Interactive effects among ecosystem services and management practices on crop production: Pollination in coffee agroforestry systems

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Crop productivity is improved by ecosystem services, including pollination, but this should be set in the context of trade-offs among multiple management practices. We investigated the impact of pollination services on coffee production, considering variation in fertilization, irrigation, shade cover, and environmental variables such as rainfall (which stimulates coffee flowering across all plantations), soil pH, and nitrogen availability. After accounting for management interventions, bee abundance improved coffee production (number of berries harvested). Some management interventions, such as irrigation, used once to trigger asynchronous flowering, dramatically increased bee abundance at coffee trees. Others, such as the extent and type of tree cover, revealed interacting effects on pollination and, ultimately, crop production. The effects of management interventions, notably irrigation and addition of lime, had, however, far more substantial positive effects on coffee production than tree cover. These results suggest that pollination services matter, but managing the asynchrony of flowering was a more effective tool for securing good pollination than maintaining high shade tree densities as pollinator habitat. Complex interactions across farm and landscape scales, including both management practices and environmental conditions, shape pollination outcomes. Effective production systems therefore require the integrated consideration of management practices in the context of the surrounding habitat structure. This paper points toward a more strategic use of ecosystem services in agricultural systems, where ecosystem services are shaped by the coupling of management interventions and environmental variables.

Apis | *Coffea canephora* | India | *Tetragonula*

Ecosystem services are widely used as an economic argument for the conservation of natural habitats, including forests (1). One such ecosystem service, crop pollination by animals, is thought to benefit 75% of the major crops, representing 35% of the world crop production (2). Pollination services have received particular attention in view of the declines in honey bees, a major crop pollinator (3). A current concern is that a continued loss of honey bees (and perhaps other bees) may undermine crop pollination services and hence crop production worldwide (4).

Although insect pollinators have been shown to improve coffee crop productivity (5), many studies have either limited the assessment of production to initial fruit set (around 5 wk after pollination) or overlooked the impact of environment and management system on production. Assessment of fruit yield within a few weeks of flowering might be misleading as coffee has a 6- to 10-mo fruit maturation period. During this production cycle a range of management practices, including fertilization and pruning, are implemented that, together with environmental conditions, might play a major role in fruit development and early fruit loss. Consequently, the early positive benefits of pollination for fruit set might have disappeared by fruit maturation and harvest (6). In consequence, it is difficult to ascribe the degree to which pollination alone contributes to coffee production. At the same time, if pollinators do enhance initial fruit set (as appears to be the case), then an improved understanding of management and environmental factors might allow pollination benefits to be retained through crop maturation. Such information would facilitate the integration of pollination services within the management system, for instance through the provision of potential nesting sites and the management of alternative floral resources.

A further consideration for coffee farmers is whether interventions that maximize pollination service benefits (e.g., shade management) incur trade-offs with other services or management priorities. It is thus conceivable that an intervention that increases pollination benefits might diminish production by, for example, reducing light or resource acquisition. A complete study of the potential benefits of pollination services to coffee production requires a more comprehensive evaluation of production at the time of fruit harvest, as well as an evaluation of the various trade-offs inherent to different management practices. Ultimately, trade-offs should be presented in crop production or monetary terms, but here we seek to understand their ecological expression.

In this study, we investigated the potential role of pollinators in promoting coffee production in the context of soil and tree management practices as well as environmental variables such as soil fertility, shade cover, and rainfall.

Results

Flowering Pattern. Agroforests in Kodagu, South India, flowered between February 10 and March 20, 2008, with each agroforest flowering on a single day within this period. Twenty-six farmers used irrigation to stimulate flowering (irrigation is otherwise not used). Two large postrainfall "mass flowering" events, covering nonoverlapping areas of 250 km^2 and 80 km^2, occurred on February 19 and March 20 and included 75 and 16 agroforests, respectively. In the first region only four farmers had irrigated their crop before the February rainfall event. The intensity of the March flowering event was less than in February as many more agroforests had already been induced to flower by irrigation. All 19 agroforests that flowered between March 15 and March 31 received rain on the flowering day, which greatly reduced the number of insect visitors (mean = 0.4 ± 0.3 SE insects per

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observation as opposed to 6.4 ± 1.2 SE insects per observation for agroforests that did not receive rain).

