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Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations

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Abstract

1 The honey bee *Apis mellifera* is native to Eurasia and Africa, although it is commonly introduced into crop fields of different parts of the world because of the assumption that it improves yield. This bee is, however, a poor pollinator of several crops compared with native insects. Indeed, honey bees can displace native pollinators and reduce their diversity. The present study evaluated the potential impacts of *A. mellifera* on the diversity of native pollinators of highland coffee (*Coffea arabica*) and its putative consequences for coffee production at the state of Veracruz, Mexico.

2 The abundance of *A. mellifera* and diversity of native pollinators were assessed during blooming at 12 shade coffee plantations and pollination experiments were conducted to determine the impacts of pollinators on coffee fruit production. Regression analyses were used to assess whether the abundance of honey bees was related to native pollinator diversity, and whether fruit production was influenced by both the diversity of pollinators and the abundance of *A. mellifera*.

3 Native pollinator diversity decreased as the number of honey bees increased. Furthermore, although coffee fruit production was positively related to the diversity of native pollinators, an increasing abundance of *A. mellifera* was correlated with a decrease in fruit production.

4 Highland shade coffee plantations are considered as reservoirs of the Mexican insect fauna. Thus, native pollinator diversity could be better preserved if beekeepers reduced the number of managed hives that they brought into plantations. This may also help to increase coffee yield by decreasing the putative negative effects of *A. mellifera* on native pollinators.

Keywords Agroecosystems, conservation biology, crop yield, ecosystem services, pollination service.

Introduction

The introduction of the honey bee *Apis mellifera* L. (Apidae) to the Americas might be considered one of the largest uncontrolled biological experiments induced by humans. Honey bees have been domesticated for the last 4000 years and introduced in almost every country of the world (Crane, 1990). Besides being appreciated for the production of honey, *A. mellifera* has historically been perceived as a beneficial insect for its role in pollination of crops and wildflowers (Watanabe, 1994; Buchman & Nabhan, 1996). Currently, the introduction of *A. mellifera* hives into crop fields is still a common practice because of the assumption that this improves the pollination and yield of crops (Torchio, 1990; Watanabe, 1994; Richards & Kevan, 2002), *Apis mellifera* appears, however, to be a poor pollinator of several crops compared with native insects, such as bumble bees and squash bees, which are more efficient in moving pollen among plants (Parker *et al*., 1987; Torchio, 1990; O'Toole, 1993; Batra, 1995). Indeed, a number of studies suggest that this bee competes with native pollinators for floral resources (Roubik, 1980; Schaffer *et al*., 1983; Steffan-Dewenter & Tscharntke, 2000; Thompson, 2006). Thus, the introduction of *A. mellifera* into agricultural fields may

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decrease the diversity of native floral visitors, which could even be more efficient pollinators of crops than honey bees.

Highland coffee *Coffea arabica* L. (Rubiaceae) is a self-compatible crop, not requiring pollination by animals to produce fruits and seeds (Fægri & van der Pijl, 1971). Nevertheless, increases in the abundance and diversity of pollinators may enhance cross-pollination and lead to higher fruit set and yield (Roubik, 2002a; Klein *et al*., 2003; Ricketts *et al*., 2004; Vergara & Badano, 2009). Mexico is the world's fifth largest producer of coffee and the third largest exporter of organic coffee (International Coffee Organization, 2006). Although the management of pollination is not a common practice among Mexican coffee producers, beekeepers usually move many hives of *A. mellifera* into coffee plantations during blooming to take advantage of the intense nectar flow (Labougle & Zozaya, 1986). Although these are managed hives, it is important to note that the vast majority of the honey bees in Mexico are Africanized hybrids. The Africanization of managed hives has occurred subsequent to 1986, when feral African honey bees were first reported in this country (Moffet *et al*., 1987). As far as we are aware, however, there are no studies evaluating the impacts of this introduction of *A. mellifera* on the productivity of Mexican coffee plantations.

In the present study, a series of correlative analyses are used to assess whether the introduction of *A. mellifera* may affect the diversity of native pollinators and, consequently, the production of fruits in highland coffee plantations of Mexico. Three basic questions are addressed: (i) is *A. mellifera* affecting the diversity of native pollinators in plantations; (ii) does the production of coffee fruits relate to the diversity of native pollinators and (iii) could high numbers of honey bees negatively influence fruit production through their effects on the diversity of native pollinators?

