Phenological floral resource complementarity is important for bee abundance

by

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Abstract

Spatial resource heterogeneity has been found to greatly influence the dynamics between diversity and function. This is particularly relevant for bee diversity and pollination services. While there has been ample research conducted to investigate these patterns, the impact of phenological resource heterogeneity (differences in availability of resources throughout time) on biodiversity and functioning has been less explored. This is important in agricultural systems, as many foraging periods of bees extend beyond the crop flowering event. In this study, we sought to understand how the bee community changed between seasons and if phenological complementarity of non-crop floral resources influenced bee diversity and abundance. We explored these questions in a region dominated by coffee agroecosystems in Mexico. This region was an ideal system for this study because the landscape offers a range of coffee management regimes that maintain heterogeneity in floral resource availability temporally and spatially.

We found that the bee community varies significantly between the seasons. There were a greater proportion of native social bees in the rainy season than the dry season. The proportion of solitary bees did not vary between the seasons. Managed social bees had a significantly greater proportion in the dry season when coffee was flowering than all other sampling times. Additionally, we found that floral resources from groundcover, but not trees, were associated with bee abundance. However, the phenological scale of the availability of these resources is important, whereby contemporaneous resource availability appears particularly important in maintaining high bee abundance at sites with lower phenological complementarity through time. We argue that in additional to spatial resource heterogeneity, resource heterogeneity through time is also critical in explaining patterns in the bee community. Farms can support pollinator services and conservation by maintaining complementarity in floral resources available from both crop and non-crop plants.

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Introduction

The Biodiversity-Ecosystem Function (BEF) framework has been explored theoretically and empirically across multiple scales and systems, with results ranging from biodiversity positively affecting ecosystem function (Tilman, Wedin, & Knops, 1996), to having neutral or negative effects on function (Cardinale et al., 2006, 2012; Sih, Englund, & Wooster, 1998). The framework considers if and how diversity of biological units (genes, species, functional groups) influence ecosystem function. If different species partition a shared niche space, reducing interspecific competition, but optimizing overall function, the diversity of species can enhance function by performing complementary roles (functional complementarity). If different species overlap in niche space, diversity does not necessarily enhance function, because more than one species is performing the same functional role (functional redundancy) (Bluthgen & Klein, 2011). Still, the insurance hypothesis, which states that biodiversity insures ecosystems against declines in functioning caused by environmental and climatic variability (Yachi & Loreau, 1999) suggests hidden, long-term complementarity behind redundancy.

The various outcomes of these studies, mostly within plant communities, have generated debate and uncertainty towards BEF. Context-dependency has been cited as an explanation for the variability in these outcomes (Cardinale et al., 2000; Wellnitz & Poff, 2001). Having greater resource heterogeneity spatially allows for greater niche partitioning among species, and thus increases the impact of diversity on function (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Tylianakis et al., 2008). Similarly, more studies have begun to examine functions beyond plant productivity and nutrient cycling, like pest control and pollination (Frund, Dormann, Holzschuh, & Tscharntke, 2013; Sih et al., 1998).

Diversity among both the plant species and pollinator species may promote functional complementarity (Ebeling et al., 2008; Fontaine, Dajoz, Meriguet, & Loreau, 2006). Diversity in plants and floral resource availability can function to sustain pollinators through varying flowering phenologies and nutritional variation. Diversity within pollinator communities maintains pollination services to plants temporally (daily, seasonally) and architecturally (Greenleaf & Kremen, 2006; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008). On the community level, diversity of plants and pollinators creates a positive feedback loop in which both parties benefit from the diversity of the other. The mechanism behind this feedback loop is centered in whether pollinators have enough floral resources to sustain the health of colonies throughout their foraging season and whether there are enough pollinator species to effectively pollinate the plant community throughout different phenological stages (Ebeling et al., 2008).

Spatial heterogeneity of floral resources is thus important in maintaining plant-pollinator interactions, particularly in agricultural landscapes (Tylianakis et al., 2008). As agriculture becomes more simplified, fewer resources are available to maintain pollinator requirements, resulting in fewer species of pollinators (Holzschuh, Steffan-dewenter, & Tscharntke, 2008; S. Jha & Vandermeer, 2010). Many important agricultural crops, like almonds, require pollination services. Others that can self-pollinate, like coffee and strawberries, benefit from animal pollination with increased weights (Klein, Steffan-Dewenter, & Tscharntke, 2003) and quality (Klatt et al., 2014). In coffee farms in Indonesia, (Klein, Steffan-Dewenter, & Tscharntke (2003) found that farms with greater resource heterogeneity supported a greater diversity of pollinators. Additionally, they found that coffee that was visited by a greater diversity of pollinators significantly increased the fruit weight of coffee (Alexandra-maria Klein, Steffan-dewenter, & Tscharntke, 2003) which has positive economic implications for farmers.

While spatial resource heterogeneity influences the dynamics between diversity and function (Tylianakis et al., 2008) the impact of phenological resource heterogeneity (differences in availability of resources throughout time) on biodiversity and functioning has been less explored (Mandelik, Winfree, Neeson, & Kremen, 2012). Bees use various plants to satisfy different resource requirements throughout their foraging season, which exceeds beyond the bloom period of most plants (Baker, 1963; Olesen, 2008). Thus, sites having floral resources available throughout the year to satisfy bee foraging, whether through plants that are always in flower or through a diversity of plants that complement respective flowering phenologies so there are always flowering resources available, are defined as having high phenological complementarity (Bluthgen & Klein, 2011). In this study we seek to understand how phenological complementarity of non-crop floral resources, which can provide resources to pollinators outside of the crop flowering season (Carvell, Meek, Pywell, & Nowakowski, 2004; Kremen, Williams, & Thorp, 2002), influences bee diversity and abundance. Coffee farms offer a valuable opportunity to explore these patterns because coffee offers ephemeral, mass flowering resources for pollinators (S. Jha & Vandermeer, 2010; A Klein et al., 2003; Ricketts, 2004; Veddeler, Klein, & Tscharntke, 2006). Additionally, coffee farms are managed under a variety of shade tree regimes (Moguel & Toledo, 1999), ranging from sun coffee to coffee grown under a diversity of shade trees. Coffee farms will offer a system in which an ephemeral resource (coffee flowers) can be studied within sites with high and low pollinator resources from other plants. This study addresses the following questions: 1) How does the community composition of bees change across seasons in a tropical coffee agroecosystem? 2) What better explains pollinator diversity and abundance sampled at a specific time, floral resources available contemporaneously with the sampling event or the level of phenological complementarity in floral resources?

For question one, we predict that the community composition of bees would change between the two different seasons. There are fewer floral resources in the rainy season, so we would expect bees that are social to be favored in the dry season, when there are more floral resources to sustain their nests. We predict solitary bees to be favored in the rainy season, when there are less social bee foraging. We do not expect the managed honeybee (*Apis mellifera scutellata*) to change during the different seasons as they are given supplemental resources.

For question two, we expect that local-floral resources during one sampling period (contemporaneous availability) are important in explaining bee abundance and diversity. We predicted that high levels of local floral resources would explain high bee abundance and diversity. Similarly, we predict that habitats with high levels of local-floral resources consistently throughout different seasons (phenological complementarity) will also generate high bee abundance and diversity. We predict that contemporaneous availability and phenological complementarity at sites will interact, where having greater phenological complementarity will limit the importance of abundant floral resources contemporaneously. Figure 1 illustrates this hypothetical expectation. Further, we predict that the effect of floral resource availability will vary depending on the sociality group (ie. Solitary, native social, or managed social).

