

Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia

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(Received 24 January 2014; revised 4 June 2014; accepted 4 June 2014; first published online 3 July 2014)

Abstract: Mass-flowering plant species are often pollinated by social bees that are able to use the abundant resource by recruiting workers from their colonies. In this study we surveyed pollinators on the mass-flowering perennial crop coffee (*Coffea arabica*) in its native range in Ethiopia. Previous studies in areas where coffee is introduced often find the social honeybee, *Apis mellifera*, to be the dominant pollinator. In those areas, the bee-species composition visiting coffee varies with a higher bee diversity closer to forest or in less modified habitats. We surveyed pollinators of coffee under different shade-tree structures, by collecting hoverflies and bees landing on coffee flowers in 19 sites in south-west Ethiopia. We found the native honeybee (*A. mellifera*) to be the dominant visitor of coffee flowers in all sites. Honeybee abundance was not affected by the local shade-tree structure, but was positively affected by the amount of coffee flower resources. Other pollinators were positively affected by complex shade-tree structures. To conclude, the honeybee is clearly the dominant pollinator of coffee in Ethiopia along the whole shade-tree structure gradient. Its high abundance could be a consequence of the provision of traditional bee hives in the landscape, which are colonized by wild swarming honeybees.

Key Words: agroforestry, *Apis mellifera* subsp. *simensis*, *Coffea arabica*, landscape ecology, moist afro-montane forest, pollination, species composition

INTRODUCTION

The co-evolution between flowering plants and pollinating insects is widely recognized. However, in spite of many intriguing examples of specialized plant-pollinator adaptations and relationships, most plants and pollinators are generalists and thus most plant-pollinator networks include numerous links (Johnson & Steiner 2000, Ollerton 1996). Certain plant species flower en masse, during a very short time span, which may reduce the chances of getting all flowers pollinated. However, pollinators like social bees which can recruit workers from their colonies are often found to be abundant at these mass flowering plants (Jha & Vandermeer 2009, Krishnan *et al.* 2012, Veddeler *et al.* 2006). The advanced communication system (waggle dance) of the social honeybee is for example suggested to have evolved because of its benefits in landscapes with patchy, high-quality resources (Donaldson-Matasci & Dornhaus 2012, Dornhaus & Chittka 2004).

Human land use not only modifies the extent and distribution of natural environments, but also alters the relative amount of resources for pollinators across time and space. This is particularly evident in agricultural systems with mass-flowering crops (Kovacs-Hostyanszki *et al.* 2013, Persson & Smith 2013). Human intervention also includes direct modifications of the pollinator community by actively managing and moving bees, especially the honey bee, *Apis mellifera* L. (Potts *et al.* 2010). These kinds of activity will affect the composition of pollinators across landscapes. It is thus important to study pollinators in human-modified landscapes from both an ecological and conservation point of view and because pollinators provide an important ecosystem service to farmers.

In this study we surveyed the pollinator community visiting the mass-flowering perennial crop coffee, *Coffea arabica* L., in its native range in Ethiopia. The main pollinators of coffee have before only been studied in its introduced range and not in its native range, where the co-evolution between the plant and the pollinators should have occurred (Ngo *et al.* 2011). In plantations

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with coffee most plants flower simultaneously and the entire coffee bloom may be completed within a couple of days (Klein *et al.* 2003a, Krishnan *et al.* 2012). The short bloom imposes high demands on the pollinator community. *Coffea arabica* attracts a range of insect pollinators (Ngo *et al.* 2011). However, in regions where coffee has been introduced, honeybees (*Apis* spp.) are often the dominant visitors, even if other eusocial bees are also frequent (Badano & Vergara 2011, Boreux *et al.* 2013, Klein *et al.* 2003a, Ricketts 2004, Roubik 2002, Vergara & Badano 2009). Higher bee diversity on coffee flowers is associated with low-impact management systems (Vergara & Badano 2009), proximity to natural forests (social bees) and local factors such as higher light intensity (solitary bees) (Klein *et al.* 2002, 2003a, b; Ricketts 2004). Thus, our selected study area is of particular interest since we have a gradient in shade tree structure, and both *C. arabica* and honeybee, *A. mellifera*, are native and found wild (Anthony *et al.* 2001, Meixner *et al.* 2011).

