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Fruit set of highland coffee increases with the diversity of pollinating bees

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The worldwide decline of pollinators may negatively affect the fruit set of wild and cultivated plants. Here, we show that fruit set of the self-fertilizing highland coffee (*Coffea arabica*) is highly variable and related to bee pollination. In a comparison of 24 agroforestry systems in Indonesia, the fruit set of coffee could be predicted by the number of flower-visiting bee species, and it ranged from *ca.* 60% (three species) to 90% (20 species). Diversity, not abundance, explained variation in fruit set, so the collective role of a species-rich bee community was important for pollination success. Additional experiments showed that single flower visits from rare solitary species led to higher fruit set than with abundant social species. Pollinator diversity was affected by two habitat parameters indicating guild-specific nesting requirements: the diversity of social bees decreased with forest distance, whereas the diversity of solitary bees increased with light intensity of the agroforestry systems. These results give empirical evidence for a positive relationship between ecosystem functions such as pollination and biodiversity. Conservation of rainforest adjacent to adequately managed agroforestry systems could improve the yields of farmers.

Keywords: agroforestry systems; *Coffea arabica*; conservation; diversity–function relationship; landscape context; pollinator limitation

1. INTRODUCTION

Almost all flowering plant species of tropical rainforests are pollinated by animals (Bawa 1990) and one-third of the human diet in tropical countries is derived from insect-pollinated plants (Crane & Walker 1983), so the worldwide decline of pollinators has potential consequences for the stability of crop yields (Allen-Wardell *et al.* 1998; Kevan & Phillips 2001). The highland coffee plant (*Coffea arabica* L.) is one of the major tropical cash crops and has been considered to be a self-fertilizing plant (Rehm & Espig 1991; Free 1993). It has only recently been shown that the fruit set of highland coffee increases with cross-pollination by bees (Klein *et al.* 2003; Roubik 2002). Pollination limitation has usually been related to the visitation rate or abundance of pollinators (Kunin 1993; Larson *et al.* 1999; Steffan-Dewenter & Tscharntke 1999; Cunningham 2000; Herrera 2000; Parker & Haubensak 2002; Roubik 2002), and only a recent study by Kremen *et al.* (2002) shows that bee diversity is essential for sustaining pollination services.

Fragmentation and destruction of natural or semi-natural habitats may result in the loss of bee diversity and disruption of plant–pollinator interactions (Rathcke & Jules 1993; Renner 1998; Cane 2001; Steffan-Dewenter *et al.* 2002), but experimental evidence is still extremely rare (Steffan-Dewenter & Tscharntke 1999; Cunningham 2000; Cane 2001; Steffan-Dewenter *et al.* 2002). The quality of the landscape matrix, with respect to the distance of crops from natural forest or other source habitats, may be important for many species (Perfecto & Vandermeer 2002). Fragmentation of tropical forest as part of the change to a mosaic of natural forest and agroforestry is known to affect pollinator communities greatly (Aizen & Feinsinger 1994). Coffee is traditionally grown under a canopy of shade trees. These traditional coffee agroforestry systems have relatively high biodiversity compared with unshaded monocultures (Perfecto & Vandermeer 1996; Moguel & Toledo 1999). One reason for the high biodiversity in shaded agroforestry systems is the structural and floristic complexity (Perfecto & Vandermeer 1996). Intermediate degrees of shade improve the coffee yield, but more than 50% shade causes high losses (Muschler & Bonnemaann 1997; Soto-Pinto *et al.* 2000). Microclimatic conditions of agroforestry systems affect flower visitation by bees (Klein *et al.* 2002), so the fruit set of coffee may also suffer.

In this study we analysed the effects of bee diversity and abundance on the fruit set of highland coffee in 24 agroforestry coffee fields, differing in shade and forest distance. We focused on the following questions.

(i) Does the fruit set of highland coffee depend on pollinating bees, and is bee diversity or bee abundance more important?
(ii) Are social or solitary bees the more efficient pollinators of *C. arabica*?
(iii) Do distance to the nearest forest and shading of coffee influence the diversity of flower-visiting bees and the resulting fruit set?