Methods

Study Area

This study was conducted in the Soconusco region of Chiapas, Mexico, (15°10'15"N; 92°20'33.192 W) a coffee growing region with varying vegetation complexity, imposed by management decisions, from June 2014 to April 2015. The rainy season takes place from May to November and dry season takes place from December to April. Twenty-five 20m x 20m plots were established based on the estimated composition of floral availability provided by plant species within each site. All sites were at least 100 m apart. We attempted to include four different plot types in order to capture variation in floral resources from trees. However, all analyses were conducted using continuous data across these four site types, rather than categorical analyses. Plot types were chosen based on temporal availability of floral resources from shade trees. The four plot types included: 1) tree species with consistent floral resources available throughout the year, or a combination of dry and rainy season flowering trees (high phenological complementarity); 2) tree species with floral resources available only in the dry season; 3) floral resources available only in the rainy season; and 4) no floral resources from trees (Table 1). Six plots were established for each plot type, except for plot type two which had seven plots. All plots had coffee, which flowers in the dry season and most treatments had floral resources available through herbaceous ground cover. Floral resources and pollinator diversity were measured in each plot in June 2014 and July 2014 (rainy season), and January 2015 and February 2015 (dry season). To test all of our predictions, we performed vegetation and pollinator surveys.

Vegetation Survey

Floral availability and pollinator diversity were measured on the same day for each plot. Floral resources from trees, herbaceous ground cover and coffee were all measured. Canopy cover was measured at five points throughout the site using a handheld spherical densitometer. All flowering trees were recorded. The proportion of trees in flower was calculated by counting the number of trees in flower over the total number of trees in the plot. Ground cover was measured by randomly placing four 1x1 m quadrats within each plot and measuring the percent groundcover in each quadrat and the percentage of flowering herbs within each quadrat. All flowering herbs were identified to a morpho-species and counted. Percent groundcover in flower was calculated by taking the proportion of flowering herbs to the total groundcover. When coffee was in flower, a ranking for coffee flowering was given to each plot ranging from 0 (no flowers) to 4 (all coffee in flower). Percentage of coffee in flower was determined by selecting three coffee bushes and counting flowers and buds. Any additional floral resources present, including epiphytes, were noted for each plot.

Pollinator Survey

Resource requirements vary throughout the season across bee species with different life histories. This is especially relevant in coffee growing regions, where coffee only flowers during two or three events for a duration of two months of the year (Philpott, Uno, & Maldonado, 2006; David W Roubik, 2002). While the coffee flowers offer an abundant and valuable resource to bees, it is ephemeral and does not sustain their foraging requirements year round. Additionally, a single floral resource may not sustain all of bees' nutritional requirements of pollen and nectar (Bluthgen & Klein, 2011). Floral resources in trees, as well as in ground cover, are thus invaluable to sustain them nutritionally and temporally. To quantify pollinator diversity at each site, pollinators were collected using pan traps and sweep nets. 30 148mL (Gordon's Food Supply) plastic bowls were placed across each plot in the shape of an x, that went through the center of each plot. One third of the bowls were painted fluorescent yellow, one third fluorescent blue and one third left white according to the standardized methods of (LeBuhn et al., 2003). Pan traps were set out before 9am and collected right before it began to rain, around 1pm in the rainy season and 2pm in the dry season. All pollinators caught were combined for each plot. All insects caught in the pan traps were preserved in alcohol in the field. Specimens were later separated and identified to species in the lab. We sweep netted for bees at each site between the hours of 9am and 11am, optimum foraging hours for bees in this region (S. Jha & Vandermeer, 2010). Each site was netted for a period of 10 minutes, on the same day that pan traps were laid out. One person performed the collection for each site. Bees that were found foraging on herbs or low trees were netted and identified on site, or kept in alcohol for later identification. During coffee flowering, coffee bushes were also observed for a period of 10 minutes. Any bees foraging on the flowers were identified in the field or kept in alcohol for later identification. Bees were identified using a combination of field guides (Michener, McGinley, & Danforth, 1994), reference collections from El Colegio Frontera Sur, and comparisons with species found at this field site from a previous study (S. Jha & Vandermeer, 2010).

Statistical Methods

We analyzed the differences in community composition between the dry and rainy season, specifically between four sampling periods, two in the rainy season (June and July) and two in the dry season (January and February), using a non-metric multidimensional scaling analysis (NMDS). We then conducted an analysis of similarity (ANOSIM) using a Bray-Curtis similarity index as the similarity measure in PAST (Hammer, Harper, & Ryan, 2001). The ANOSIM compares the mean distance within group to the mean distance between groups; this statistically determines separation in species composition between the two different seasons (Jimenez-Soto & Philpott, 2015).

To see what was explaining the differences in community composition between the sampling months, we ran individual ANOVAs to see how sampling month influences the proportion of native social bees, native solitary bees, and managed social bees. We then performed post-hoc Tukey's tests to determine which months were driving the differences. All variables were natural log transformed to meet the assumptions of the test.

To compare how contemporaneous floral resources and the level of phenological complementarity at sites influence bee abundance and richness, as well as to see if they interact, we created three metrics to quantify floral resource availability at sites. The purpose of these metrics was to create standard values that we could compare across sites as well as sampling times. The first metric combined individual floral resource variables across the four sampling periods to quantify phenological resource availability. This metric was then divided into metric 1a, which represents phenological resource availability from trees, and metric 1b, which represents phenological resource availability from groundcover. The second metric combined floral resources from trees at each sampling time to quantify contemporaneous resource availability [metric 2a]. The final metric combined floral resources from groundcover to also quantify contemporaneous resource availability [metric 2b] (Table 2).

These metrics were determined using a threshold analysis approach (Byrnes et al., 2014; Lefcheck et al., 2015). This approach assigns value to variables that exceed a threshold percentage. The threshold is a percentage of the maximum value of the variable across sites sampled. The method to calculate the metrics varies slightly between metric one and metric two. For metric one, the response variables are first assessed individually across sampling times (Fig. 2). If the response variable exceeds the selected threshold percentage, then that variable receives a value of 1 for that month and if it is below then it receives a value of 0, with a maximum value of 4 and minimum value of 0. To select the best threshold percentage, all possible threshold percentages from 5-95% were run to generate values for the relevant variable and compared with bee richness (Fig. 3). The percentage used to calculate the metric was selected based on which percentage's value was best correlated with bee richness, or had the highest slope (Fig. 3). Metric one was then separated into metric 1a, which has a final range from 0-11, and metric 1b, which has a final range from 0-6, by adding the values of the included variable into the final metric. Metric 1a is a combination of two variables (flowering tree abundance and richness) across four sampling times, and one variable (proportion # trees in flower) across three sampling times. We did not have data for the third variable in July, which is why it is only quantified in the metric for three sampling times. Groundcover species richness and percentage of groundcover in flower, which are represented by metric 1b, were only quantified in June, January and February.