Our aim with this study was in addition to identifying the main day-time pollinators of coffee in its native range, to also evaluate the effect of variation in local shade-tree structure on the pollinator communities visiting coffee flowers. We had three hypotheses. First, social bees, including honeybees, are the main pollinators of coffee, since they can recruit workers from their colonies and may collect the mass of resources available during a short time. Second, species richness of pollinators is higher in sites with more complex shade-tree structures, since some species may be absent in more altered, simplified habitats. Third, honeybees are less affected by shade-tree structure compared with other pollinators, since they are very mobile and are provided with nests (traditional beehives that could be colonized by wild swarming bees) in most parts of the landscape.

METHODS

Study landscape

Gera and Goma districts (7.8°N; 36.4°E) are located in one of the main coffee-growing areas in Ethiopia. The landscape is dominated by small-scale agriculture and moist afro-montane forests. The western part of the landscape has larger remnants of continuous forest, whereas the forests in the eastern part of the landscape are highly fragmented (Figure 1). Honey production is widespread in Ethiopia and in our study landscape, with both modern and traditional beehives. Traditional beehives are most common and are made of split logs, carved and tied together and thereafter tied to a branch in a tree without further management. The honeybee, *Apis mellifera*, is native to Ethiopia (Meixner *et al.* 2011) and

the honey production with traditional beehives depends on colonization by wild swarms of honeybees (Dietemann *et al.* 2009). No other bee species are used for honey production. However, honey hunting from wild stingless bees does occur (Kajobe & Roubik 2006). The coffee normally starts to flower in January or February, after the first heavy rains, and flowers one to four times before the main rainy season starts in June or July. The landscape is dry during this time of the year, and there are few other herb and shrub species flowering because of the dryness and high grazing pressure by livestock. However, most tree and fruit-tree species have their main flowering period in the dry season.

Coffee production system

Coffea arabica is the only coffee species cultivated in the landscape and it is grown mainly in the forest or in forest patches in the agriculture-semiforest mosaic. The coffee production systems are recognized as semi-forest or semi-plantation coffee depending on the forest management intensity and plant diversity (Hundera *et al.* 2013). In most coffee stands, understorey vegetation is repeatedly removed to reduce nutrient competition for the coffee plants and to facilitate picking of coffee berries from the ground (Schmitt *et al.* 2010). Pruning of shade trees and coffee plants is not a common management practice; instead old coffee plants are removed and replaced with coffee seedlings occasionally. The coffee was organically managed, i.e. no pesticides or chemical fertilizers have been used, with the exception of two coffee state farms that had access to fertilizers and herbicides.

Study design

Before the onset of the coffee flowering in 2011, we identified coffee sites that differed in diversity of shade-tree species, interspersed over the landscape. When the coffee flowering started, we selected coffee sites for sampling of coffee pollinators depending on the availability of flowering coffee. Each site had more or less synchronized blooms with fresh flowers for only 1–2 d, but the flowering pattern over the landscape was not fully synchronized, letting us sample for approximately 5 d during each coffee flowering period. We aimed to cover a long gradient in shade-tree diversity and to visit as many sites as possible. Altogether we sampled 19 coffee sites during the two flowering events, in mid-February (10 sites) and at the end of March 2011 (nine sites). Sites were separated by at least 650 m when sampled in the same flowering period. The shortest distance between two sites sampled in different periods was 150 m. The distance between the two furthest sites was 46 km (Figure 1).