2. MATERIAL AND METHODS

(a) *Study area and experimental sites*

Coffee pollination was studied from November 2000 to March 2001 and from July 2001 to October 2001 at the margin of the Lore-Lindu National Park, Central Sulawesi (Indonesia), 100 km south of the city of Palu, in the villages Wuasa, Watumaeta, Alitupu and Kaduwaa. The 24 study sites, i.e. agroforestry coffee fields, were characterized according to shade level and

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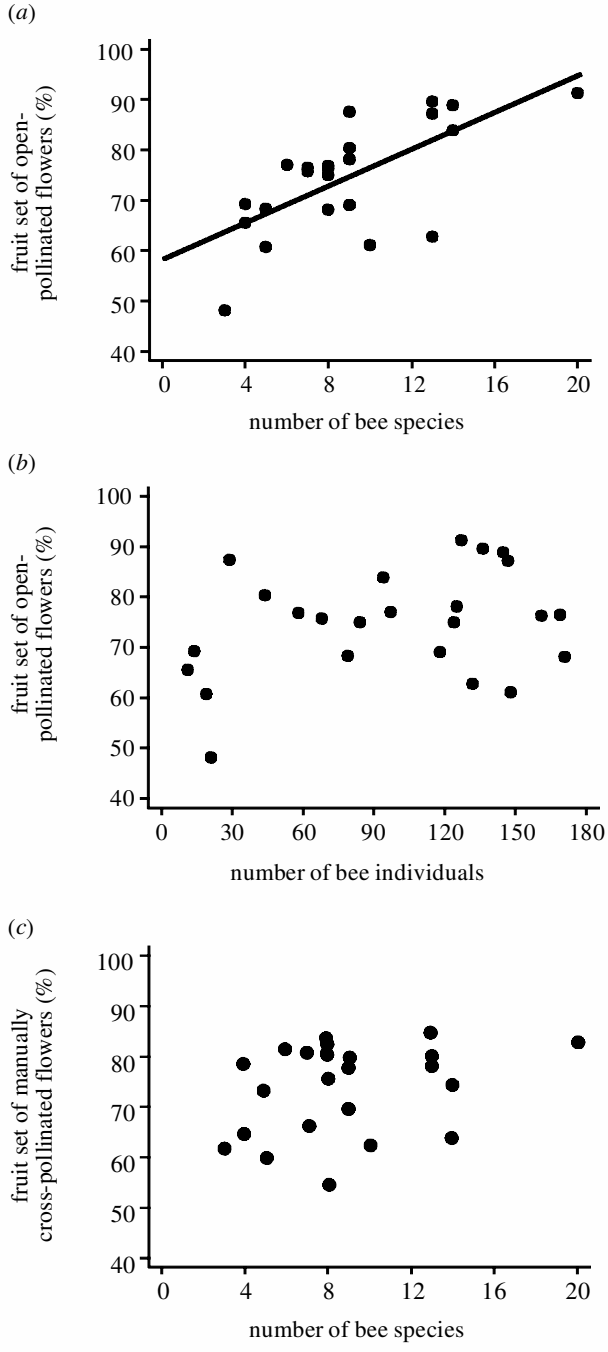

Figure 1. Fruit set of *C. arabica* in relation to species number and abundance of bees in each of the 24 agroforestry systems (bees observed three times on full-blooming coffee plants). (*a*) Fruit set as a function of open-pollination and bee species richness ($y = 58.56 + 1.81x$, $F = 17.90$, $r^2 = 0.449$, $n = 24$, $p < 0.001$). (*b*) Fruit set as a function of open-pollination and bee abundance ($F = 2.49$, $r^2 = 0.102$, $n = 24$, $p = 0.13$). (*c*) Fruit set as a function of manual cross-pollination and bee species richness ($F = 0.14$, $r^2 = 0.309$, $n = 24$, $p = 0.14$).