Materials and methods

The present study was conducted in the central area of the State of Veracruz (19°12′22″–27′29″N, 96°53′04″–59′17″W), where an important proportion of the Mexican coffee is produced. Twelve highland coffee plantations were selected in this area during 2003. The area of these plantations varied in the range 5–10 ha. In accordance with the criteria proposed by Moguel and Toledo (1999), and later modified by Gordon *et al*. (2006), we identified three types of coffee management systems among the selected plantations. Four plantations belonged to the 'rustic shaded coffee', where plantations are located beneath the canopy of native tropical forests after removing the understory. Four plantations belonged to the 'commercial polyculture', where the native forest is removed and replaced with a set of non-native tree species with high economic value (pepper and cedar, among others). Finally, four plantations belonged to 'specialized shade', where native forest is removed and replaced by tree species belonging only to the Fabaceae family.

To estimate the diversity of pollinating insects and the number of *A. mellifera* workers, their flower visitation rates were recorded in May 2004, during coffee blooming. For this, four coffee plants were selected at each site by using points at random directions and distances from the centre of plantations, and selecting the nearest flowering coffee plant to each point. Because coffee flowers usually remain open for 2 days but are attractive to pollinators only during the first day (Free, 1993), this procedure was repeated as many times as necessary until finding four plants with recently open flowers.

At each plantation, the four selected plants were sequentially observed during 25-min periods on the same day; the first plant was observed between 09.00 and 09.25 h, the second plant between 11.00 and 11.25 h, the third plant between at 13.00 and 13.25 h and, finally, the fourth plant was observed between 15.00 and 15.25 h. We performed observations on different plants at the different times of the day to avoid biases as a result of possible accidental manipulation of the flowers. Observations started at 09.00 h because insect activity earlier in the day is very low (Vergara *et al*., 2008). Therefore, 1 day per plantation (12 days in total) was spent. On each selected plant, direct observations of floral visitors were conducted on an imaginary area that included 40% of its branches. All observations were conducted on clear sunny days by the specialist (C. H. Vergara) to identify the pollinator species *in situ*. In all cases, the observer was located at 0.5 m from flowers and recorded the number of individuals of each insect species visiting flowers. Only those insects that made contact with the sexual parts of flowers were considered as pollinators, and only these data were included in the analyses. Some insects that are traditionally considered as floral robbers, such as species of the genus *Trigona* subgenus *Trigona*, were included because they were detected collecting nectar or pollen legitimately and making contact with sexual parts of flowers.

Data from the four plants selected at each plantation were later pooled to estimate the total number of individuals of each native species and *A. mellifera* workers. Native pollinator diversity at each plantation was estimated using two measures: species richness and the Shannon–Wiener index. *Apis mellifera* itself was not included in these estimations. Species richness (S) was estimated by counting the number of the different flower visitor species. The Shannon–Wiener index was estimated as $H' = -\Sigma pi\ \ln(pi)$, were pi is the relative abundance of the i_{th} species; pi values were calculated as the ratio between the number of individuals of the i_{th} species and the total number of insects recorded at the respective plantation.

Linear regression analyses were conducted to assess whether variations in the number of *A. mellifera* were related to changes in the diversity of native pollinators. The dependent variables here were S or H', whereas the predictive variable was the number of *A. mellifera* recorded at each the respective plantation ($n = 12$). Nevertheless, because both pollinator diversity and *A. mellifera* abundance may be influenced by differences in management systems (Vergara & Badano, 2009), we compared the values of S and H' among management systems to validate these correlative analyses. For this, one-way analysis of variance (ANOVA) was used to compare S, H' and the number of *A. mellifera* among the four management systems. In these analyses, if S, H' and the number of *A. mellifera* are not indicated to differ among management types, then the correlative analyses described above can be assumed as valid.