For metric 2a, the three variables that characterize floral resources from trees were quantified together to select the best threshold percentage (Fig. 4). Values were assigned to each site for every time period based on how many of the three variables exceeded the threshold. All possible threshold percentages, from 5-95%, were run to generate values for the metric, which were then compared to bee richness in order to select the most predictive percentage (Fig. 5). The percentage used to calculate the metric was selected based on which percentage's value was best correlated with bee richness, or had the highest slope (Fig. 5). Metric 2a has a range from 0-3. This was then repeated for metric 2b, which included the two variables that quantified floral resources from groundcover (Fig. 4). Metric 2b has a range from 0-2.

We then tested all of the final metric values for collinearities. We analyzed the effect of contemporaneous and phenologically complementary floral resource availability on the following response variables: bee abundance, bee richness, native social bee abundance, native solitary bee abundance, and managed social bee abundance. These were analyzed using generalized linear mixed effect models ('glmer' function in package lme4) with a Poisson error distribution and logit link function (Bolker et al., 2008). Contemporaneous floral resources from trees, phenologically complementary floral resources from trees, their interaction, as well as contemporaneous floral resources from groundcover, phenologically complementary floral resources from groundcover, their interaction, and presence of coffee, were all analyzed as fixed effects. Plot, as a factor of season, was considered a random effect. The models were fitted by maximum likelihood with a Laplace Approximation and all terms that were not statistically significant were removed to improve model fit, using Akaike's Information Criterion (AIC). Statistical analyses were performed with the software R-Studio v. 0.98.1103 for Macintosh and PAST v. 3.04.

Results

We identified 796 bees of 31 species in 3 families. The most common family was Apidae (62.9%), followed by Halictidae (37%) and Megachilidae (0.1%). The most abundant species was *Apis mellifera scutellata*, the Africanized honeybee, which are managed on the farm. The second most abundant species was *Ceratina ignara*, a solitary Apidae species. Across plots during one sampling period, bee abundance ranged from 0 to 35. Bee richness ranged from 0 to 12. A total of 312 bees were caught during the rainy season and 484 bees were caught during the dry season. Flowering vegetation varied between sites and seasons. Flowering tree richness ranged rom 0 to 4 species in flower at a given sampling time at one plot. Flowering tree abundance ranged from 0 to 10 trees. The proportion of trees in flower ranged from 0 to 63%. The percentage of groundcover in flower ranged from 0 to 35% and the richness of groundcover in flower ranged from 0 to 7 species (Table 3).

Changes in the bee community based on season

Bee community composition differed between the two seasons, and differed between each sampling month (R=0.2406). The NMDS comparing the four months showed an apparent difference (stress=0.4606; Fig. 6). The ANOSIM found a significant difference in the bee community between June and July, both in the rainy season (p=0.0018). The community also differed significantly between January and February, both in the dry season (p=0.0066). Additionally, the communities differed between the dry and rainy seasons (Table 4).

Changes in total bee abundance and richness between the seasons

Floral resources from trees did not significantly affect total bee abundance, so we removed these variables from the model. Contemporaneous and phenologically complementary floral resources from groundcover interacted to influence bee abundance (z=-2.841; p<0.01; Table 5). At sites with low phenological complementarity in ground cover resources, high contemporaneous floral resources from groundcover positively associated with bee abundance. However, at sites with floral groundcover resources available throughout the two seasons (high phenological complementarity), contemporaneous floral resources did not positively correlate with total bee abundance. Thus, contemporaneous floral resource availability from groundcover was important in explaining bee abundance at sites that did not maintain consistent floral resources throughout the year (Table 5; Fig. 10 and 11). Coffee flowering positively influenced total bee abundance (z=11.334; p<0.001; Table 5); season also positively influenced bee abundance with higher abundances found during the dry season (z=3.567; p<0.001; Table 5).

Floral resources from trees did not significantly influence bee richness and were removed from the model. Coffee (z=6.059; p<0.001; Table 5) and season (z=3.781; p<0.001; Table 5) positively correlated with bee richness. High phenological complementarity in floral resources from groundcover was positively correlated with bee richness as well (z=4.5050; p<0.001; Table 5), but contemporaneous floral resources from groundcover did not influence bee richness (Table 5).

Changes among different sociality groups between the seasons

The proportion of solitary bee abundance did not change between the four sampling months, or the two different seasons (F=0.673, p=0.571; Fig. 7. The proportion of native social bee abundance at one time was higher in the rainy season than in the dry season (F=3.849, p=0.0126; Fig 8). Finally, the proportion of managed social bee (*Apis mellifera scutellata*) was significantly higher during the period in which coffee was flowering (F=13.79, p<0.001) (Fig. 9).

Contemporaneous and floral resources from groundcover that were phenologically complementary interacted to influence bee abundance (z=-2.627; p<0.001). At sites with low phenological complementary floral ground cover resources, high contemporaneous floral resources from groundcover positively impacted native bee abundance. At sites with floral groundcover resources available throughout the two seasons (low phenological complementarity), contemporaneous floral resources did not positively impact native bee abundance (Fig. 12 and 13). Thus, contemporaneous floral resource availability from groundcover was important in explaining native bee abundance at sites that did not maintain consistent floral resources throughout the year (Table 5; Fig. 12 and 13). Coffee flowering (z=6.212; p<0.001) positively influenced native bee abundance. Additionally, there were more native bees in the dry season than in the rainy season (z=3.822; p<0.001).

Solitary bee abundance was explained by the presence of coffee in flower (z=8.858; p<0.001; Table 5) and the season, where there were more individuals in the dry season (z=3.855; p<0.001; Table 5). Floral resources from trees and groundcover did not explain solitary bee abundance at either time scale.

Season was important for managed bee abundance, as there were greater numbers during the dry season (z=-2.001; p<0.05; Table 5). Presence of coffee in flower was also positively correlated with managed bee abundance (z=8.342; p<0.001; Table 5).

Discussion

Phenological resource complementarity is an example of the biodiversity-ecosystem function relationship, in which complementarity in floral resources through time functions to satisfy foraging requirements of bees throughout their foraging season. In coffee agroforests, coffee is grown under shade trees and in the presence of herbaceous groundcover. These agricultural systems have the potential to support bee resource requirements, depending on the intensity of their management. We found more bees to be active during the dry season, which can be explained by the presence of flowering coffee, a high quality, but ephemeral, floral resource. Still, bees were found foraging in the rainy season, as well as in the dry season outside of the coffee flowering event. The bee community differed between the two seasons, as well as between sampling events. The presence of bee foraging during the two seasons, as well as differences in the bee community, exemplifies the importance of understanding phenological resource complementarity, particularly in tropical agroecosystems. We found that contemporaneous floral resource availability and phenological resource complementarity from groundcover interact to explain bee abundance. We did not find floral resources from trees to be important in explaining bee abundance or richness.

Changes in the bee community based on season

We found that the bee community composition differs between the two seasons, and the four sampling months. Each sampling month had different combinations of floral resources available. The floral resources available are determined by flowering phenologies of trees and coffee, as well as the management of the herbaceous ground cover on the farm. Under normal management, the herbaceous groundcover is completely removed several times per year, rapidly removing available floral resources for bees from this source. We speculate that the context of floral resource sources available at a sampling time impact how bees interact to forage for resources and thus determine their presence on them. Native bees foraging on high quality resources will be displaced in the presence of managed honeybees (Roubik & Wolda, 2001). But if there are other resources available concurrently with the displacement, they will persist by foraging on the other resources, possibly of lower quality. Thus if one group is displaced by another on coffee, they can still be found foraging on trees or herbaceous groundcover if it is in flower. Since each sampling time has a different combination of floral resource sources (ie. groundcover, trees, coffee), with varying abundances and richness, we see strong differences in community composition of bees during the different seasons.