vegetation. Light intensity per study site was measured with a luxmeter (digital light gauge with four ranges from 0–1999 W m^{-2}) under standardized conditions (on the ground and on sunny days, local time 0900–1500) and the mean of 20 measurements was calculated. The vegetation was mapped twice per study site, within a 25 m^2 plot for herbs and within a 100 m^2 plot for shrubs and trees, resulting in estimates of the number of total plant species and the percentage of vegetation cover. Percentage cover of coffee plants in flower and percentage cover of all non-coffee plants in flower (which were all herbs) were recorded for each site to estimate the resource availability for flower-visiting bees. Distance to the nearest forest ranged from inside the forest margin to a distance of 1415 m, measured with a GPS (Global Positioning System 12, Garmin International Olathe, Kansas, USA).

(b) *Flower-visiting bees and fruit set*

Flower-visiting bees on *C. arabica* were observed from 28 December 2000 to 9 January 2001. The flowers generally open just before dawn and last for 2 days, but usually, depending on the weather conditions, a coffee flower is attractive to flower-visiting bees for only 1 day. At each study site we observed flower visitors for 25 minutes on each of three different days. Every day we observed a different full-blooming coffee plant from the one observed the day before and with about 100 flowers, on sunny days between 0900 and 1400 (local time). All flower visitors were counted within these 75 minutes. After each 25-minute observation period, bees were caught for 5 minutes by sweep-netting, for species identification. Social bees were identified with the help of a collection from Gard Otis, University of Guelph, Canada. Solitary bees were identified by Donald B. Baker, Oxford University Museum of Natural History, UK.

For each of three treatments, open-pollination, cross-pollination by hand and self-pollination by hand, we selected four coffee shrubs per study site (four sets of three branches in each of the 24 sites, resulting in a total of 288 branches). Bags of very fine nylon mesh gauze (10 μm) were used for the hand- and self-pollination experiments to exclude wind-pollination and were fixed on the coffee branches 1–6 days before flowering, following Willmer & Stone (1989). Sticky glue was put on the branch beneath the bagged flowers to exclude ants. Pollen was transferred to stigmas with a brush on the first day of flower opening. The numbers of flowers on the observed bagged and open branches were counted, and the branches were tagged. Hand-pollination and open-pollination experiments were conducted in the same week as flower-visitors were counted. Five weeks after the end of the major flowering period, the bags were removed and the numbers of green ovules were counted on tagged hand- and open-pollinated branches.

At the beginning of June 2001, 10 coffee plants at one site (unshaded polyculture) were selected to test experimentally the pollen transfer efficiencies of different bee species. Twenty branches with dense and mature buds were bagged on each of the 10 plants 4 days before flowering, using fine nylon mesh gauze (10 μm). When the flowers started to open, the bags were removed (one by one), so the bees could visit the still virginal flowers. Immediately after one bee had visited a single flower, the flower was marked with a species-specific colour and the branch was bagged again. After five weeks, we removed the bags from the fruiting branches and counted the numbers of green ovules in marked flowers only. Normally two ovules develop into a coffee fruit. Sometimes only one of the two ovules in a coffee flower develops into a fruit, a condition known as 'pea berry' (Raw & Free 1977). We found only 0.92% of such 'pea berries' in 12 000 coffee fruits. Therefore we neglected possible differences between 'pea berries' and complete fruits in our study. Terminal flowers may have smaller fruits and a lower probability of fruit set than basal flowers (Corbet 1999), but in our experiments we observed only terminal flowers, so these possible differences did not affect our results.