Diversity and visitation rates of pollinators may also be influenced by other important concomitant factors, such as the distance between crops and patches of native vegetation

(Rathcke & Jules, 1993; Klein *et al*., 2003) and/or by the abundance of floral resources (Fægri & van der Pijl, 1971). Therefore, the putative effects of these variables were also assessed to avoid biases in the interpretation of the results from correlative analyses. The distance (in metres) between the edge of each plantation and the closest patch of native forest was determined by analyzing high resolution satellite images (IKONOS-2, 1 pixel per m^2) with the software ERDAS IMAGINE 8.4 (ERDAS Inc., Atlanta, Georgia) and subsequently processed with ARCVIEW 3.2 (ESRI Software, Redlands, California). To estimate the abundance of floral resources, all plants in bloom (herbs, shrubs, including coffee plants, and trees) were recorded in 5×100 m^2-quadrats per site, and a percentage of covering was estimated by five different observers. An average percentage value was then calculated for each site. With these data, simple linear regression analyses were performed, where diversity measures (S and H') and the number of *A. mellifera* recorded at each plantation were the dependent variables, and the distance to forest patches and abundance of flowers were the predictive variables.

In May 2004, four coffee plants were randomly selected at each plantation to assess whether fruit production was related to native pollinator diversity and the number of *A. mellifera* workers. These plants were chosen by using the same protocol described above, although they were different from those on which pollinator observations were performed to avoid confounding effects as a result of the presence of the observer. Later, a branch with floral buds was selected on each plant, taking care that all selected branches were approximately at the same height in the plant and had the same length and sun light exposure. All floral buds on each branch were counted and the branch was labelled with small plastic flags. These labelled buds remained exposed to pollinators throughout the entire floral cycle (open pollination treatment). Additionally, a second branch was chosen on each plant to assess the autogamic production of fruits. Here, all floral buds on the branch were counted and labelled, and branches were later covered with a (Nytex mesh, Mumbai, Maharashtra, India) bag to prevent the access of pollinators (self pollination treatment).

The fruit set rate (FS) and the fruit retention rate (FR) were later calculated for each plant of each treatment. These two measures were used because FS indicates the immediate effect of pollination on fruit development, whereas FR estimates the final fruit production after physiological limitations of plants have acted. To estimate FS, the number of developing fruits on each branch was recorded 7 weeks after labelling floral buds, and it was calculated as the ratio between the number of developing fruits and the initial number of floral buds on each branch. To estimate FR, the number of fruits that reached maturity was recorded 6 months after labelling flowers, and FR was calculated as the ratio between the number of mature fruits and the number of fruits initiated per branch. Values of FS and FR were averaged across the four plants considered at each plantation to avoid pseudo-replication in the statistical analyses.

A series of simple linear regression analyses were conducted to determine whether coffee fruit production measures were related to the diversity of native pollinators and the number of *A. mellifera* workers. First, we only focused on the open pollination fruit production, where FS and FR acted as dependent variables and S, H' or the number of *A. mellifera* were used as predictive variables. Second, to ensure that the observed changes in coffee fruit production were a result of the pollinators, we calculated the differences between the estimators of coffee fruit production obtained from open pollination (FS_{open} and FR_{open}) and their respective values obtained from self pollination (FS_{self} and FR_{self}). Therefore, for each plantation these differences were calculated as: $\Delta FS = (FS_{open} - FS_{self})$ and $\Delta FR = (FR_{open} - FR_{self})$, where larger values of ΔFS and ΔFR are indicative of bigger impacts of open pollination for fruit production. In all cases, these values of FS and FR are the averages from the four plants considered at each plantation for each pollination treatment to avoid pseudo-replication. Values of ΔFS and ΔFR were later regressed against S, H' and the number of *A. mellifera* as described above to assess the potential effects of these variables on coffee production.

Because management systems may also influence fruit production rates, and this may bias the interpretation of the results, values of FS_{self} and FR_{self} were also compared across management systems with one-way ANOVAS as described above. If no significant differences are detected, it could be assumed that management systems have negligible effects on fruit production. All statistical analyses described above were conducted using the software R, version 2.3 (R Foundation for Statistical Computing, Austria).

Results

A total of 1602 pollinator insects were detected on coffee flowers, although the abundance of honey bees was 8.9-fold higher than the abundance of all other pollinators (Table 1). Although *A. mellifera* was the most common species, 14 other insect species were recorded visiting coffee flowers (Table 1). Both species richness ($F_{1,10} = 16.271$, $P = 0.002$, $R^2 = 0.619$) and

Table 1 Total number of visits of the different pollinating insects recorded on the 12 coffee plantations included in the present study