Insect Visitors. Three social bees accounted for 99% of flower visitors: *Apis dorsata*, the giant Asian honey bee (47% of visitors), *Apis cerana* (24%), and *Tetragonula iridipennis* (27.9%). All these bees were observed to carry pollen and contact the stigma during flower visits. Two *Ceratina* and one *Xylocopa* species were occasional visitors to coffee flowers (1% of visits). As bee diversity was low, we evaluated pollination and fruit set on the basis of overall bee abundance, assuming that each pollinator species is equivalent in terms of pollination effectiveness. As there is no information available on the equivalency of pollinator effectiveness of these flower visitors, we feel the assumption of equivalence is preferable to the introduction of potential errors based on speculation.

There was high variation in pollinator abundance, with 45 agroforests (40%) receiving no visitors at all during the observation periods. In such cases it was very obvious that there were almost no pollinators across the entire agroforest, and thus a "0" value is not simply an artifact of a limited observation time but is an accurate representation of extremely low bee visitation.

Shade Cover and Shade Tree Densities. Shade varied from 15% in the most open agroforests to 76% in the most shaded, with an average at 45%. Densities of *Grevillea robusta* and native shade trees differed at plot and agroforest scales due to uneven distribution of trees within agroforests (Fig. S1). On the basis of data collected from the 113 agroforests we estimated shade tree species richness across a range of agroforest areas (Fig. S2).

Responses of Bees to Management and Environmental Variables. Widespread rainfall throughout the study region triggered simultaneous flowering across multiple agroforests, whereas irrigation allowed farmers to control the timing of coffee flowering, which was often at times when few other agroforests were flowering. Bee abundance varied as a function of the number of agroforests flowering simultaneously (Fig. 1). Agroforests flowering asynchronously via irrigation (i.e., only 1, 2 or 3 agroforests flowering at any one time) had significantly higher bee abundance (15.2 ± 3.0 bees) than agroforests that flowered following rain (16 or 75 agroforests flowering concurrently; 2.3 ± 0.7 bees) (Kruskal–Wallis test: $\chi^2 = 28.31$, df = 1, $P < 0.001$). Bee abundance was negatively correlated with the number of flowers and the density of native shade trees (at agroforest and plot scales) and was positively influenced by the number of *A. cerana* hives and temperature at the time of observation (Table 1).

Relating Bee Abundance and Plantation Management to Coffee Production. The interaction between bee abundance and number of flowers had a positive impact on the number of coffee berries harvested. Thus coffee production increased with increasing bee abundance, and this effect was amplified by an increase in the initial number of flowers (Fig. 2). Bee abundance reduced berry drop rate before the monsoon as well as the number of peaberries (Table 2).

Fertilization and nitrogen availability had negligible effects and were therefore not included in any final models. Lime application, however, positively increased mature fruit production (Table 2).

Discussion

After accounting for several management and environmental variables, it is clear that bees provide a pollination service to coffee that is reflected in a higher number of harvested berries. The contribution of pollinators must, however, be qualified in that pollinator visitation is highly dependent on a particular management intervention: irrigation. Irrigation can be used to increase pollinator abundance, creating patches of intense flowering that are asynchronous with the surrounding coffee farms (Fig. 1). Other management interventions, notably liming, also substantially affect coffee yields independently of any effect on bees and far more substantially than any variation in bee abundance. Different amounts of fertilizer application had no effect on production, probably because farmers apply more fertilizer than is actually necessary. In Kodagu, P fertilization ranged from 24.7 to 498.2 kg·ha^{-1}·y^{-1} (mean of 177.1 ± 7.5), whereas the recommended application for coffee production is 20–45 kg·ha^{-1}·y^{-1} (7, 8). There was an indication that fruit abortion was greater ($P = 0.08$), and mature berries smaller ($P = 0.064$), at higher coffee plant densities, although these effects are marginally significant (Table 2). The large majority of coffee