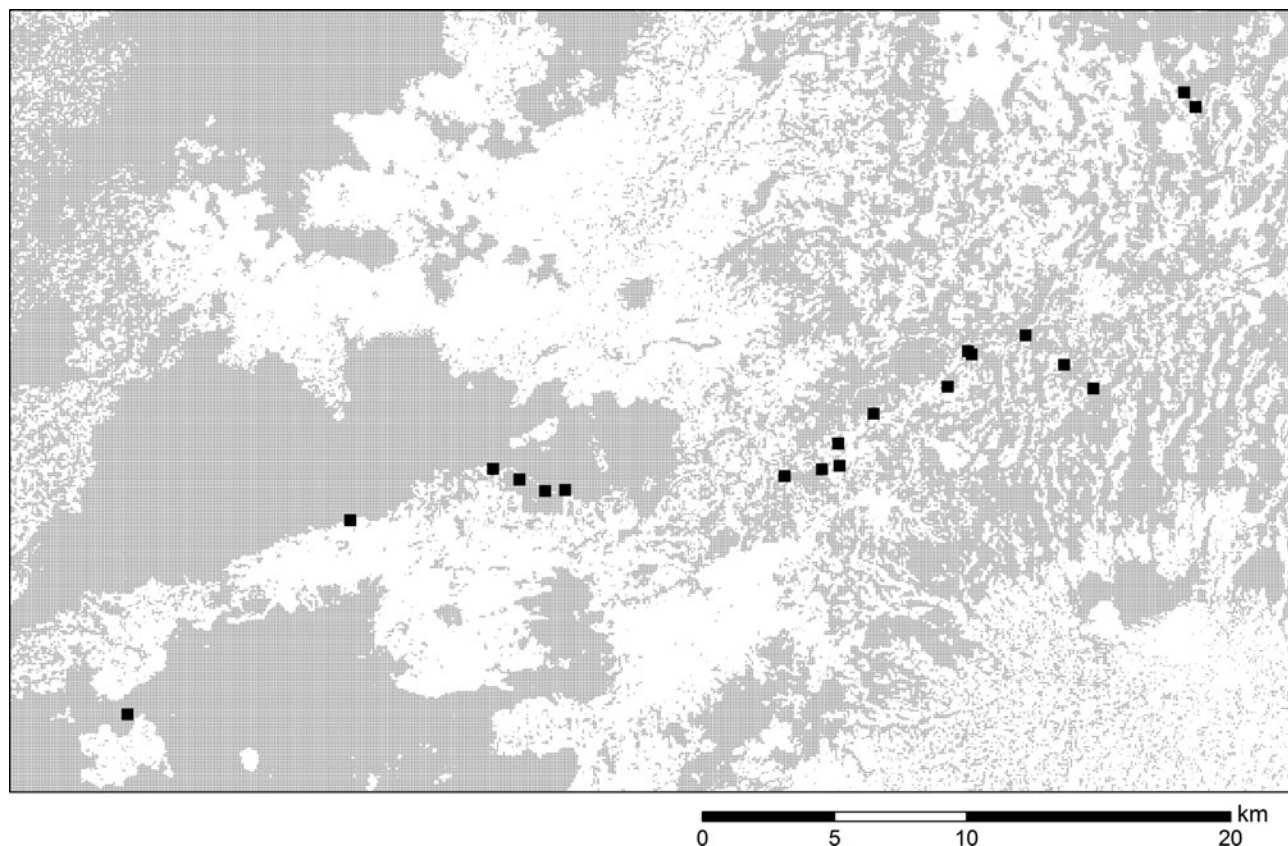


Figure 1. The study landscape in south-western Ethiopia. The western part of the landscape contains larger remnants of moist afro-montane forest (forested areas are in grey), whereas all forests in the eastern part have been converted into fragmented semi-plantation coffee stands. The black squares are the 19 sites we visited for sampling of coffee pollinators.

In each coffee site, we established a 40×40 -m plot where we collected the following environmental variables: canopy cover, by visual estimation in percentage; number of coffee plants; number of shade trees (>10 cm dbh) and number of tree species. We estimated the freshness and number of open coffee flowers on a scale between 1 and 5, where 1 represented few and 5 many fresh flowers. An estimate of the total amount of coffee flower resources in the site was achieved by multiplying the coffee flower variable with our visual estimate of the coffee ground cover (%). We noted presence of honeybee hives in the vicinity of the sites and surveyed other flowering plants. Each flowering plant was noted as very common (3) (>1000 flowers or flower heads), frequent (2) (100–1000), or rare (1) (10–100). The numbers for each flowering plant species were summed per site to get an estimate of the amount of alternative flower resources.