Order/family	Species	Abundance (n)
Hymenoptera/ Apidae	*Apis mellifera mellifera* L.	1441
	Plebeia frontalis Friese	6
	Scaptotrigona mexicana Guérin	37
	Trigona (*Trigona*) *nigerrima* Cresson	16
	Trigona (*Trigona*) *corvina* Cockerell	6
	Ceratina sp.	3
Hymenoptera/ Halictidae	*Augochlora* sp.	2
Hymenoptera/ Vespidae	*Polistinae* sp. 1	11
	Polistinae sp. 2	17
Diptera	*Syrphidae* sp. 1	24
	Syrphidae sp. 2	11
	Syrphidae sp. 3	8
	Calliphoridae sp.	8
	Bibionidae sp.	11
Coleoptera/ Melolonthidae	*Macrodactylus fulvescens* Bates	1
	Total number of insects recorded	1602

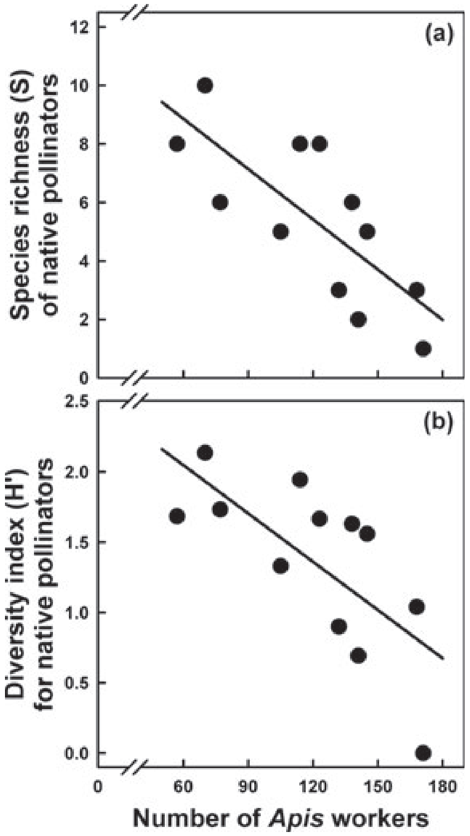

Figure 1 (a) Number of *Apis mellifera* workers versus number of native species and (b) diversity of native pollinators detected at each coffee plantation.

the Shannon–Wiener diversity index of native pollinators ($F_{1,10} = 13.674$, $P = 0.004$, $R^2 = 0.578$) showed a negative relationship with increasing number of *A. mellifera* workers (Fig. 1). We did not find differences in the richness of native pollinator ($F_{2,9} = 3.673$, $P = 0.068$), values of the Shannon–Wiener index ($F_{2,9} = 3.738$, $P = 0.067$) and the number of *A. mellifera* workers ($F_{2,9} = 0.905$, $P = 0.438$) among management systems (data not shown). The distance between coffee plantations and the closest patch of native forest also did not affect these variables (pollinator richness: $F_{1,10} = 1.850$, $P = 0.203$, $R^2 = 0.156$; diversity index: $F_{1,10} = 2.973$, $P = 0.115$, $R^2 = 0.229$; *A. mellifera* abundance: $F_{1,10} = 0.005$, $P = 0.947$, $R^2 = 0.001$; data not shown). Moreover, none of these variables related to the abundance of floral resources (pollinator richness: $F_{1,10} = 3.015$, $P = 0.113$, $R^2 = 0.275$; diversity index: $F_{1,10} = 3.637$, $P = 0.086$, $R^2 = 0.267$; *A. mellifera* abundance: $F_{1,10} = 1.455$, $P = 0.255$, $R^2 = 0.127$; data not shown). All these results then indicate that the previously reported relationships between the diversity of native pollinators and the number of *A. mellifera* are not affected by management systems, distance to native forest or the abundance of floral resources.

Increases in species richness ($F_{1,10} = 17.126$, $P = 0.002$, $R^2 = 0.631$; Fig. 2a) and the Shannon–Wiener diversity index for native pollinators ($F_{1,10} = 13.530$, $P = 0.004$, $R^2 = 0.575$; Fig. 2b) were positively related to fruit set rates (FS). Conversely, increases in the number of *A. mellifera* workers were negatively related to $FS(F_{1,10} = 5.698$, $P = 0.038$, $R^2 = 0.363$; Fig. 2c). Similarly, the fruit retention rate (FR) rose with increases in both species richness ($F_{1,10} = 17.777$, $P = 0.001$, $R^2 = 0.640$; Fig. 3a) and diversity of native pollinators ($F_{1,10} = 18.332$, $P = 0.001$, $R^2 = 0.647$; Fig. 3b), whereas it decreased with increasing number of *A. mellifera* workers ($F_{1,10} = 21.915$, $P < 0.001$; $R^2 = 0.686$; Fig. 3c).