Changes in total bee abundance and richness between the seasons

Total bee abundance did not respond to floral resources from trees, which was unexpected as previous studies have shown the importance of trees in predicting bee abundance and richness (Jha & Vandermeer, 2010; Klein et al., 2003), particularly because one of these studies was performed across the same farms that were used in this study. However, the variation we found in floral resources from trees across our sites was much smaller than this previous study, which may have reduced its signal. Between these studies, one of the farms we sampled significantly reduced the number of shade trees in an effort to intensify farm management (I. Perfecto, *pers. communication*). Some shade trees were also cut before we sampled in February 2015 (K. Fisher, *pers. observation*)[1]. Additionally, bees may respond to a larger spatial scale than we used for this study (Jha & Vandermeer, 2010). Floral resources from groundcover however, were very important in explaining total bee abundance throughout the year. These resources interacted between the two time scales, where contemporaneous resource availability was more impactful at sites with lower phenological complementarity. This suggests that sites with higher phenological complementarity can sustain bee foraging requirements, even at times where contemporaneous resources are low.

Bee richness responded to high phenological complementarity of floral resources from groundcover, but not contemporaneous availability. This may be because different bee species' dependence on groundcover is context dependence. If higher quality resources are being exploited by competitive foragers, less competitive foragers may shift to other resources like groundcover (Cairns, Villanueva-Gutiérrez, Koptur, & Bray, 2005; Klein et al., 2003). Sources of high quality resources vary depending on the season, so different bee species will rely on groundcover at different times. This is supported from season being important in explaining bee richness.

Changes between different sociality groups between the seasons

The differences are more explicit when we compare the proportions of different sociality groups across the sampling times. Floral resource availability influenced bee groups differently as we expected, except for their response to coffee flowering, which was always positively correlated. This is expected, as coffee is a mass flowering, high quality resource that is abundant throughout the landscape when it flowers. Bee social groups have different recruitment strategies in response to mass flowering crops: managed social bees forage with a concentration effect, whereas native solitary and social bees exhibit a dilution effect in their foraging response to increases in floral resources. Additionally, the groups respond to resources at different scales (Jha & Vandermeer, 2009).

The highest proportion of native social bees was found in the rainy season, which had the lowest number and richness of trees in flower (SOM, Table S-1). This was unexpected, as previous studies have found this group to respond the strongest to increases in floral resource availability from trees. But neither contemporaneous nor phenological complementary floral resources were found to affect native bee abundance. Like total bee abundance, native social bee abundance responded to an interaction between contemporaneous ground cover and high phenological complementarity in groundcover.

Both flowering and non-flowering resources from trees have been found to be important (Jha & Vandermeer, 2010). Native social bees may be more active in the rainy season because they are nest building or foraging for resources other than nutritive resources. Native social bees, of the genus Meliponini, have been found to collect plant resins for communication (Leonhardt, Blüthgen, & Schmitt, 2009) and possibly for immune defenses (Leonhardt, Wallace, Bluthgen, & Wenzel, 2015). Additionally, they were actively foraging on the available floral resources from groundcover vegetation, the availability of which is determined by the management regime and not phenological patterns.

Another possibility as to why native bees were lower in the dry season is that they may be avoiding floral resources that are occupied by other species (Johnson and Hubbel, 1974; Nagamitsu and Inoue, 1997), particularly exhibiting resource shifts in order to avoid competition with the Africanized honeybees (Cairns, Villanueva-Gutiérrez, Koptur, & Bray, 2005; Roubik, Moreno, Vergara, & Wittman, 1986; Roubik, 1978) which was most abundant in the dry season when coffee was flowering. Native social bees have been found to respond negatively to greater distance to forest (Brosi & Briggs, 2013; Klein, Steffan-Dewenter, & Tscharntke, 2003; Ricketts, 2004). In a previous study, distance to forest did not impact bee abundance. This was explained by the diversity of within farm resources being sufficient in sustaining resource requirements (Jha & Vandermeer, 2010). But since the significant tree removal in 2012, the forest fragments adjacent to the farms may now be relatively more valuable than they were during the previous study. The native social bees may have shifted to forest fragments during this time, which would explain their low numbers on the farm.

Native solitary bees did not change in their proportion of abundance during the four sampling times. Native solitary bees only responded to presence of coffee and season, which contradicts other studies, which have found solitary bees to respond strongest to herbaceous groundcover. Solitary bees require a diverse array of floral resources to sustain local densities (Klein et al., 2003). The sites we sampled may have maintained a high enough combination of resources for solitary bees throughout the year, which made it difficult to observe a signal from one resource level. Solitary bees have been found to respond the strongest to flowering herb density (Klein et al., 2003) and species richness of flowering herbs (Jha & Vandermeer, 2010), which were both available at similar densities throughout the four sampling periods. The most abundant solitary bee species was of the genus *Ceratini*. Canopy cover has been found to be important for these bees because it provides access to nesting sites (Jha & Vandermeer, 2010). Canopy cover did not change between the sampling periods. The consistency in these resources may explain why the solitary bee community remained at similar proportions throughout the sampling periods. The solitary bee community also remained in similar proportions during the coffee flowering event, in contrast to native social bees and managed honey bees. While most solitary bees forage on coffee flowers (Klein et al., 2003), they will switch to groundcover resources when social bees are foraging (Willmer and Stone, 1989; Klein et al. 2002). This may explain why they were still found foraging at sites in similar proportions during this time.

Managed honeybees were found in the highest proportions during the dry season when coffee was flowering (February). This is contrary to what we expected, as we predicted that their proportion would remain the same as they were given supplemental resources at the apiaries during our sampling periods (E. Jiminez-Soto, *pers. comm*). There are several apiaries scattered across the farms where we sampled. Social bees have been found to positively correlate with blossom cover of coffee (Klein et al., 2003). The Africanized honeybee exhibits a concentration effect in response to mass flowering, where they increase visitation with increases in floral resource abundance (Jha & Vandermeer, 2009; Veddeler et al., 2006). Managed bees only responded to coffee availability and season. The significant increase in their foraging during February is best explained by the presence of coffee flowering. Coffee flowers are high quality and abundant resources for bees when they are available. As the managed honeybees have been found to be the best competitor in obtaining high quality floral resources (Cairns et al., 2005; Roubik et al., 1986; Roubik, 1978) it is reasonable that they would significantly respond to coffee flowering. Additionally, this group was found to be at a significantly higher proportion during the coffee flowering event, substantiating their concentration effect foraging strategy. This explanation also substantiates why the native social bees were so low during this time, as they shift resource use in response to other foragers, especially Africanized honeybees (Cairns, Villanueva-Gutiérrez, Koptur, & Bray, 2005; Roubik & Wolda, 2001).

