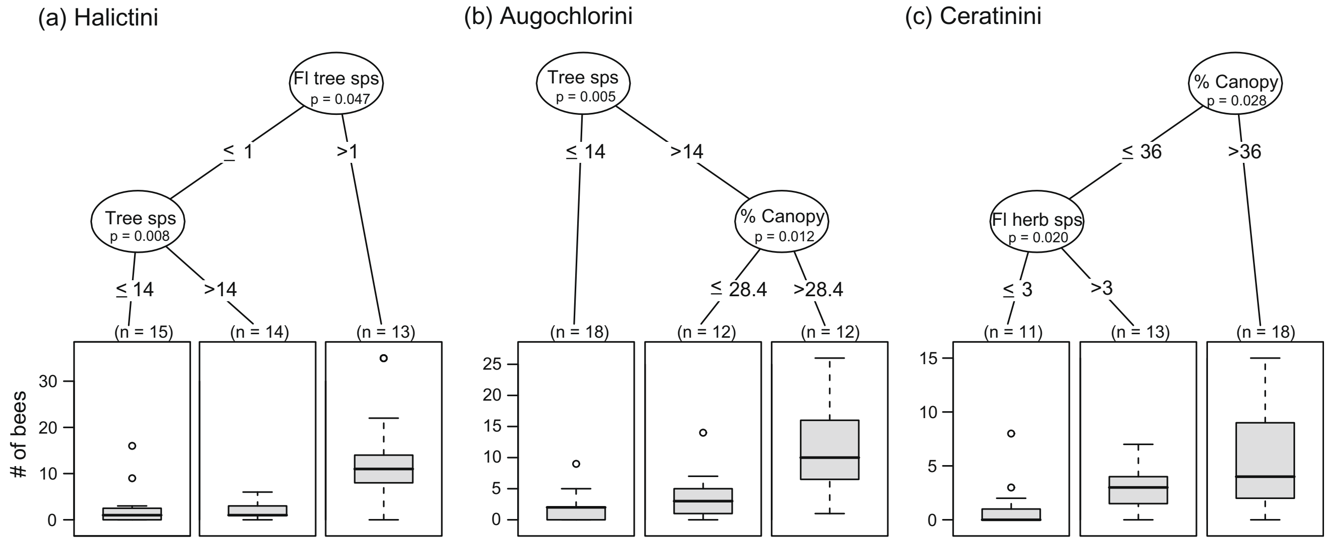

Fig. 7. Conditional inference tree for (a) Halictini bee abundance, (b) Augochlorini bee abundance, and (c) Ceratinini bee abundance. The encircled variables are those showing the strongest association to the response variable (Halictini bee abundance, Augochlorini bee abundance, and Ceratinini bee abundance, respectively). The *p*-values listed at each node represent the test of independence between the listed variable and the response variable. Box plots at the terminal nodes show the distribution of the abundance data within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median, while whiskers represent the extent of data within the 1.5× inner-quartile range. Circles above and below the whiskers represent data points outside of this range. The number of sites that fall within each branch (*n*) are listed above the box plots.

of previous research emphasizes the availability of semi-natural habitat as a primary factor mediating bee abundance and richness within agricultural systems (reviewed in, Kremen et al., 2004; Klein et al., 2008; Ricketts et al., 2008). This distinction in response to semi-natural habitat fragments is best explained by differences in bee community composition and nest site availability between these studies.

In this study, the bee community is dominated by small-bodied tribes, the Halictini, Augochlorini, and Ceratinini, which tend to have shorter foraging ranges (i.e., Greenleaf et al., 2007) and thus are likely to respond to local habitat factors. In contrast, larger bodied, longer-ranging tribes, like the Apini and Meliponini, which predominate in many tropical ecosystems, exhibit increased abundance with greater local forest availability (e.g., Klein et al., 2003b; Ricketts, 2004; Brosi et al., 2008). Additionally, the Mexican shade coffee landscape exhibits high levels of overstory and understory plant richness within the agricultural matrix (Moguel and Toledo, 1999) and low levels of regional forest cover (reviewed in Ramirez-Marcial et al., 2001), potentially rendering within-farm resources more available than those in regional forest patches. Past studies have shown that bee communities may not exhibit increased abundance or diversity with increasing forest proximity,