The differences in fruit production between open and self pollination indicated that significantly larger amounts of fruits were produced (ΔFS) and retained until reach maturity (ΔFR) at plantations with higher richness (ΔFS: $F_{1,10} = 16.426$, $P = 0.002$, $R^2 = 0.621$; ΔFR: $F_{1,10} = 13.278$, $P = 0.004$, $R^2 = 0.570$) and diversity (ΔFS: $F_{1,10} = 9.331$, $P = 0.012$, $R^2 = 0.482$; ΔFR: $F_{1,10} = 7.482$, $P = 0.021$, $R^2 = 0.428$) of native pollinators (Figs 4 and 5). By contrast, both ΔFS

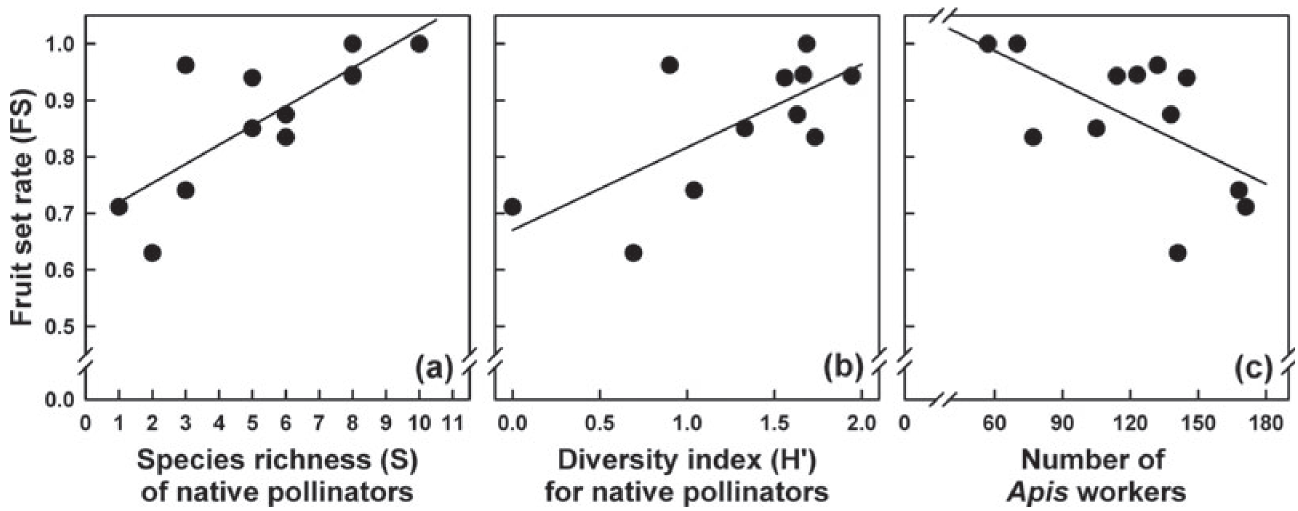

Figure 2 Average fruit set rate estimated for each plantation (*FS*) versus (a) species richness of native pollinators, (b) proportional diversity of native pollinators and (c) number of *Apis mellifera* workers.