Three persons simultaneously collected insects landing on coffee flowers. All insects were collected with aerial nets and stored in alcohol. The sampling was conducted during four trials; each trial lasted 15 min. The collectors were standing on the same location for the whole

15-min trial and moved to a new position for the next trial. In total we spent 3 h per site sampling coffee visitors. The sampling at each coffee site ended with 15 min of sampling of pollinators that were not foraging on coffee flowers, hereafter referred to as the surrounding sampling. The surrounding sampling was skipped in four sites since the understorey vegetation very recently had been cleared. On most days, two sites were sampled, one site before and one after noon. Sampling normally started around 9 h 30 and was finished around 15 h 30. Sampling was not conducted on rainy days. Each site was sampled once due to the trade-off between number of sites and replication, where we aimed for maximizing the number of sites. Pollinators were sorted into genera and identified to species or morphospecies.

Data analysis

The abundance, which is the number of collected individuals, of honeybees and other pollinators were analysed separately. In other pollinators we included all bee species (except honeybees) and hoverflies, since

these groups are well-known pollinators. The number of species and abundance of the other pollinators were closely correlated ($r = 0.96$), therefore we only used total abundance as a response variable for the other pollinators. The overall low abundances did not permit us to investigate rarefied species richness and the different groups (hoverflies, solitary bees and other social bees) could not be analysed separately for the same reason. Thus, we had three response variables: abundance of honeybees on coffee, abundance of other pollinators on coffee and abundance of other pollinators in the surroundings of the coffee (not on the coffee).

We identified four variables that reflected the shade-tree structure of the site: canopy cover, number of trees, number of tree species and if the site was part of a contiguous forest or of the agriculture-agroforestry mosaic (categorical variable). These variables, except canopy cover, covaried ($P < 0.05$). The variable number of trees had the longest gradient; therefore we chose it to be included in the models to represent the shade-tree structure of the sites, and disregarded the other variables. However, to verify that the estimated variable captured the shade-tree structural complexity we also developed a forest index based on all four variables using ordination techniques. We did a principal components analysis (PCA), using the standardized values of the four variables, in the *vegan*-package in R. The PCA site scores from the first PCA axis, which explained 63% of the total variance, were used as a forest index. Higher scores represented more forest-like conditions.

All analyses were done in the statistical software R 3.0.1 (R Development Core Team). Five explanatory variables that we hypothesized to influence the pollinator community were included in the full models for all response variables: (1) number of trees or forest index, (2) coffee flower resources, (3) other flower resources, (4) time of the day (rounded to nearest hour of sampling start) and (5) presence of beehives (yes or no). All analyses were run twice, including either number of trees or forest index, i.e. these variables were not used simultaneously since they should reflect the same thing: shade-tree structures. The model for each response variable was simplified using the *drop1*-function to drop non-significant variables until a final model was found. Variables were dropped only if the models' residuals did not get distorted. The final models were verified by applying forward selection by adding each dropped variable singly. The full models were inspected for violations of the assumption of normal distribution by plotting the residuals against each explanatory variable and the model's fitted values. The models with the abundance of honeybees and other pollinators on coffee did not meet the assumptions. Therefore the abundances of honeybees were \log_e -transformed. The abundances of other pollinators on coffee were analysed with a Poisson generalized model (GLM). Since overdispersion

Table 1. Environmental variables in the coffee sites ($n = 19$) in south-western Ethiopia measured in a 40×40 -m plot. The variable coffee flower resources is the estimated amount of open fresh coffee flowers multiplied with the coffee ground cover (%).

Variable	Mean	Range
Altitude (m asl)	1890	1530–2090
No. trees	15	6–26
No. tree species	5	2–12
Canopy cover (%)	49	40–70
No. of vegetation layers	2.6	2–3
Coffee ground cover (%)	68	50–85
No. coffee plants < 1.5 m	88	4–414
No. coffee plants > 1.5 m	359	45–610
Coffee flower resources	225	100–400
No. of flowering species	2.8	0–7

was detected in this model, the standard errors were corrected by using a quasi-GLM model where the variance is given by the dispersion parameter times the mean (Zuur *et al.* 2009). In the result section, β -values and standard errors are presented from standardized variables ($X'_n = \frac{X_n - \text{mean}(X)}{\text{sd}(X)}$).