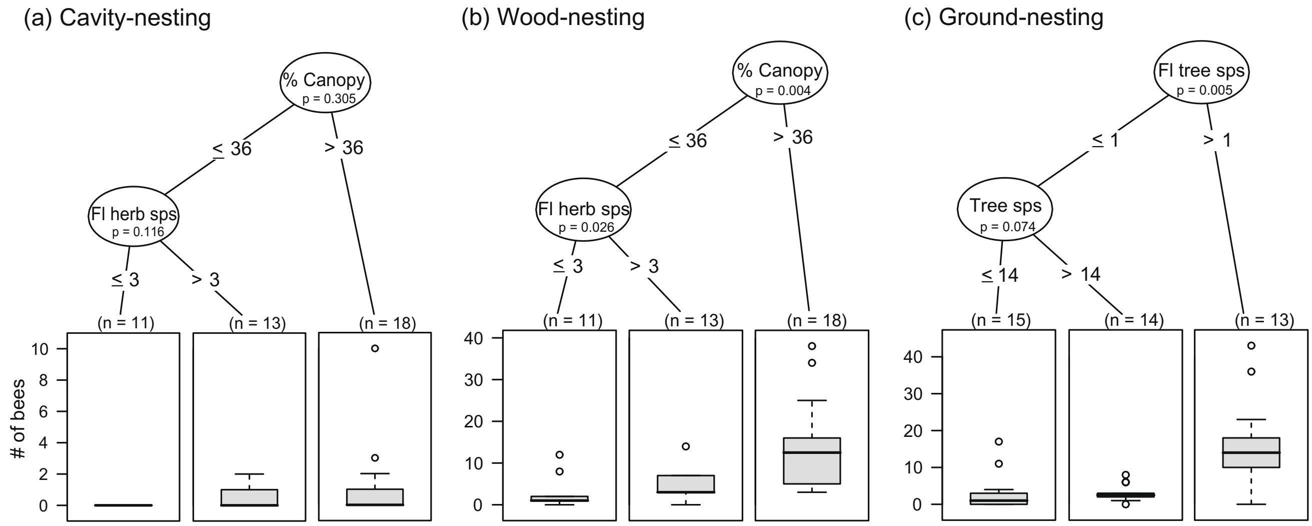

Fig. 8. Conditional inference tree for (a) cavity-nesting bee abundance, (b) wood-nesting bee abundance, and (c) ground-nesting bee abundance. The encircled variables are those showing the strongest association to the response variable (cavity-nesting bee abundance, wood-nesting bee abundance, and ground-nesting bee abundance, respectively). The *p*-values listed at each node represent the test of independence between the listed variable and the response variable. Box plots at the terminal nodes show the distribution of the abundance data within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median, while whiskers represent the extent of data within the 1.5× inner-quartile range. Circles above and below the whiskers represent data points outside of this range. The number of sites that fall within each branch (*n*) are listed above the box plots.

but may exhibit a shift in bee community composition (e.g., Cane et al., 2006; Brosi et al., 2008). We did not find strong evidence for a shift in bee community composition and suggest that this is due to the low amount of regional forest cover and similarity in nesting resources between forest and shade coffee habitats. Thus, our findings may be more typical of bee communities within heavily deforested agroforestry regions, an increasingly common landscape in the tropics (Perfecto et al., 1996; Donald, 2004). While native forest preservation is paramount to biodiversity conservation, most coffee cultivators can only implement land-use change within their own farms (Philpott et al., 2008b). Our study indicates that local habitat factors, managed within agroforestry systems, can have strong impacts on local bee abundance and diversity.

4.2. Sociality groups

Overall, solitary bees showed the greatest response to high levels of canopy cover and high understory flowering plant richness. While previous studies in tropical agricultural systems have also found increased solitary bee abundance with greater flowering herb cover, they additionally document decreases in solitary bee abundance with decreasing light availability (Klein et al., 2002, 2003b; Tylianakis et al., 2006). Alternatively, our hierarchical analysis indicates that flowering herb diversity is most critical in sites with very low canopy cover, but that solitary bee abundance is highest in habitats with at least moderate (36%) canopy cover. For social bees, we documented strong preferences for high tree species richness and high species richness of trees in flower, resources which provide both nesting and foraging sites. As in Klein et al. (2002), we found that social bee abundance increased with increasing local vegetation diversity and density. However, our results specifically show that social bee abundance is related to the species richness of shade trees within an agroecosystem. Furthermore, we demonstrate that trees both within and outside of their flowering periods are important for this group.