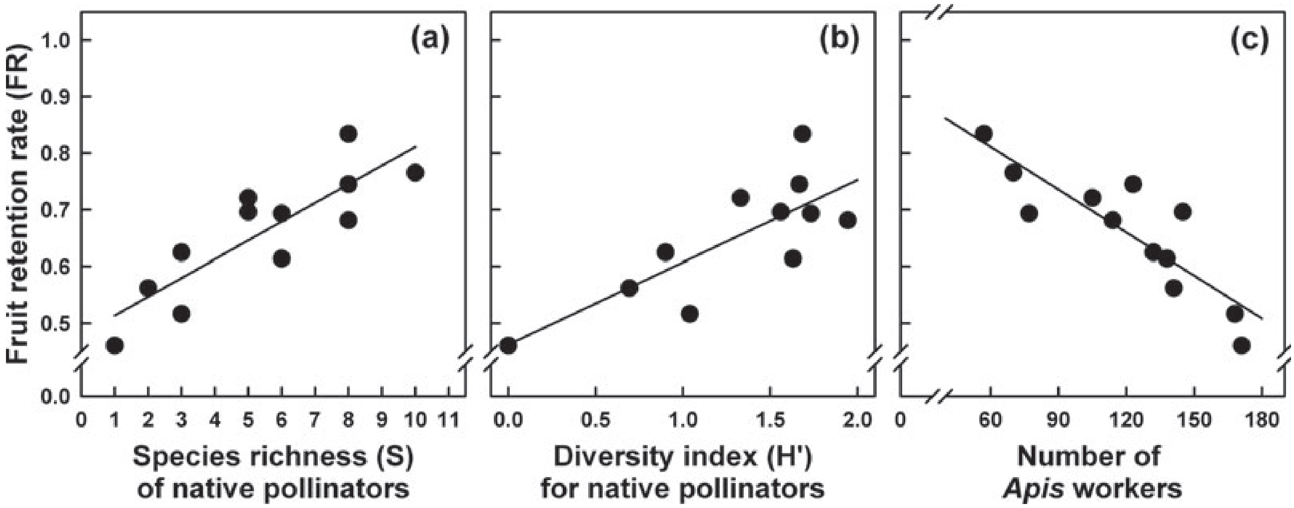

Figure 3 Average fruit retention rate estimated for each plantation (*FR*) versus (a) species richness of native pollinators, (b) proportional diversity of native pollinators and (c) number of *Apis mellifera* workers.

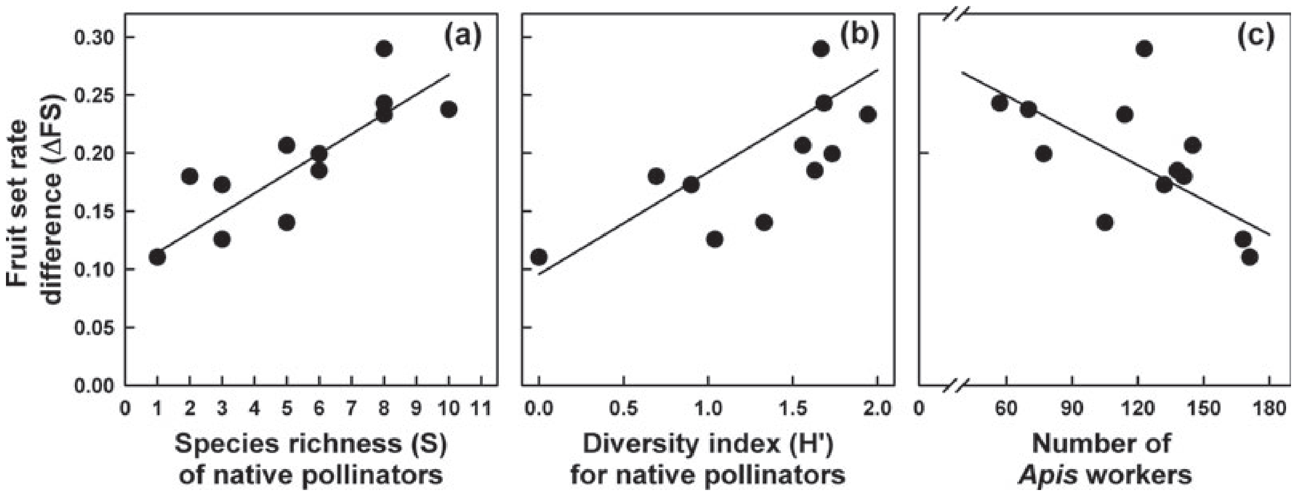

Figure 4 Differences between the fruit set rate obtained from open and self pollination treatments at each plantation [$\Delta FS = (FS_{open} - FS_{self})$] versus (a) species richness of native pollinators, (b) proportional diversity of native pollinators and (c) number of *Apis mellifera* workers.

and ΔFR were negatively related to increasing numbers of *A. mellifera* in plantations ($\Delta FS : F_{1,10} = 29.132,\ P < 0.001,\ R^2 = 0.744$; $\Delta FR : F_{1,10} = 20.253,\ P < 0.001,\ R^2 = 0.699$) (Figs 4 and 5). Autogamic fruit set ($F_{2,9} = 3.255,\ P = 0.086$) and fruit retention rates ($F_{2,9} = 2.802,\ P = 0.133$), obtained from the self-pollination treatment, did not differ among management systems. This indicates that management systems have negligible effects on autogamic fruit production across plantations and, therefore, pollinators are what make the difference in fruit production.