Conclusion

Resource heterogeneity, which is determined by management decisions in agricultural landscapes, is a key drive of species richness and abundance (Macarthur and Macarthur, 1961; Tylianakis et al, 2008). It has been shown that changes in land use can lead to resource mediated pollinator declines (Holzschuh et al, 2008; Kennedy et al., 2013; Weiner et. al, 2014). Previous studies have found that floral resource heterogeneity at the local and landscape spatial scale interacts to explain bee abundance, where bee abundance is positively impacted by improvements in local resource availability in more simplified landscapes (Roschewitz et al, 2005; Tscharntke et al, 2005). They did not find that local resource availability was as important in farms that were in more heterogeneous landscapes, as the surrounding landscape served as refuges. Similarly, we found that contemporaneous resource availability was more important for bee abundance at sites that had lower phenological complementarity. We argue that in addition to spatial resource heterogeneity, resource heterogeneity through time is also critical in explaining bee richness and abundance. Farms can support pollinators by maintaining complementarity in floral resources available from both crop and non-crop plants. Future studies should investigate the mechanism driving these patterns. Particularly, how specific bee groups shift resource use depending on the context of resource availability, resource requirements at that life history stage (nesting, nutritive, immune, etc.) and competition with other bees.

Tables

Always in Flower	Flowers in Dry Season	Flowers in Rainy Season	Never Flowers
Conostegia xalapensis *Miconia argentea* *Yuca elephantipes*	*Inga lauriana* *Inga micheliana* *Inga rodrigueziana* *Inga vera* *Schizolobium parahybum* *Alchornea latifolia* *Cybistax donnell-smithii* *Solanum* sp.	*Trema micrantha* *Spathodea campanulata*	*Quercus corrugata* *Pinus pseudostrobus*

Table 1: Table showing trees in phenology categories based on season.

	Phenological Resource Availability [Metric One]			**Contemporaneous Availability [Metric Two]**	
	Resource Variable	*Threshold Value*		*Resource Variable*	*Threshold Value*
Metric 1a	**Flowering tree species richness**	0.62	Metric 2a	Floral resources from trees	0.15
Metric 1a	**Flowering tree abundance**	0.34	Metric 2b	Floral resources from groundcover	0.21
Metric 1a	**Proportion # Trees in Flower**	0.1			
Metric 1b	**Groundcover species richness**	0.58			
Metric 1b	**% Groundcover in Flower**	0.4			

Table 2: Table describing the threshold value selected for each variable for both metrics. The maximum value of the mean for each variable was first determined. Then all threshold values from 5-95% of the maximum value of the mean were run. Threshold values were selected based on the value that had the strongest correlation (highest slope) with bee richness.

Variable	June	July	January	February	Total
Flowering Tree Richness	0-1	0-1	0-4	0-2	0-4
Flowering Tree Abundance	0-6	0-6	0-10	0-9	0-10
Avg. % Tree in Flower	0-42.85%	0-40%	0-62.5%	0-56.25	0-63%
% Groundcover in Flower	0-27.08%	0-23.09%	0-35%	0-27.5%	0-35%
Richness of Groundcover in Flower	0-7	0-4	0-5	0-7	0-7
Bee Abundance	0-24	0-23	0-11	0-35	0-35
Bee Richness	0-9	1-7	0-6	0-12	0-12

Table 3: Results of ranges found for each site during each sampling time and for all sampling times combined. Ranges include both vegetation and bee variables.

	June	July	January	February
June	x	0.0018	0.0013	0.0001
July	0.0018	x	0.0092	0.0001
January	0.0013	0.0092	x	0.0066
February	0.0001	0.0001	0.0066	x
R=0.2406				

Table 4: ANOSIM results

		Estimate	**Std. Error**	**z-value**	**Pr(|>z|)**
Bee Abundance	Intercept	0.44633	0.2093	2.132	0.03299*
	Present GC	0.96316	0.3643	2.643	0.00820**
	Temporal GC	0.25514	0.0533	4.782	1.74e-06***
	Groundcover Interaction	-0.27721	0.0975	-2.841	0.004496**
	Coffee	1.50044	0.1323	11.334	2e-16***
	Season	0.90673	0.25420	3.567	0.00036***
Bee Richness	Intercept	0.12450	0.19885	0.626	0.5312
	Temporal GC	0.18067	0.04011	4.505	6.64e-06***
	Coffee	1.08261	0.17868	6.059	1.37e-09***
	Season	0.72223	0.19104	3.781	0.000157***
Native Bee Abundance	Intercept	-0.42266	0.30883	-1.369	0.171121
	Present GC	1.38322	0.48690	2.841	0.004499**
	Temporal GC	0.18791	0.07882	2.384	0.017132*
	Groundcover Interaction	-0.34787	0.13243	-2.627	0.008619**
	Coffee	1.30688	0.21036	6.212	5.22e-10***
	Season	1.28609	0.33652	3.822	0.000133***
Solitary Bee Abundance	Intercept	-0.3431	0.2888	-1.188	0.234926
	Coffee	1.8663	0.2107	8.858	<2e-16***
	Season	0.8649	0.2243	3.855	0.0001166***
Managed Honey Bee Abundance	Intercept	-0.3351	0.2893	-1.158	0.2467
	Coffee	1.9062	0.2285	8.342	<2e-16***
	Season	-1.8905	0.9447	-2.001	0.0454*

Table 5: GLMM Results
Significance Levels: p<0.1; *p<0.05; **p<0.01; ***p<0.001

Figures

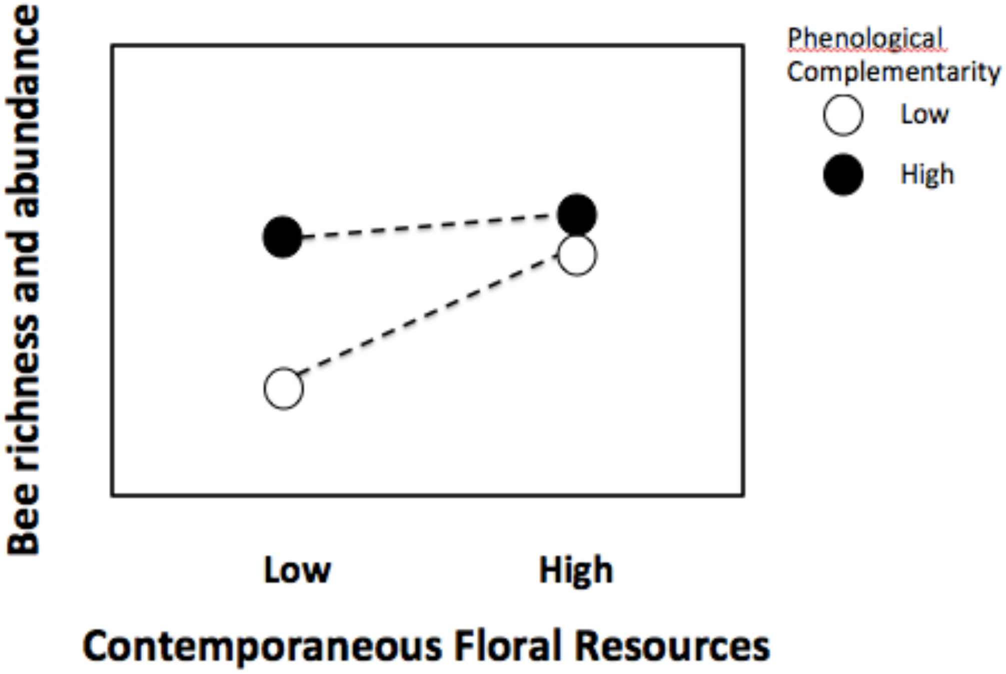

Figure 1: Hypothetical graph showing expected relationship between floral resource availability and bee richness/abundance. At sites with low phenological complementarity, it is expected that there will be a dramatic increase in bee richness/abundance when contemporaneous floral resources shift from low to high (ie. When coffee flowers). At sites with high phenological complementarity, it is expected that there will not be a significant increase in bee richness/abundance when there is a shift from low to high contemporaneous floral resources (ie. When coffee flowers).