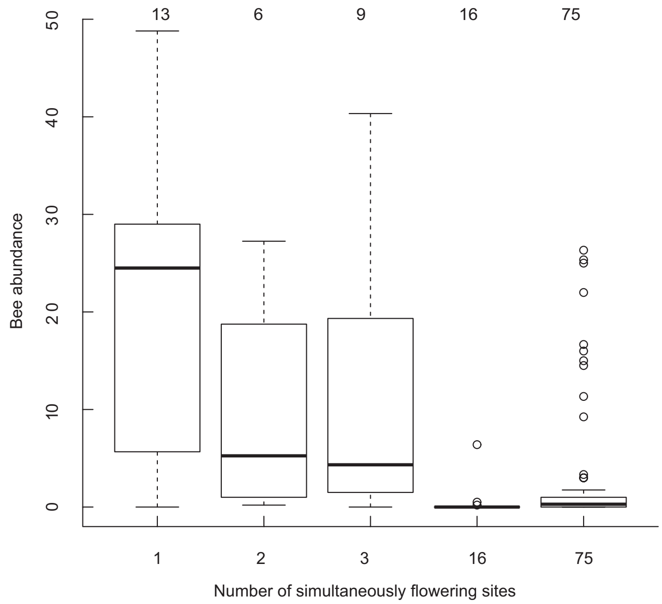

Fig. 1. Bee abundance as a function of the number of agroforests flowering on the same day. All agroforests in categories 1–3 were irrigated, and the number of each category signifies the number of agroforests in flower at that time. The numbers at top of the graph indicate how many agroforests flowered under such conditions: Agroforests flowering alone (category "1") numbered 13, those flowering simultaneously with one other agroforest (category "2") totaled 6, and those flowering with two other agroforests (category "3") totaled 9. Four of the 16 coflowering agroforests (category "16") were irrigated. Flowering in the 75 coflowering agroforests was stimulated by rainfall.

Table 1. Management practices and environmental variables significantly affecting bee abundance at coffee flowers (zero-inflated negative binomial model)

	df	Sign	χ^2	*P* value
Bee abundance at coffee flowers (count model)				
Irrigation	1	+	15.35	<0.001
No. flowers	1	–	5.06	0.024
Density of native shade trees at agroforest scale	1	–	6.57	0.010
Number of *Apis cerana* hives	1	+	8.31	0.004
Bee abundance at coffee flowers (binomial model)				
Irrigation	1	+	25.63	<0.001
Density of native shade trees at plot scale	1	–	10.75	<0.001
Temperature at observation time	1	+	13.91	<0.001

The "Sign" column indicates the effect of the independent variable on bee abundance/presence.

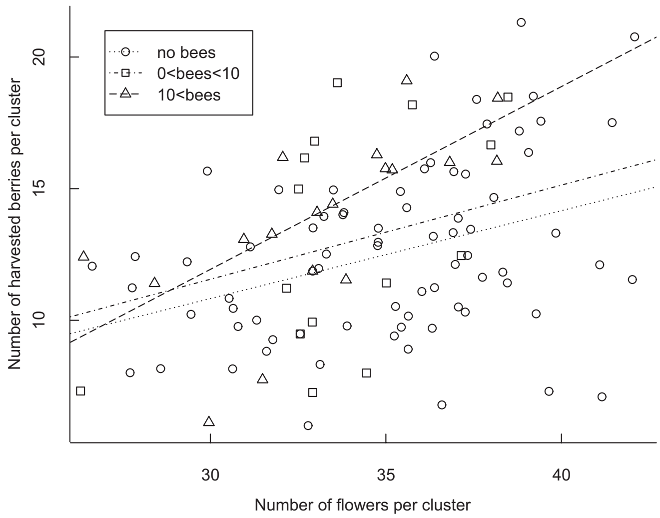

Fig. 2. Interaction graph representing coffee production as a function of the initial number of flowers, for different values of bee abundance. For clarity, the abundance of bees observed per hour is presented as three categories: no bees, <10 bees, and ≥10 bees.

plants were established at least 30 y before the study, and this predates changes to shade tree densities (9); consequently there is no clear relationship between shade tree and coffee densities. Nevertheless, the data also suggest that increasing native shade tree density does increase the number of harvested berries ($P = 0.06$; Table 2). In all these cases, however, effect size is small. The role of bees for coffee production in Kodagu needs to be set in the context of these management interventions that affect production either by influencing pollination or otherwise.