RESULTS

All sites had a high cover of coffee (50–85%) but varied widely in number of trees and number of tree species per site (Table 1). Altogether, 1226 pollinators were collected on coffee flowers in the 19 sites. The honeybee, *A. mellifera*, probably subsp. *simensis* Meixner, Leta, Koeniger & Fuchs, was the dominant pollinator and accounted for 96% of the collected pollinators. We found six hoverfly species and 16 bee species visiting coffee (Table 2). The only captured eusocial bee species were the honeybee and *Meliponula cf. ogouensis*. In the sampling from the surrounding of coffee plants, honeybees were rare and other bees generally more common than on coffee (per 15 min-period, mean: 0.8 other pollinators on coffee, vs. 5.6 other pollinators surrounding coffee, $P = 0.003$, Appendix 1).

The honeybee abundance was positively affected by the amount of coffee flower resources (LM: $\beta = 0.50$, $SE = 0.18$, $t = 2.8$, $df = 17$, $P = 0.013$, Figure 2c), but not by the shade-tree structure (Figure 2a, b). In contrast, other coffee pollinators were positively affected by more complex shade-tree structure in the coffee sites (quasi-GLM with number of trees: $df = 17$, $P < 0.001$ (Figure 2d); quasi-GLM with forest index: $df = 17$, $P = 0.001$ (Figure 2e)). The other pollinators were not affected by the amount of coffee flower resources in the sites (Figure 2f). Traditional beehives were present in the close surroundings of six sites, but the number of honeybees or other pollinators on coffee were equally abundant in sites with and without traditional beehives. We found no correlation between the number of honeybees and other

Table 2. The taxa observed on coffee flowers. A variety of literature was used for the identification including the key to bee genera and subgenera of sub-Saharan Africa (Eardley *et al.* 2010). * = observed on coffee off the time of standardized sampling. ** = observed on coffee but not included as pollinators in the analyses.

Insect order	Family	Species/morphospecies	Abundance
Hymenoptera	Apidae	<i>Apis mellifera</i> Linnaeus	1178
Hymenoptera	Apidae	<i>Meliponula</i> cf. <i>ogouensis</i> Vachal	3
Hymenoptera	Apidae	<i>Xylocopa caffra</i> (Linnaeus)	1
Hymenoptera	Apidae	<i>Xylocopa inconstans</i> Smith	1
Hymenoptera	Apidae	<i>Xylocopa torrida</i> (Westwood)	1
Hymenoptera	Halictidae	<i>Lasioglossum</i> sp. A	1
Hymenoptera	Halictidae	<i>Lasioglossum</i> sp. B	1
Hymenoptera	Halictidae	<i>Lasioglossum</i> sp. C	1
Hymenoptera	Halictidae	<i>Patellapis</i> sp. A	2
Hymenoptera	Halictidae	<i>Patellapis</i> sp. B	1
Hymenoptera	Halictidae	<i>Patellapis</i> sp. C	1
Hymenoptera	Halictidae	<i>Patellapis</i> sp. D	2
Hymenoptera	Halictidae	<i>Seladonia</i> sp. A	1
Hymenoptera	Halictidae	<i>Seladonia</i> sp. B	2*
Hymenoptera	Megachilidae	<i>Megachile nasalis</i> Smith	2
Hymenoptera	Megachilidae	<i>Megachile</i> cf. <i>venusta</i> Smith	1
Hymenoptera	Megachilidae	<i>Megachile curtula</i> Gerstaecker	1
Diptera	Syrphidae	<i>Baccha</i> sp.	3
Diptera	Syrphidae	<i>Betasyrphus</i> sp.	6
Diptera	Syrphidae	<i>Eristalinus</i> (<i>Eristalodes</i>) sp.	10
Diptera	Syrphidae	<i>Eristalis</i> sp.	2
Diptera	Syrphidae	<i>Ischiodon aegyptius</i> (Wiedemann)	1
Diptera	Syrphidae	<i>Phytomia</i> sp.	4
Diptera	Calliphoridae	<i>Stomorphina</i> sp.	**
Diptera	Calliphoridae		**
Diptera	Calliphoridae (Rhiniinae)		**
Diptera	Muscidae		**
Diptera	Sarcophagidae	<i>Sarcophaga</i> sp.	**
Diptera	Tephritidae		**
Lepidoptera	Nymphalidae	<i>Amauris echeria</i> Stoll	**
Lepidoptera	Pieridae	<i>Mylothris rueppellii</i> Koch	**

pollinators on the coffee ($t = 0.19$, $df = 17$, $P = 0.85$). The final model for pollinators from the surrounding sampling included no significant variables (Figure 2g–i).