Discussion

The results obtained in the present study suggest that the introduction of *A. mellifera* in Mexican coffee plantations may negatively impact the diversity of native pollinators and, hence, decrease fruit production. To our knowledge, this is the first time that such a negative effect of *A. mellifera* on coffee yield has been documented. Because these suggestions are only supported by correlative analyses, it could, however, be argued that external uncontrolled factors might bias the interpretation of the obtained relationships. Nevertheless, the main concomitant factors that were identified in plantations as potential sources of bias (distance to the closest patch of native forest, abundance of floral resources and differences in management systems) were indicated to have no effects on the study variables. This suggests that the analyses, the results and their interpretation are sound.

The decreased diversity of native pollinators at higher numbers of *A. mellifera* could be attributed to the foraging behaviour of this bee. Honey bees are mass-recruiters that intensively collect nectar and pollen on the flowers they visit, focusing their activities on a single patch of flowers until completely depleting these resources (Roubik, 1980; Butz-Huryn, 1997;

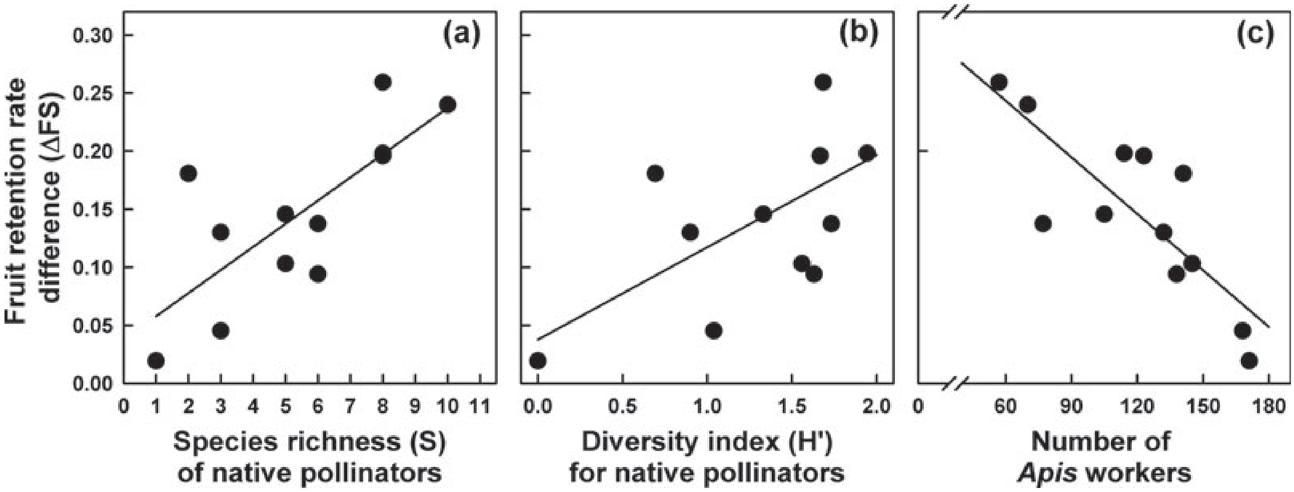

Figure 5 Differences between the fruit retention rate obtained from open and self pollination treatments at each plantation [$\Delta FR = (FR_{open} - FR_{self})$] versus (a) species richness of native pollinators, (b) proportional diversity of native pollinators and (c) number of *Apis mellifera* workers.

Hansen *et al*., 2002). Therefore, *A. mellifera* may competitively displace other pollinators from food sources. Moreover, the amount of floral resources removed by *A. mellifera* usually rises with increased visitation rates of honey bees (Schaffer *et al*., 1983; Paton, 1993), indicating that this is a density-dependent process. In the present study, most of the managed colonies that beekeepers move into coffee plantations are strong units (i.e. each colony has over 40 000 workers). Thus, the number of foragers per colony and the total number of foragers per flower appear to be sufficiently high to cause the rapid depletion of floral resources.