Pollinator Diversity and Abundance. Bee populations in Kodagu appear lower than that required to ensure full pollination of coffee flowers, as only 40% of agroforests received bee visits. Moreover, the number of pollinating species is low compared with that recorded by other studies, with only three social bee species accounting for 99% of flower visits. Most other studies, often on *Coffea arabica*, recorded over 20 bee species even though the scale of the studies (i.e., number of agroforests) was far lower than our own (Table S1). A low diversity of flower visitors in Kodagu might be explained by a regionally depauperate bee community, but this does not seem to be the case as many bee species have been recorded in adjacent forest patches during the coffee flowering period (10). The application of pesticides could affect bee populations elsewhere, but in Kodagu pesticides are almost never used as *Coffea canephora* is naturally resistant to pests (11), which is indeed the main reason why farmers choose to plant it over *C. arabica*. Whereas solitary bee species might have comparatively low resource requirements and might therefore benefit little from foraging outside forest fragments, social bees (including *Apis* and *Tetragonula*) have high resource demands to support large colonies and are likely to benefit more from a mass flowering resource such as coffee (12). Moreover, populations of ground-nesting solitary bees are not likely to be favored within coffee agroforests because management interventions include soil tillage and weeding that could destroy bee nests. In contrast, *A. cerana* and *T. iridipennis* are regularly found nesting within agroforests. This combination of factors might explain the low diversity of the coffee-pollinating community in Kodagu.

In most other studies (except that in ref. 13), variables related to shade (i.e., shade tree diversity and density, and shade cover) were positively associated with pollinator abundance and diversity (Table S1). This was not the case in Kodagu, where shade did not affect bee abundance at coffee, although native tree density (highly correlated with tree species richness) negatively affected bee abundance. It is possible that floral resources available within the many forest patches across the landscape, as well as the flowering shade trees within coffee agroforests, are sufficiently abundant in Kodagu that resources offered by coffee flowers fail to attract pollinators. Indeed, the distribution of forest patches in Kodagu, in terms of their distance to coffee plantations, has little effect on pollinator visitation to coffee (10), a result contrary to other studies that suggest declining

Table 2. Effects of management practices and environmental variables on coffee production

	Sign	*F*	*P* value
Harvested berries ($R^2 = 0.40$, df = 98)			
No. flowers * bee abundance	+	13.4	<0.001
Lime application	+	22.7	<0.001
Rain on the flowering day	–	8.7	0.003
Density of native shade trees	+	1.9	0.06
Fruit drops between April and June 2008 ($R^2 = 0.33$, df = 85)			
Previous no. fruits	+	17.4	<0.001
Bee abundance	–	19.1	<0.001
Rainfall up to June	–	8.6	0.003
Density of coffee trees	+	3.1	0.080
Log of fruit drops between July and September 2008 ($R^2 = 0.62$, df = 85)			
Previous no. fruits	+	113.2	<0.001
Lime application	–	4.8	0.031
Shade	–	2.2	0.14
Berry dry weight ($R^2 = 0.18$, df = 97)			
No. fruits harvested	–	16.0	<0.001
No. weedings per year	+	5.1	0.026
Density of coffee trees	–	3.5	0.064
Density of *G. robusta* at plot scale	–	–5.4	0.022

Results of linear model analyses are presented after model reduction based on the Akaike information criterion (single terms present in interactions are not presented when interactions are significant; *Materials and Methods*). Adjusted R^2s are in parentheses after the name of the response variable tested. The sign indicates whether the relationship between variables is positive or negative.

pollinator services with increasing distance to forest (14, 15). This is probably because forest cover is still extensive across Kodagu, and even plantations far from forest patches are not sufficiently isolated to suffer from deficiencies in pollinator visitation. Bee diversity and abundance at coffee flowers might, therefore, be a function of the abundance and distribution of alternative floral resources within agroforests or across the landscape, and where these resources are abundant the attractiveness of coffee as a resource might be diminished (10, 16). Should this be the case, then the validity of encouraging forest conservation through an associated crop pollination service will depend on the context of land cover distributions.

A comparison across studies serves to illustrate this point. The Kodagu coffee region retains relatively high natural forest cover (46%) and shade tree richness across the landscape is around 45 species per hectare (Fig. S2). By comparison, a Costa Rican study (17) was carried out in a 1,100-ha *Eucalyptus*-shaded coffee plantation located between only two forest fragments of 46 and 110 ha. Hence the high diversity of bees (40 species) at coffee flowers in the Costa Rican study might be explained by the availability of a major floral resource (the extensive mass-flowering coffee crop) in relation to limited alternative resources within the two forest patches and monospecific shade layer. Similarly, Jha and Vandermeer (18) recorded 17 bee species at coffee in "heavily deforested" Mexican sites, with 12–18 shade tree species per hectare, and tree densities of 139–256 trees per hectare, again representing far fewer resources for bees than at Kodagu (tree richness, 45 species per hectare; tree density, 32–796 trees per hectare). The relationship between pollinator diversity/abundance at crop flowers and shade tree density/diversity is therefore complex and is likely to reflect an interaction among native tree diversity/abundance and area and distribution of forest cover across the landscape.