DISCUSSION

In all surveyed sites, the honeybee was present and was the dominant visitor of coffee flowers with a dominance sometimes even higher than in other studies on coffee in its introduced range (Klein *et al.* 2003a, Ricketts 2004). Its abundance was as expected related more to flower resources than shade-tree structure reflecting its high mobility (Beekman & Ratnieks 2000, Ricketts 2004). However, other pollinators on coffee were favoured by forest complexity. This finding highlights that biodiversity and total pollinator abundance need not always correlate positively.

Honeybee abundance in our study landscape is promoted through the provision of traditional nests during parts of the year, even though colonies have to find alternative nest sites to survive during times

when hives are not erected. Since honeybees are very mobile and can travel several kilometres from their hive (Beekman & Ratnieks 2000), our survey of beehives in the vicinity of the sites may not necessarily reflect the number of beehives that actually had access to the coffee sites. Normally, the traditional beehives are set out in the coffee areas just before the onset of flowering, to utilize the abundant nectar resources coffee provides, and are colonized by swarms of wild honeybees. The rapid colonization of traditional beehives may reflect a shortage of natural, high-quality nesting places for honeybees in the landscape, and the provision of beehives could possibly explain the high abundance of honeybees on coffee. This idea is strengthened by our observation of a very low abundance of honeybees on coffee in the same landscape in January 2013 coinciding with an unusually early coffee flowering period and a delayed erection of beehives. The temporal variability in bee densities suggests that we need additional studies on the population dynamics of the honeybee in our study area to understand how the temporal variation in coffee flowering and management regimes impacts honeybee abundance on coffee.