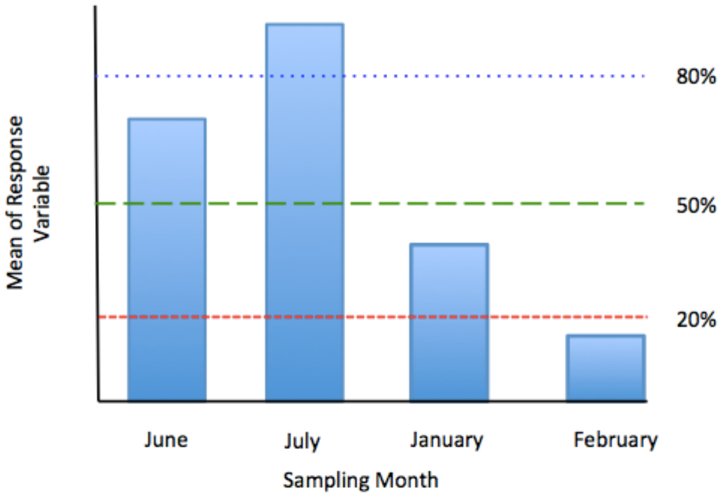

Figure 2: Conceptual illustration of method used to define metric one. The individual response variable (flowering tree or flowering groundcover characteristic) being evaluated is shown for each sampling month. The percentages are possible threshold percentages that represent a percentage of the maximum value for that variable across sampling sites. If the response variable exceeds the selected threshold percentage, then that variable receives a value of 1 for that month and if it is below then it receives a value of 0, with a maximum value of 4 and minimum value of 0. If the threshold was set at 20% for illustration, then the metric value for the response variable would be 3.

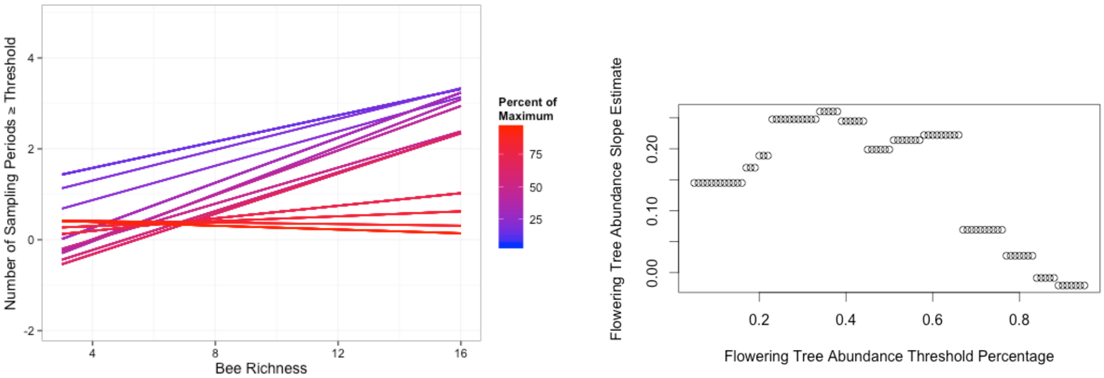

Figure 3: Results of correlations between bee richness and the number of sampling periods that exceed the designated threshold percentage for every threshold percentage from 5-95%. Threshold percentages were chosen based on which percentage had the highest correlation with bee richness (Left). Linear coefficients for every threshold percentage [5-95%]. Threshold percentage was selected for each variable for metric one based on the threshold with the highest linear coefficient (Right).

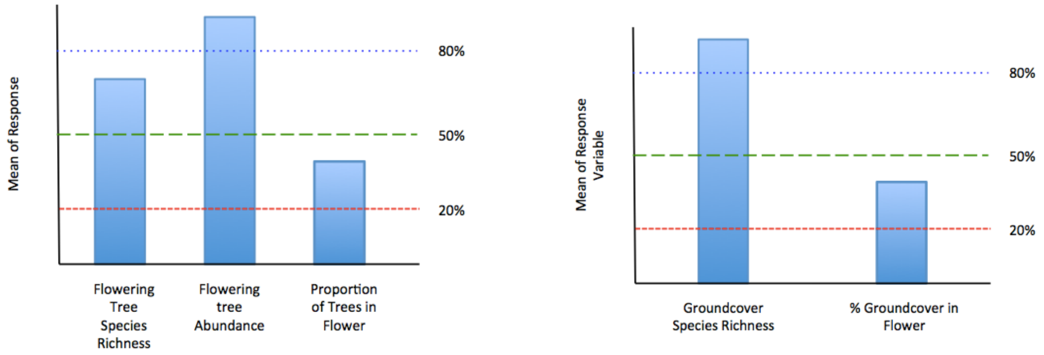

Figure 4: Conceptual illustration of method used to define metric 2a. The individual variables used to formulate this metric, floral resources from trees, are shown on the x-axis. The percentages are possible threshold percentages that represent a percentage of the maximum value for the individual variable across sampling sites. If the response variable exceeds the selected threshold percentage, then that variable receives a value of 1 and if it is below then it receives a value of 0, with a maximum value of 3 and minimum value of 0 (Left). Conceptual illustration of method used to define metric 2b. The individual variables used to formulate this metric, floral resources from ground cover, are Groundcover Species Richness and % Groundcover in Flower. The percentages are possible threshold percentages that represent a percentage of the maximum value for the individual variable across sampling sites. If the response variable exceeds the selected threshold percentage, then that variable receives a value of 1 and if it is below then it receives a value of 0, with a maximum value of 2 and minimum value of 0 (Right).

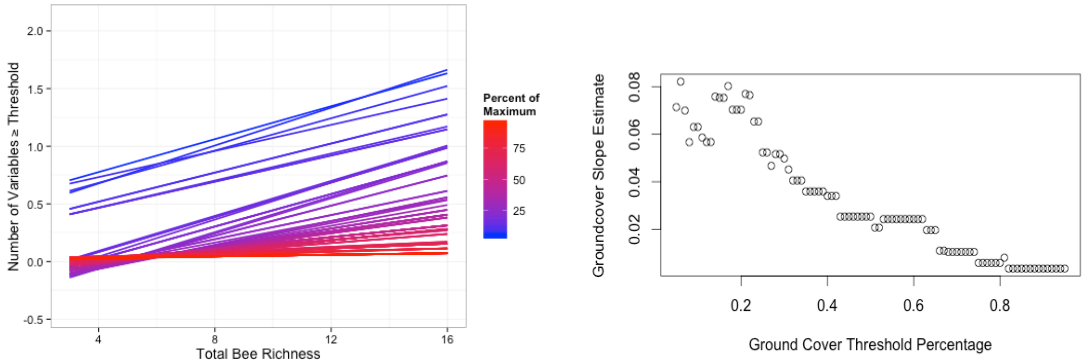

Figure 5: Results of correlations between bee richness and the number of variables that exceed the designated threshold percentage for every threshold percentage from 5-95%. Threshold percentages were chosen based on which percentage had the highest correlation with bee richness (Left). Linear coefficients for every threshold percentage [5-95%]. Threshold percentage was selected for metric 2a and 2b based on the threshold with the highest linear coefficient (Right).