Managing Flowering Asynchrony for Pollination Benefit. The large number of synchronously flowering agroforests following rainfall causes social bee foraging to be spread over many agroforests and thus limits bee abundance at any one agroforest (Fig. 1) (18, 19). In Kodagu, pollination effectiveness is not only a function of pollinator abundance, but also a function of a single irrigation treatment by which farmers induce flowering outside the main rainfall period and correspondingly benefit from large numbers of bees attracted to their agroforests (6.6 times more bees on average). Crop pollination might therefore be managed by providing the capacity to irrigate agroforests sequentially and patchily across the landscape before the predicted start of rainfall. We suggest that such irrigation management could be applied to *robusta* coffee systems elsewhere where rainfall during a distinct dry season triggers flowering; its relevance to *arabica* coffee remains to be explored. Besides concentrating pollinators within flowering agroforests, irrigation allows synchronous berry maturation and crop harvesting, hence limiting the costs of multiple harvestings (20). Moreover, asynchronous flowering among agroforests allows for a better distribution of labor that is limited during the harvesting period. As irrigation is applied only once to stimulate flowering, its effects on pollination and coffee production can only be attributed to its role in inducing flowering.

Independently of irrigation, the number of *A. cerana* hives maintained by farmers within agroforests and on adjacent farms positively affected the abundance of *A. cerana* at coffee flowers. Maintaining such hives can, therefore, benefit coffee pollination and provides an alternative to irrigation for farmers who are unable to invest in irrigation.

Bees and Coffee Production. Bees contributed significantly to coffee production by increasing the number of berries produced (Fig. 2). This finding, which is consistent with previous studies on coffee pollination (10, 17, 21, 22), demonstrates that bees improve coffee production even after accounting for the full maturation time and management practices. Pollinators might have a qualitative as well as a quantitative effect in that biotic pollination might increase pollen genetic diversity and hence viability of resulting fruits (23). It certainly seems that bee pollination improves fruit retention before the monsoon (Table 2), although it did not significantly affect berry dry weight or the proportion of large beans, as reported by other studies on *C. arabica* (24, 25).

The contribution of bees to crop production does, however, need to be considered with respect to the number of flowers within each inflorescence (Fig. 2). When the number of flowers per cluster is relatively low (at around 30), bee visits make no apparent contribution to coffee production. Berry production increases with flower number regardless of bee visitation, but the rate of increase is higher when bees are present in large numbers (Fig. 2). Thus, when coffee inflorescences include 40 flowers, visitation by bees increases berry production by more than 25%. This represents a substantial increase in coffee production for farmers, and the result emphasizes the need for management that increases both flower number (perhaps by fertilization or the adoption of improved coffee varieties) and bee visitation. This might prove challenging on account of the odd result that bee visitation is negatively correlated with flower number (Table 1).

Role of *Grevillea*. The density of *Grevillea* planted in agroforests had a negative effect on berry dry weight, a measure of coffee quality. We cannot easily explain this result, nor can we even ascribe it directly to *Grevillea* density, which negatively covaries with native tree cover. Nevertheless, *Grevillea* cover is more open and is unlikely to be as effective in providing a favorable understory microclimate that buffers coffee from weather fluctuations. *Grevillea* also drops its leaves frequently and the resulting litter often smothers the coffee plants. Farmers state that both these factors adversely affect berry development, although we have no empirical evidence to support this. We also recognize that *Grevillea* trees provide many benefits to farmers as timber revenue and as a stand for pepper (9, 26); the potential negative effects of *Grevillea* need to be set against its benefits.

Conclusion

Ecosystem services unfold not in isolation but through interactions with multiple management interventions that play a part in farmers' decision making. Coordination of irrigation to cue flowering among coffee farmers, for example, might attract more bees by sequentially staggering the flowering times of agroforests and thereby avoiding competition among them for pollinators. The potential benefit of this to coffee production in Kodagu is substantial, not only by greatly increasing bee visits to individual plantations, but also in consideration that 60% of farms currently suffer from extremely low bee visitation. At the same time it is important to recognize that other interventions, such as liming, can also substantially increase production irrespective of (and additive to) bee visits.