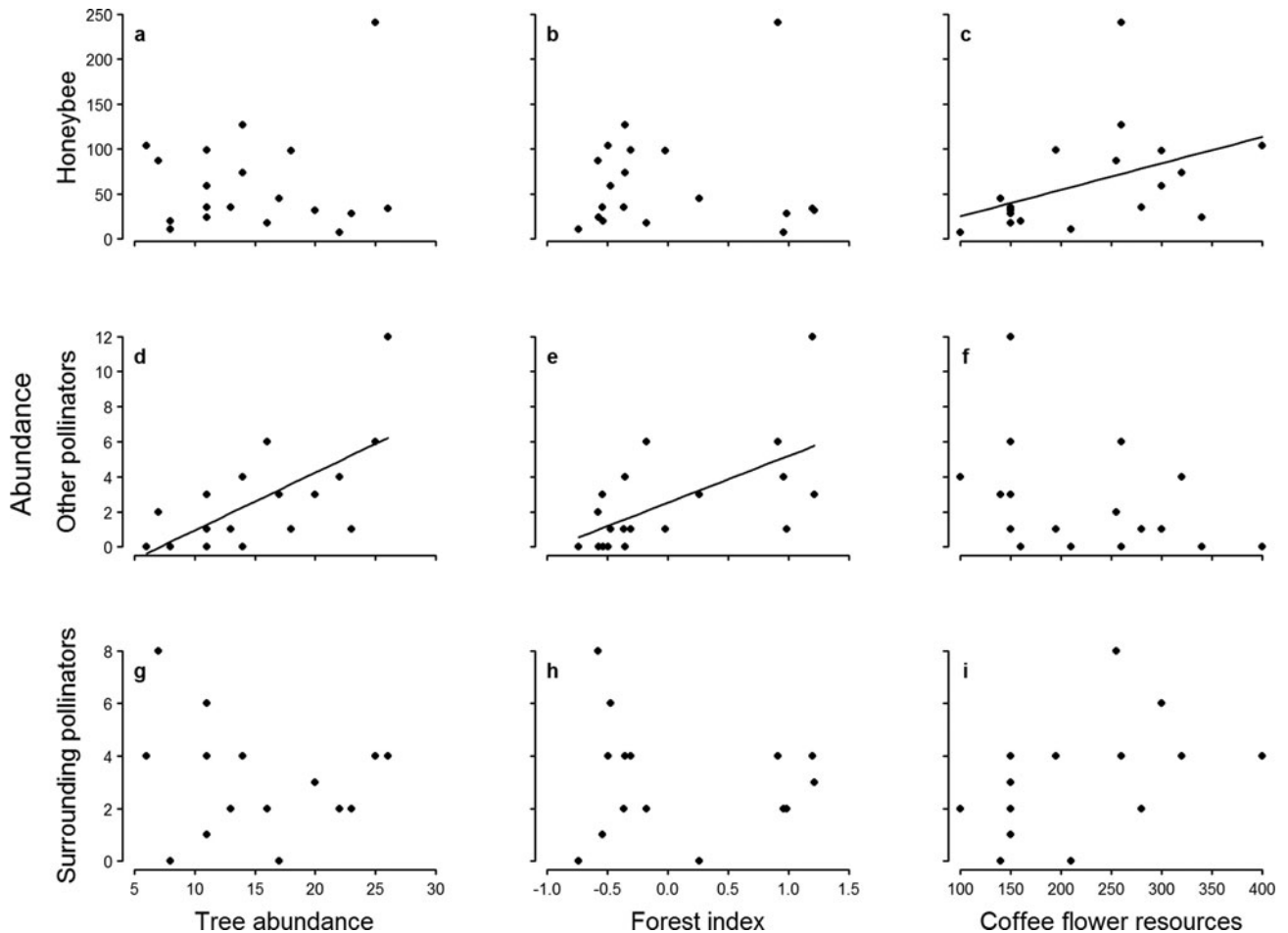


Figure 2. The relationships between pollinator abundances and three habitat and landscape variables in a coffee landscape in south-west Ethiopia for the honeybee (a–c), other pollinators on coffee (d–f), and pollinators in the surroundings of the coffee (g–i). The relationship is shown for number of trees (a, d, g), forest index (b, e, h) and coffee flower resources (c, f, i). Significant relationships ($P < 0.05$) are indicated with a solid line. Other pollinators include hoverflies and bees except the honeybee ($n = 19$). Surrounding pollinators are other pollinators sampled around the coffee plants ($n = 15$).

The ability to recruit workers to mass-flowering crops is known from other social bee species, and the eusocial stingless bees are, in many regions, found to be important and common pollinators of coffee (Klein *et al.* 2003a, Ricketts 2004). However, in our study, only one other eusocial bee species was found on coffee flowers, a *Meliponula* sp. with three individuals in one site. It thus seems that other social bee species in this landscape do not utilize the pulse of resources offered by the coffee flowering. Other pollinators on coffee, such as other bee species and hoverflies, were rare compared with honeybees. However, in contrast to the case for honeybees, these other pollinators were positively affected by more complex shade-tree structures. This finding is in accordance with studies from other regions (reviewed in Klein *et al.* 2008) and highlight the importance of maintaining natural environments from a biodiversity conservation approach. The low number of other pollinators however suggests

that they probably have little importance in this system (at least this year) for providing pollination services. On the other hand, in parts of the introduced range of coffee, coffee fruit set is positively affected by a high bee diversity, and a visit by a solitary bee has been found to be more effective than a visit by a honeybee (Klein *et al.* 2003a, Vergara & Badano 2009). The effectiveness of honeybees as coffee pollinators is ambiguous, as high abundances of honeybees have been reported with both increased and decreased coffee yields (Badano & Vergara 2011, Roubik 2002). Different pollinator species probably complement each other (Albrecht *et al.* 2012) or increase pollination effectiveness (Brittain *et al.* 2013). However, since we did not measure the pollination efficiency of the coffee visitors we cannot evaluate the contribution by the honeybee and the other bees' impact on coffee harvest.