4.3. Tribes

Across all three tribes, the availability of nesting and foraging resources were critical factors predictive of bee abundance. The Halictini is a ground-nesting polylectic tribe that includes both solitary and social species, and exhibits relatively low diversity in the new world tropics (e.g., Michener, 2000). In this study, halictines exhibited strong habitat responses to the species richness of trees in flower. Given their ground-nesting behavior, this result indicates that floral resource richness is a primary driver of halictine bee abundance within coffee-growing regions. The Augochlorini are a polylectic tribe that nest in the ground and in decaying plant matter (e.g., Eickwort and Sakagami, 1979; Michener, 2000). Augochlorines are most diverse in the new world tropics, where they have received attention for the broad array of nest architecture types that potentially drive their diversification (reviewed in Engel, 2000). We found that Augochlorines exhibited higher abundance in habitats with high tree diversity, followed by high canopy cover. Given this response to nesting resource diversity and density, our results suggest that Augochlorine nesting ecology may be important, not only for tribe diversification, but also for governing local abundance. The Ceratinini, a small-bodied polylectic tribe that primarily includes stem-nesting solitary bees (e.g., Okazaki, 1992; Michener, 2000), responded most to high canopy cover and then to herb species in flower. While greater canopy cover provides greater access to stem nesting sites, responses to flowering herb species richness reveals that diverse floral resources are also critical in sustaining local densities of ceratinine bees.

4.4. Nesting guilds

Cavity-nesting bees were most abundant in habitats with high canopy cover and high levels of flowering herb species richness, likely a response to greater cavity availability (e.g., Potts et al., 2005) and greater food resource availability. Wood-nesting bees were also more abundant in coffee systems with greater canopy cover and herb species richness, a finding supported by past studies documenting wood-nesting bee preferences for regenerating scrub lands (Potts et al., 2005) and abandoned coffee farms (Tylianakis et al., 2005). Ground-nesting bee abundance did not respond to bare ground-availability (as seen in Wuellner, 1999; Potts et al., 2005) or availability of semi-natural habitat (as seen in Kim et al., 2006), but alternatively, responded to high species

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richness of trees in flower, indicating a dependence on non-crop floral resource availability.

4.5. General patterns

Overall, our results suggest that coffee flowering alone does not drive neotropical bee abundance and species richness within coffee agroforestry systems. Though coffee flowering provides bees with abundant floral resources, these resources are only available for a short period of time (e.g., Klein et al., 2003a; Ricketts, 2004; Veddeler et al., 2006). Alternatively, non-crop vegetation, such as flowering field margins, hedgerows, and local forest patches, provide pollinators with floral resources during and outside of the crop flowering season (e.g., Kremen et al., 2002; Carvell et al., 2004; Kim et al., 2006; Ockinger and Smith, 2007; Dover and Settele, 2009). While past studies have documented the importance of flowering coffee and non-coffee understory plants for bee communities (Klein et al., 2003b; De Marco and Coelho, 2004; Veddeler et al., 2006), we found that shade trees were the most critical factors for native bee abundance and species richness within agroforestry systems. Floral density did not play a critical role in this system. Instead we document greater bee abundance and species richness in habitats with greater species richness of trees in flower, a novel finding to our knowledge.

5. Conclusions

Across ecological systems and organisms, resource heterogeneity is a key driver of species richness and abundance (e.g., Macarthur and Macarthur, 1961; Shmida and Wilson, 1985; Tylianakis et al., 2008). Not surprisingly, declines in habitat heterogeneity are critically linked to biodiversity loss within agricultural landscapes (Benton et al., 2003). We found that the most important factors predictive of bee abundance in coffee agroforestry systems were related to the diversity of vegetation within the agroforestry system. These results indicate that coffee farmers do not need to rely solely on landscape-level forest patches to provide pollinator resources. Instead, coffee farmers can contribute to biodiversity conservation by creating heterogeneous and resource-rich agricultural matrices (i.e., Perfecto and Vandermeer, 2008). Specifically, coffee farmers can promote bee abundance and diversity within their own farms by diversifying their shade trees, allowing these trees to age, and by creating a mosaic of light gaps and flowering herb patches that will attract foraging pollinators. Given the immense benefit of insect pollination to coffee yields (Klein et al., 2003a; Ricketts et al., 2004), there is great incentive for farmers to improve agroforestry management, dually garnering ecosystem services and supporting biodiversity conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.017.

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