Counterintuitively, pollinator services to crops might be depressed in a landscape that is rich in natural forest habitat and diverse in tree species if natural floral resources are sufficiently plentiful to supply the needs of pollinators. There is evidence for this from Kodagu (10) as well as elsewhere (16). Thus, crops might benefit most from pollination services when native trees (in forests or in agroforests) are neither too abundant nor too scarce. Controversially, it might be argued that the abundance and richness of native trees in coffee agroforests in Kodagu is actually detrimental to coffee pollination through competition for pollinators (10), even though shade has other benefits for coffee production. Although this might encourage management interventions to reduce the number of native trees (or at least those that flower at the same time as coffee), it should also be recognized that shade has other benefits (e.g., moderation of microclimate and provision of other nontimber forest products), as well as serving to support the wider landscape biodiversity (27).

There is considerable variation in farmer management practices, and current practice is often far from optimal for maximizing production: only some farmers apply lime, only some irrigate, and almost all apply more fertilizer than is necessary. Shade tree density is highly variable, and bee hives are maintained in some farms but not in others. This wide variation in management practices might reflect a lack of understanding of what constitutes best practice, barriers to the adoption of best practice or, alternatively, that maximizing coffee production is not a high priority for these farmers. The latter is very unlikely given that coffee constitutes the main financial resource of most farmers, who expressed frequent concerns about productivity. Barriers to adoption of irrigation certainly exist in the form of access to water and capital to invest in irrigation technology, but this does not explain lack of adoption of simple inputs such as liming that substantially contributes to production. We suggest that the diverse management practices observed in Kodagu mainly reflect the still limited understanding by scientists and farmers of the complex interactions and resulting outcomes of different management practices.

Materials and Methods

The study took place in Karnataka, India, in the district of Kodagu, on the eastern slopes of the Western Ghats. *Coffea canephora*, which is cross-pollinated, flowers 8 d after rainfall (or irrigation) between February and March. The flowers are borne in inflorescences distributed along branch nodes. Anthesis across an agroforest occurs simultaneously on a single day. In Kodagu, *C. canephora* is grown under varying densities (32–796 trees per hectare) and types of shade tree. In past decades, coffee farmers have increasingly replaced native shade trees with the exotic tree *Grevillea robusta*.

In 2008, we collected data on pollination and coffee production at 113 agroforests. Agroforests were selected on the basis of the age of the *C. canephora* trees (20–40 y), reflecting the period of peak production. Agroforests selected for study were separated from each other by at least 1 km, but were otherwise randomly selected. Individual coffee agroforests ranged in size from 0.3 ha to, exceptionally, 32 ha, with a mean of 3.8 ha (SE = 0.42). This size range is typical for smallholder coffee production in Latin America and Southeast Asia. Farm size itself, however, is not particularly informative as plantation boundaries typically abut, and the contiguous area under agroforest cultivation often exceeds the size of any individual farm.

On-Site Factors. Shade was determined by recording canopy cover in the immediate vicinity of our coffee trees, using a densiometer (28). We also recorded the density of *G. robusta* and native trees with diameter at breast height (DBH) exceeding 10 cm, based on two 10-m radius plots (2×314 m^2) in each agroforest. The plots were located at either end of the rows of coffee trees used to assess pollination and fruit production. Within the same plots we recorded the species of shade trees that exceeded 10 cm DBH. We also collected estimates of shade tree densities given by farmers for their whole agroforest. These estimations are coarser but take account of a larger spatial scale, and both measured and estimated densities were included when analyzing the impact of environmental variables on bees.

Soil was sampled from each agroforest in March 2008. At each site, we collected three soil cores 2.5 cm in diameter and 20 cm deep. The samples were taken 10 m apart, with each sample being within a few meters of the sampled coffee plants. The three samples were pooled, thoroughly mixed, and air dried. From each site 500 g of soil was sent for analysis of nutrients and pH by Multiplex Biotech Pvt Ltd. Rainfall data for 2007 and 2008 were collected from 24 farmers who used rainfall gauges provided by the Coffee Board of India. From these data, we interpolated rainfall patterns across the region, using the inverse distance weighting method (29).

Information on farm management practices was collected through interviews with all 113 farmers. Specifically, we sought information on application of fertilizer and lime, irrigation that is applied once to induce flowering, pruning and weeding, and tree management.