Table 1. Pollination efficiencies of social and solitary bees. Fruit set after a single visit of a specific bee species to a single virginal previously bagged coffee flower was analysed. The number of single visits for each species and the proportion of flowers that developed fruits are given. In addition, the frequency of flower visitation within the total of 75 min per study site is given for the 24 study sites.

bee species	number of replicates	fruit set (%)	frequency of flower-visitors
social bees			
Apis nigrocinta	51	76.5	343
Apis dorsata binghami	56	82.1	229
Apis cerana	13	84.6	269
Trigona (*Lepidotrigona*) *terminata*	20	80.0	106
Trigona sp. 3	12	75.0	23
Trigona (*Heterotrigona*) sp. 1	12	66.7	19
Trigona (*Heterotrigona*) sp. 2	12	58.3	154
	sum: 176	mean: 74.7 ± 3.51	sum: 1143
solitary bees			
Amegilla sp.	14	85.7	57
Chalicodoma (*Callomegachile*) *clotho*	5	60.0	28
Ceratina sp.	10	90.0	26
Creightonella frontalis	20	90.0	101
Halictidae gen. sp.	11	90.9	146
Heriades sp.	28	92.9	113
Xylocopa (*Koptotorsoma*) *aestuans*	4	100	33
Xylocopa (*Zonohirsuta*) *dejeanii nigrocerulea*	9	88.9	53
	sum: 101	mean: 87.3 ± 4.16	sum: 557

(c) *Statistics*

Statistical analyses were performed using the software 'STATGRAPHICS PLUS for Windows 3.0' (Manugistics 1997). All data were tested for normality and transformed if necessary. The independent variables blossom cover of coffee and blossom cover of herbs were always $\log_{10}$-transformed and the independent variable forest distance was always square-root-transformed (Sokal & Rohlf 1995). After transformation to normality we tested correlations between five independent habitat factors. In stepwise multiple linear regression analyses with backward selection we examined which independent habitat factors were most important for the dependent variables: number of all bee species and individuals, and separately for social and solitary bee species and individuals. The best-fitting habitat factor was shown in simple linear regression with the dependent variable. We used *t*-tests to compare the means of fruit set between social and solitary bees. To analyse the effect of bee diversity on the spatial variability of fruit set, we calculated the coefficient of variation (CV) of fruit set resulting from open-pollination for three bushes per study site. We estimated the total species richness of flower-visiting bees per site with 100 randomizations at 5-minute intervals, using the estimator ACE (abundance-based coverage estimator of species richness) and the program ESTIMATES, v. 5 (Colwell 1997). The proportion of sampled and estimated species richness was calculated for each study site and a mean value for all sites is shown. Arithmetic means ± standard errors are given.

3. RESULTS

The number of flower-visiting bee species in each of the 24 agroforestry systems was closely related to fruit set and explained 45% of the variance (figure 1*a*), whereas the number of bee individuals was not related to fruit set (figure 1*b*). The number of bee species and the number of bee individuals were positively correlated ($F = 8.98$, $r^2 = 0.289$, $n = 24$, $p = 0.007$). Fruit set was correlated with both the number of social bee species ($F = 12.33$, $r^2 = 0.359$, $n = 24$, $p = 0.002$) and the number of solitary bee species ($F = 8.91$, $r^2 = 0.288$, $n = 24$, $p = 0.007$). This pattern of pollinator limitation was further tested with manual cross-pollination of flowers. In this case, fruit set was not correlated with the number of bee species (figure 1*c*), so the highly significant correlation between bee diversity and fruit set was not confounded by factors such as nutrient limitation or plant growth. In addition, we calculated the difference between fruit set after open-pollination and fruit set after experimental cross-pollination. This difference increased with increasing bee diversity ($F = 5.60$, $r^2 = 0.203$, $n = 24$, $p = 0.027$), thereby giving direct evidence of pollination limitation. The CV of fruit set for open-pollinated flowers was negatively related to bee diversity ($F = 6.76$, $r^2 = 0.235$, $n = 24$, $p = 0.016$), indicating that high bee diversity reduced the spatial variability of fruit set.

The mechanism of this relationship between diversity and ecological function was investigated using further pollination experiments. We observed 277 flower visits from 15 species on virginal (previously bagged) coffee flowers. The pollination efficiency of solitary bee species was significantly higher than that of social bee species. On average, flower visitation by solitary bees resulted in 87.3% fruit set and visitation by social bees resulted in 74.7% fruit set ($t = -2.31$, $n = 7$ social + 8 solitary bees, $p = 0.019$; see table 1).