The highly efficient foraging behaviour of *A. mellifera* has been shown to have little effect on the diversity of floral visitors in Eurasia, where honey bees are native and have coexisted with other bee species during their evolutionary history (Steffan-Dewenter & Tscharntke, 2000). *Apis mellifera* is, however, an introduced species in Mexico and its density-dependent effects may be responsible, at least in part, for the reduced diversity of native pollinator observed in coffee plantations. This suggestion concurs with the results of studies performed in other sites where this bee has been introduced, including countries of America and Oceania, where the presence of *A. mellifera* reduces visitation rates of native pollinators to wild plants (Aizen & Feisinger, 1994; Paini, 2004).

Interestingly, the abundance of *A. mellifera* was also negatively related to the proportional abundance of native insects, as reflected in the Shannon–Wiener index. This index can be interpreted as the amount of uncertainty regarding the species to which an individual randomly selected from a community belongs, which is a measure of the amount of information contained in a community (Margalef, 1957; Peet, 1974). In the present study, the negative relationship found between the values of this index and the abundance of *A. mellifera* suggests that honey bees are decreasing the biodiversity of coffee plantations. This is a important note of caution for those conservation biologists who propose that ‘environmentally friendly’ agroecosystems, which preserve part of the native biodiversity, should be the focus of conservation efforts in developing countries because they ensure both economic benefits and biodiversity conservation (Greenberg *et al*., 1997; Roberts *et al*., 2000; Bhagwat *et al*., 2005; Daugherty, 2005). In the particular case of Mexico, the third most megadiverse country of the world, shade coffee plantations have been indicated to act as reservoirs of native fauna, including insects, birds and mammals (Gallina *et al*., 1996; Moguel & Toledo, 1999; Perfecto *et al*., 2003). The results obtained in the present study suggest that protecting insect biodiversity within Mexican coffee agroecosystems is important for both conservation purposes and for maintaining ecosystem services. Special attention should, however, be paid on the quality and composition of those species. In the present study, one additional exotic bee species, *A. mellifera*, appears to be detrimental for both native insect diversity and pollination services.

Honey bees could alter the pollination rates of plants in several different ways, hence affecting crop yield. They may add to the services provided by native pollinators and augment crop yield; for example, in coffee plantations of Venezuela (Manrique & Thimann, 2002) and Panama (Roubik, 2002b), the introduction of *A. mellifera* hives increased coffee yield. However, this does not appear to be the case in Mexico. The results obtained in the present study suggest that *A. mellifera* reduces pollinator diversity in coffee plantations without providing equivalent pollination services. This suggestion arises from the fact that fruit production was positively related to increases in both species richness and proportional diversity of pollinators, whereas it was negatively related with the abundance of *A. mellifera*. This is not in agreement with the widely accepted assumption that honey bees increase coffee yield. For example, Roubik (2002a) performed a global assessment of the impact of *A. mellifera* on coffee production and indicated that the establishment of Africanized honey bees in the Neotropics coincided with a substantial increase of coffee yields. It was proposed that, for most tropical Latin American Countries, there is a possible positive cause–effect relationship between these variables. In the particular case of Mexico, however, Roubik (2002a) shows a decrease in coffee yield for the post-Africanization period.

The results obtained in the present study suggest that the presence of honey bees in Mexican coffee plantations may preclude fruit production. Indeed, this negative effect appears to be related to decreases in the diversity of native pollinators with increased abundance of *A. mellifera*. This could be a result of the features of Mexican beekeeping compared with the rest of the Latin American countries. Beekeeping in Mexico involves much larger numbers of hives, as well as the migration of colonies after nectar flows. Therefore, the decrease in coffee yield observed in the present study may not be related to differences in the composition of native pollinator communities regarding other countries. To our knowledge, however, there are no specific studies addressing this topic.

Although the results obtained in the present study indicate the negative effects of *A. mellifera* on insect diversity and pollination services, any conclusions made are subject to limitations. First, they are reliant on a series of correlative analyses performed with observational data. Therefore, the current conclusions would remain as hypotheses until manipulative experiments in which the abundance of *A. mellifera* is controlled are conducted. Second, determining whether honey bees competitively displace native insects would also require more detailed observations of pollinator activities within flowers, aiming to assess whether *A. mellifera* effectively depletes floral resources (nectar and pollen). Finally, all these assessments should be performed at other sites, or even other countries, to determine whether these putative negative effects of *A. mellifera* can be considered as a general phenomenon.

Acknowledgments

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