Pollination Service. At each site we conducted simultaneous observations of 15 min at three to eight flowering coffee trees. Each observation encompassed a total of 30 inflorescences (6 inflorescences on each of five branches). We recorded all insect species visiting coffee flowers and the number of flowers visited per individual, which allowed us to determine species diversity and abundance, as well as the visitation rate. The 15-min observation time that is consistent with other studies (15, 17) was chosen on the basis of preliminary observations at 70 coffee trees, which indicated that results derived from a 15-min observation period did not differ from those derived from a longer 30-min period (10). Due to a varying number of observations per agroforest, we averaged all of the data at 1 h observation per agroforest.

Observations were carried out between 0900 and 1600 hours, and observations were distributed almost equally between morning and afternoon (52% vs. 48%, respectively). All observations were conducted during periods of fine weather (sunny), although on some observation days it rained later in the day. In our analysis we differentiate between days of rain and no rain.

Coffee Production. Fruit production was assessed on 10 trees within each of the 113 agroforests at four stages during fruit development (see below). The first coffee tree was randomly selected in the agroforest. We then selected another 4 coffee trees, choosing every other tree in the same row. We repeated this selection procedure in a parallel row, although two rows removed from the first. Distance between sampled trees was 7–12 m. Average planting density was 1,240 ($\pm$20, SE) coffee plants per hectare.

The number of buds from 30 inflorescences (on five branches) from the 10 trees at each agroforest was counted. Developing and mature fruit on the same inflorescences were counted on four subsequent occasions: early fruit set (mid-March to early May), pre-monsoon fruit set (June), post-monsoon fruit set (September), and final production (December to January). We also considered pre-monsoon fruit drop (early fruit set minus pre-monsoon fruit set) and monsoon fruit drop (post-monsoon fruit set minus pre-monsoon fruit set). Once collected, berries were dried in an oven at 60 °C for 24–36 h until moisture content was around 12%, as required by the coffee sector. For each of the 10 trees, we evaluated berry production per inflorescence in absolute terms (most relevant from a farmer's perspective). The ratio of fruits to flowers was not used as this would have obscured the interaction effect of flower number and bee visitation with regard to fruit production. The initial number of flowers and previous counts were included as covariates in the corresponding models.

Statistical Analysis. Data were analyzed using R, using linear models when production variables were the dependent variables or zero-inflated negative binomial (ZINB) models when "bee abundance at coffee flowers" or "number of visited flowers" were analyzed. ZINB models can deal with a large number of zero values in the dataset, as well as overdispersion of the data (30), and are therefore more appropriate than generalized linear models for our dataset. We averaged results from trees within agroforests to overcome nonindependence of data and unbalanced sample sizes. We tested the homoscedasticity of the models and log-transformed the independent variables when necessary.

Correlations between independent variables were checked using the generalized variance inflation factor (GVIF) and in the case of correlation (GVIF > 3), the variable of least importance for the study was removed. The models were simplified by removing the least significant variable as long as the reduced model did not significantly differ from the previous one. For analyses without interaction terms we used a type II sum of squares in the ANOVA summary. When an interaction term was included, we used a type III sum of squares. In such cases, the individual effect of the single terms that were part of the interaction was not considered (31).

For fruit set analyses, we included management practices and environmental variables based on information provided from farmers. These variables were liming (yes/no), fertilizer application, soil pH, coffee production in the previous year, rainfall in previous and current years, rain on the day of flowering (yes/no), weedings per year, shade cover, and coffee tree density.

We investigated the impact of nine variables on bee abundance: shade, shade tree density at agroforest scale (data from interviews) and plot scales (field measurements) for *G. robusta* and native trees, temperature at the time of observation, number of domesticated *A. cerana* hives maintained by farmers and their neighbors, feral *A. dorsata* hives within 300 m of the agroforests, and irrigation. Shade tree densities (of *G. robusta* and native trees) and shade cover were treated as independent variables as there was no collinearity among them (*G. robusta* tends to be planted at much higher densities in agroforests than native shade trees, but casts less shade).