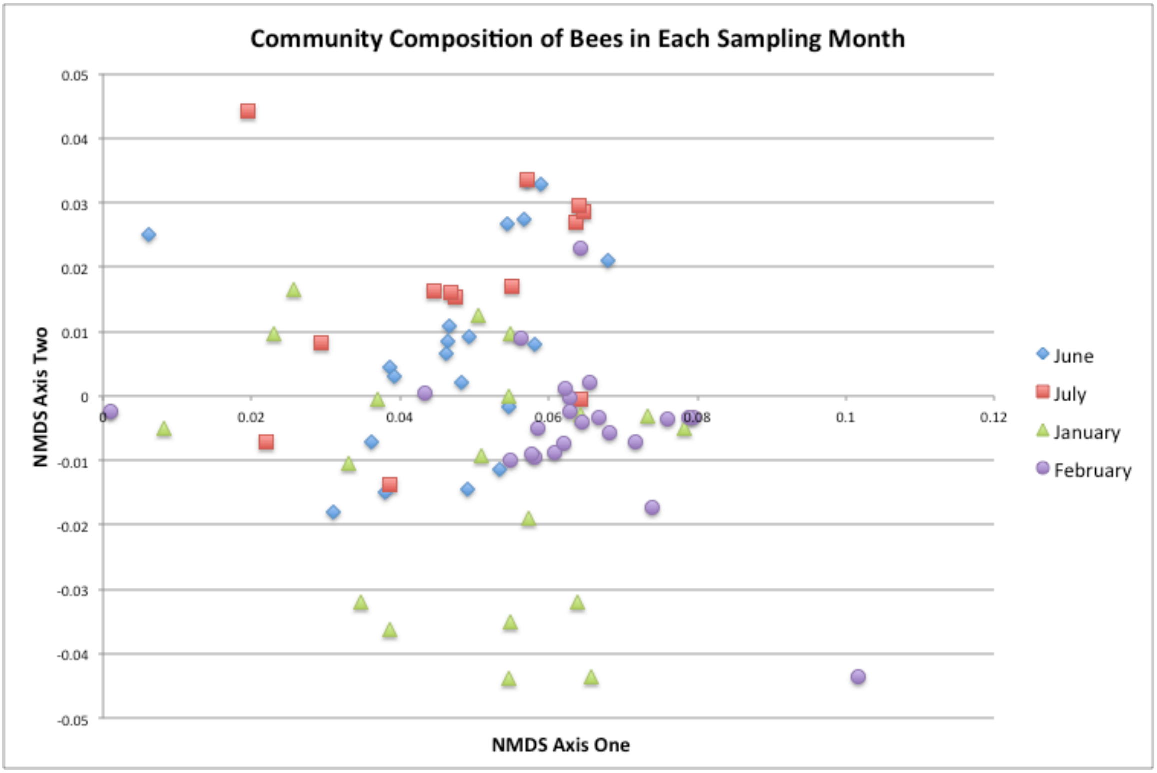

Figure 6: Results of Non Metric Multi-dimensional scaling analysis performed between each sampling period. There is an apparent difference in the bee community between each sampling time (Stress=0.2406).

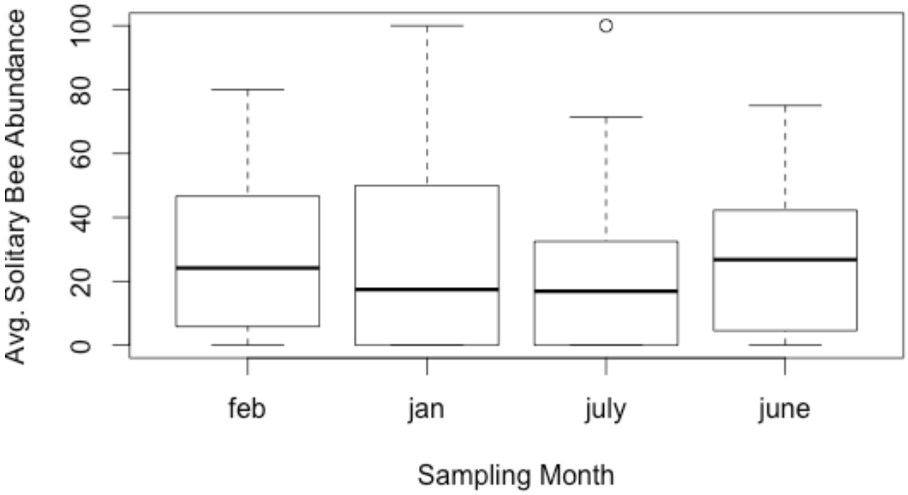

Figure 7: Box and whisker plots show the average proportion of native solitary bee abundance for each sampling month. There was no significant difference in proportion of any sampling month (F=0.673, p=0.571).

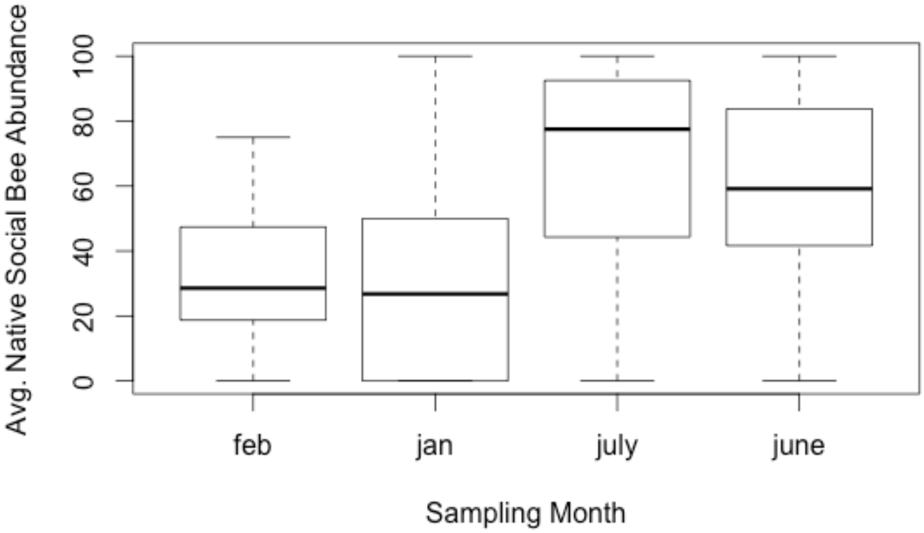

Figure 8: Box and whisker plots show the average proportion of native social bee abundance for each sampling month. There was no significant difference in proportion within each season. But the abundance was significantly higher in the months of the rainy season compared to the months of the dry season (F=3.849, p=0.0126).