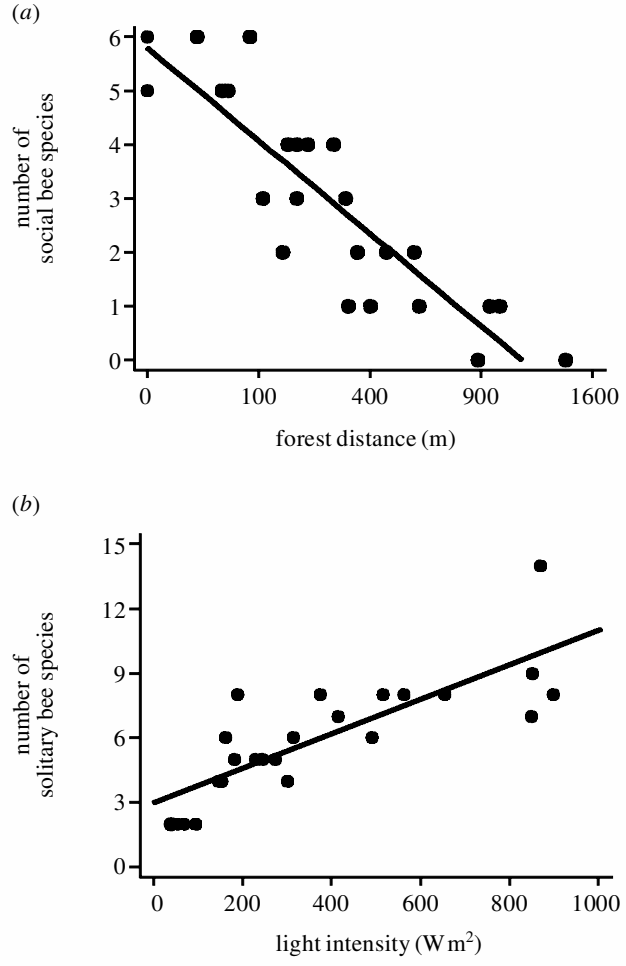

Figure 2. Number of bee species in relation to characteristics of the 24 agroforestry systems (bees were observed three times per 25 min on full-blooming coffee plants). (*a*) The number of social bee species in relation to forest distance ($y = 5.79 - 0.17\sqrt{x}$, $F = 79.24$, $r^2 = 0.782$, $n = 24$, $p < 0.001$). (*b*) The number of solitary bee species in relation to light intensity ($y = 2.97 + 0.01x$, $F = 40.33$, $r^2 = 0.65$, $n = 24$, $p < 0.001$).

We found 1143 individuals of seven social bee species (Hymenoptera: Apidae) and 895 individuals of 22 solitary bee species (Hymenoptera: Apidae, Megachilidae, Halictidae), which appeared to be a good estimate of bee diversity (on average $96.4 \pm 0.88\%$ species saturation; Colwell 1997). The diversity of flower-visiting bees was related to characteristics of the 24 agroforestry systems. The number of plant species, blossom cover of *C. arabica*, blossom cover of all plants, light intensity and distance to the forest were not significantly correlated with each other and were used as the five predictor variables. In stepwise multiple regression, the number of social bee species could be best explained by the distance to the forest margin (figure 2*a*), and the number of solitary bee species could be best explained by a combination of light intensity and plant diversity, the latter explaining a further 9.4% (out of a total of 74%) of the variance (figure 2*b*; table 2). The number of all flower-visiting bee species increased with light intensity and decreased with distance to the forest margin, the latter explaining a further 24.4% (out of a total of 78%) of the variation. Accordingly, fruit set of coffee significantly increased with increasing light intensity and decreased with increasing isolation distance from the forest margin, the latter explaining a further 9.2% (out of a total of 46%) of the variation (table 2). Fruit set of flowers that were manually cross-pollinated or self-pollinated was not related to forest distance or light intensity (table 2). The mean fruit set after self-pollination by hand has been observed to be 62.4% in all agroforestry systems (Klein *et al.* 2003).