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Supporting Information

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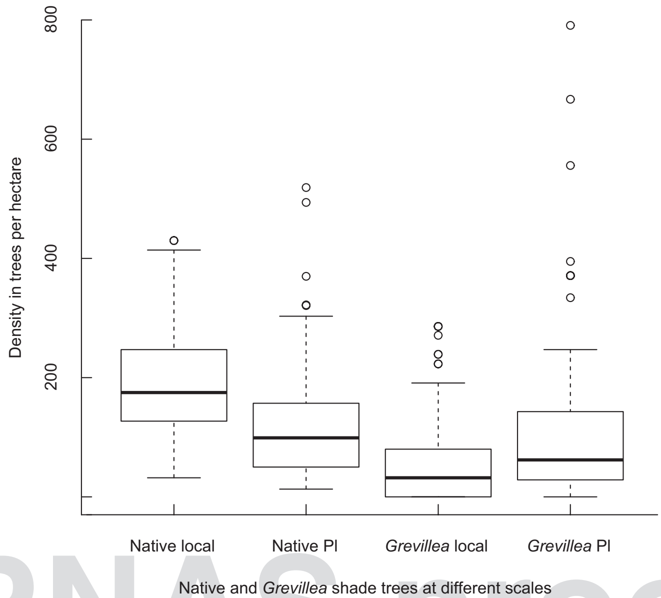

Fig. S1. Densities (trees per hectare) of native and *G. robusta* shade trees at the plot scale ("local", measured around the selected coffee trees) and the plantation scale ("Pl", given by farmers for the entire plantation).

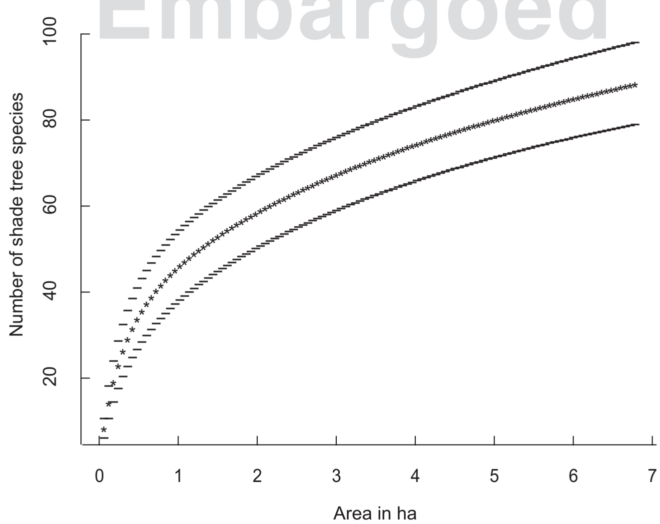

Fig. S2. Accumulation curve of shade tree species richness over area in hectares for Kodagu, calculated with EstimateS 8.2 (http://purl.oclc.org/estimates). *x* axis shows the area in hectares, *y* axis represents the species richness. The 95% confidence interval is represented for each modeled point.

Table S1. Bee diversity and shade variables across coffee pollination field studies

Location	Coffee spp.	Total species	Social bees	Solitary bees	Other species	Shade, %	Shade variables	Shade effect on bee richness	Study sites	Reference
Kodagu	*canephora*	5	3	2	0	15–75	S, STD, SD	–	113	This study
Mexico	*Coffea* spp.	44	36	8	NA	19–71	S, STD, SD	+	7	Jha and Vandermeer (1)
Mexico	*canephora*	17	12	NA	NA	60	S, STD, SD*	+	2	Jha and Vandermeer (2)
	arabica	8	5	NA	NA	25	S, STD, SD*			
Mexico	*arabica*	8	5	3	8	4 classes	S, SD*	+	16	Vergara and Badano (3)
Mexico	*arabica*	5	3	2	9	High	S, STD, SD*	None	2	Philpott et al. (4)
	arabica	3	2	1	2	Low	S, STD, SD*			
Brazil	*arabica*	6	4	2	NA	None	NA	NA	6	De Marco and Coelho (5)
Ecuador	*arabica*	29	19	10	NA	NA	S (tree scale), SD	+	22	Veddeler et al. (6)
Costa Rica	*arabica*	40	11	29	NA	NA	NA	NA	1	Ricketts (7)
Panama	*arabica*	22	19	3	1	2 classes	NA	NA	10	Roubik (8)
Indonesia	*arabica*	29	7	22	NA	NA	NA	NA	24	Klein et al. (9)
Indonesia	*canephora*	22	7	15	NA	5 classes	S, STD, SD*	+	12	Klein et al. (10)

Shade variables are S, shade; STD, shade tree density; and SD, shade diversity. Jha and Vandermeer (1) cataloged bees throughout the year and not only at the time of coffee flowering. NA, not assessed.
*Variables are confounded in these studies.

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