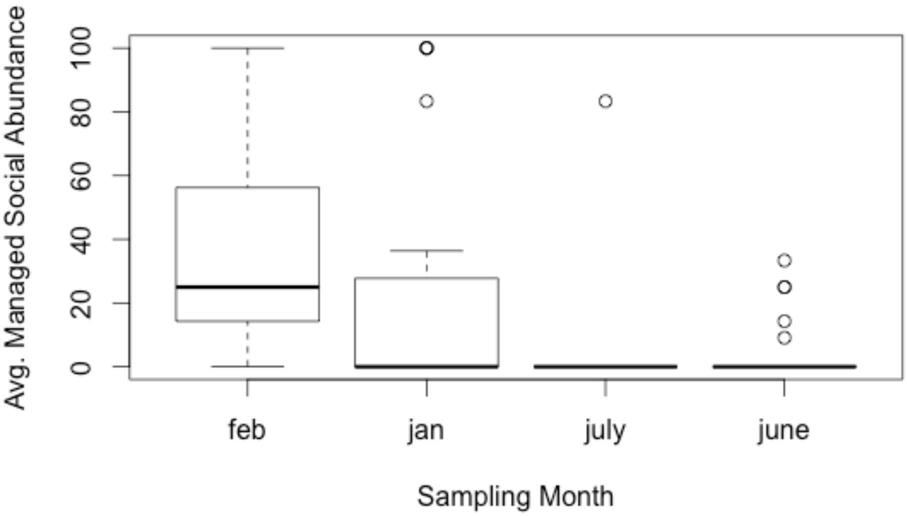

Figure 9: Box and whisker plots show the average proportion of managed social bee abundance for each sampling month. There is no significant difference in proportion between January, July and August, but there is a significantly higher proportion of managed honeybees in February compared with the other months (F=13.79, p<0.001).

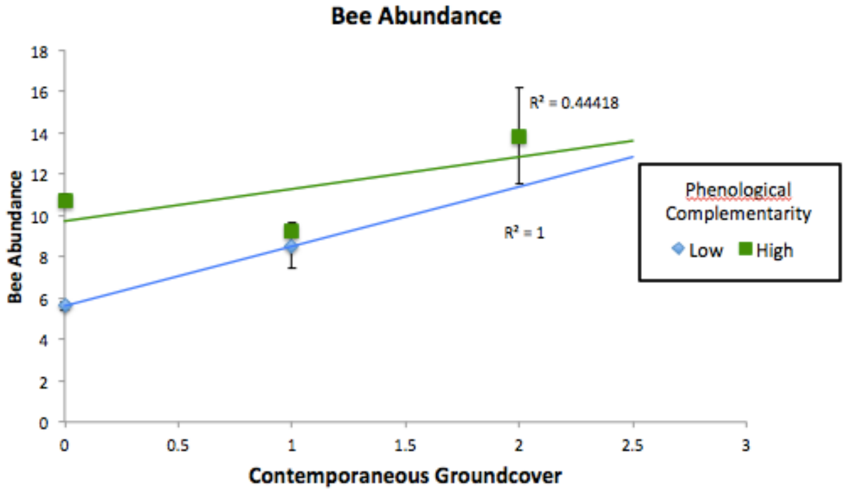

Figure 10: The effect of the interaction between floral resources from groundcover on total bee abundance. The x-axis represents metric 1 for contemporaneous groundcover. When there is lower phenological complementarity, contemporaneous groundcover is more important in explaining bee abundance.

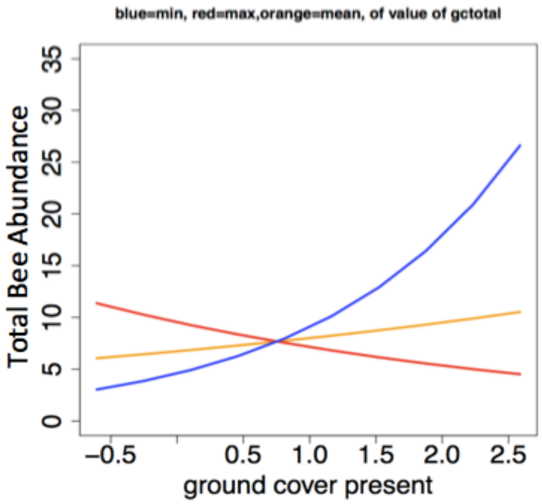

Figure 11: Interaction graph from table 3 with total bee abundance as ouput variable. The lines represent the minimum, maximum and average of metric 2b for floral resources from groundcover. The x-axis represents metric 1 for contemporaneous groundcover. The interaction suggests that when there is higher phenological complementarity (red line), the contemporaneous groundcover floral resources are negatively correlated with bee abundance. When there is lower phenological complementarity (blue), high contemporaneous floral resources is important in explaining high bee abundance.

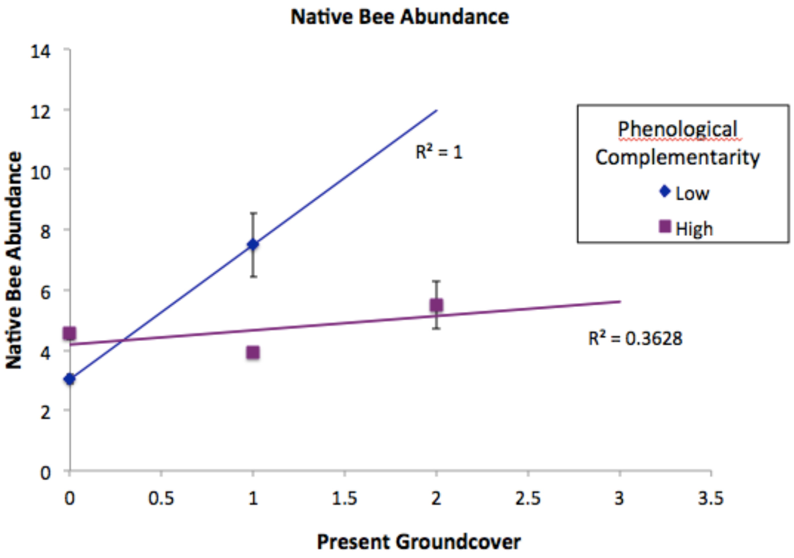

Figure 12: The effect of the interaction between groundcover floral resources on native bee abundance. When there is lower phenological complementarity from groundcover, contemporaneous groundcover is more important in explaining native bee abundance.

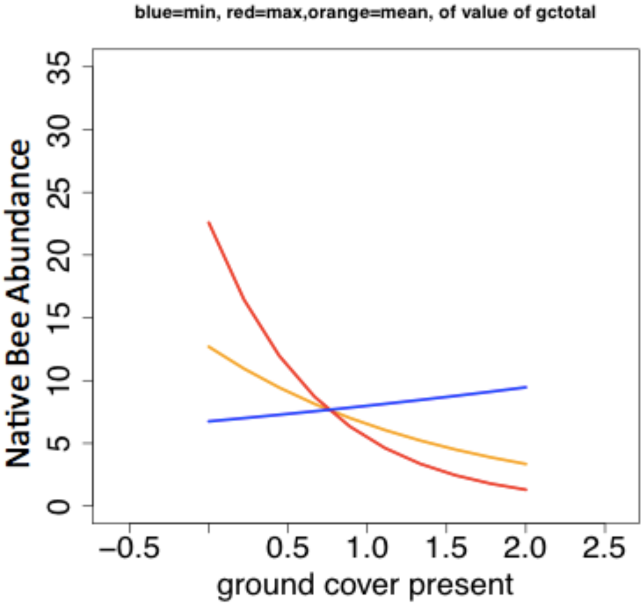

Figure 13: Interaction graph from table 5 with native bee abundance as ouput variable. The lines represent the minimum, maximum and average of metric 2b for floral resources from groundcover. The x-axis represents metric 1 for contemporaneous groundcover. The interaction suggests that when there is higher phenological complementarity (red line), the contemporaneous groundcover floral resources are negatively correlated with bee abundance. When there is lower phenological complementarity (blue), high contemporaneous floral resources is important in explaining high bee abundance.

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