The low abundance of alternative floral resources during the dry season can lead to the impression that

there was a general lack of resources and pollinators in our study landscape during our survey, which would explain the low diversity of other pollinators on coffee. However, some tree species, including several fruit trees, mainly flower during the dry season and both this and other studies suggest that other pollinators are present in the surrounding vegetation. The sampling of pollinators surrounding the coffee showed the presence of pollinators other than honeybees and a separate study in the same landscape similarly found other pollinators on a perennial herb (Fabaceae: *Senna didymobotrya* (Fresen.) Irwin & Barneby) that flowered simultaneously to coffee plants (U. Samnegård, unpubl. data). Sampling on this plant, using a similar sampling effort as in this study, revealed higher abundances of many bee species also found in low numbers on coffee. Moreover it showed that an overall higher diversity was present in the landscape (>530 bees other than honeybees of ≥ 27 species were sampled). Thus, it appears that even though other bees were present in the landscape, they select for other floral resources or were unable to utilize the resources from the coffee. We found no negative correlations between the number of honeybees and other pollinators on coffee, suggesting that the honeybee in this system does not affect other pollinators negatively (Stout & Morales 2009).

The Ethiopian system seems vulnerable since it is so heavily dependent on one major pollinator. Nevertheless, it is worth noting that African honeybees have a higher genetic variation than introduced and domesticated honeybees, which makes them more resistant to diseases and mites (Dietemann *et al.* 2009). Since many wild honeybee populations are still present, a collapse seems unlikely in the near future and thus this system with only one main pollinator may not be as fragile as it first appears. However, the observation from January 2013, with no bees on the coffee when almost no traditional beehives were erected, is calling for more studies on interactions of coffee and bees across space and time in these landscapes. The landscape in south-western Ethiopia is rapidly changing, with deforestation in many areas (most pronounced at altitudes above the coffee-growing areas, Hylander *et al.* 2013) and simplification of the forest structure in most coffee-growing areas (Hundera *et al.* 2013). These are worrying trends since other pollinators seemed to depend on complex environments and because the wild honeybee depends on a variety of trees during other seasons (Dornhaus & Chittka 2004). This study is the first to investigate pollinators visiting coffee in Ethiopia. We suggest that future work here should focus on wild honeybee population dynamics across landscapes, inter-annual pollinator patterns and comparisons across larger geographic settings with longer gradients in coffee shade-tree structures and management systems in Ethiopia.

ACKNOWLEDGEMENTS

We thank Connal Eardley for assistance with bee identification and Gerard Pennards for Diptera identification. We also thank Konjit Dereje, all assistants in the field, the coffee owners for their permission to let us work with their coffee, and the IBC in Addis Ababa for their help and cooperation. The study was financed by grants from SIDA and Formas (to K.H.).

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Appendix 1. The bee taxa collected in the surroundings of coffee plants in 15 sites in south-western Ethiopia. A variety of literature was used for the identification including the key to bee genera and subgenera of Sub-Saharan Africa (Eardley *et al.* 2010).

Family	Species	No. collected
Apidae	<i>Braunsapis</i> sp. 2	1
Apidae	<i>Ceratina ericia</i> Vachal	2
Apidae	<i>Ceratina moerenhouti</i> (Vachal)	1
Apidae	<i>Xylocopa caffra</i> (Linnaeus)	1
Halictidae	<i>Lasioglossum</i> sp. C	2
Halictidae	<i>Lasioglossum</i> sp. D	2
Halictidae	<i>Lasioglossum</i> sp. E	1
Halictidae	<i>Lasioglossum</i> sp. F	4
Halictidae	<i>Lasioglossum</i> sp. G	2
Halictidae	<i>Lasioglossum</i> sp. H	2
Halictidae	<i>Lasioglossum</i> sp. I	1
Halictidae	<i>Patellapis</i> sp. A	2
Halictidae	<i>Seladonia</i> sp. A	4
Halictidae	<i>Seladonia</i> sp. B	16
Halictidae	<i>Seladonia</i> sp. C	1
Halictidae	<i>Seladonia</i> sp. D	1
Megachilidae	<i>Anthidium</i> sp.	1
Megachilidae	<i>Othinosmia</i> sp.	1