4. DISCUSSION

Our results show that the fruit set of highland coffee could be predicted by the diversity, not abundance, of flower-visiting bees, so the collective role of a species-rich bee community was important for pollination success. The fruit set of open-pollinated flowers ranged from 60% to 90%, whereas cross-pollination by hand resulted on average in 75% fruit set and did not depend on pollinator diversity or habitat factors, indicating that pollination limitation played a major role. Both social and solitary bee species contributed to this diversity effect, but the underlying mechanism could be elicited only partly in this study. In general, two mechanisms could be important. First, complementary effects can be expected in a species-rich pollinator assemblage, thereby better covering spatial and temporal variability of flower resources, compared with one or a few pollinator species. Second, a sampling effect could result in the availability of more-efficient pollinator species in diverse bee communities.

Comparing abundant social and rare solitary bee species, we showed that single flower visits of solitary bees resulted in fruit set with a higher probability than with social bee species. Hence, the contribution of each rare bee species may have been small, but the collective role of these rare species turned out to be of quantitative importance. Given the same number of flower visits, the species-rich solitary bees contributed more to fruit set than the abundant social bees, partly explaining the positive relationship between fruit set and bee diversity. Multiple flower visits providing a surplus of pollen appeared to be rare, as shown by (i) the low fruit set of many sites, and (ii) the short lifespan of each flower, because a coffee flower is attractive to bees for only 1 day. Flower visits are extremely rare when coffee flowers open on a rainy day, and a second or even third visit to one flower is highly improbable. This is a common situation, because coffee flowers start opening at the same time as the rainy season starts. In our study, we observed flower visitors when it was dry and sunny, so we could observe a large number of pollinating bees.

Earlier studies have shown that, for several crops, solitary wild bees are more efficient pollinators than social honeybees (Corbet 1991). This could be explained by the following findings.

(i) Honeybees visit more flowers per unit time than other bees, and remain longer at branches with dense flowers, thereby consecutively visiting more flowers on the same plant (Heard 1994). Thus, there is a higher probability that honeybees transfer pollen of the same plant individual. Within-plant (geitonogamous) pollination has been shown to result in lower fruit set than cross-pollination for *C. arabica* (Klein *et al.* 2003).

Table 2. Results of stepwise multiple regression analyses of the effects of light intensity, forest distance, blossom cover of coffee, blossom cover of herbs and number of plant species on species richness and abundance of solitary and social bees and fruit set of open-pollinated, cross-pollinated and self-pollinated coffee. Only significant relationships are shown. Cross- and self-pollination did not show a relationship with any variable.

dependent variables	habitat factor (independent variables)	t	p	r^2
number of all bee species	light intensity (W m^{-2})	5.19	< 0.001	
	forest distance (m)	−4.81	< 0.001	
	final model			77.79
number of all bee individuals	light intensity (W m^{-2})	4.98	< 0.001	52.98
number of solitary species	light intensity (W m^{-2})	5.29	< 0.001	
	number of plant species	2.75	0.012	
	final model			74.07
number of solitary individuals	light intensity (W m^{-2})	3.83	< 0.001	39.96
number of social species	forest distance (m)	−8.90	< 0.001	78.26
number of social individuals	light intensity (W m^{-2})	−5.71	< 0.001	59.67
fruit set of open-pollination	forest distance (m)	−2.83	0.010	
	light intensity (W m^{-2})	2.11	0.047	
	final model			46.35
fruit set of cross-pollination			n.s.	
fruit set of self-pollination			n.s.	

(ii) Honeybees are known often to collect only nectar and to contact the stigma less often (Corbet 1987). A pollination experiment involving cashews in northeast Brazil showed that a solitary bee species was more efficient in depositing pollen on stigmas than the European honeybee (Freitas & Paxton 1998).

(iii) Long-tongued bees reach a hidden stigma more often than bees with a short tongue (Corbet 1996). In our study, most solitary bee species on coffee had longer tongues than the social bees (A.-M. Klein, personal observation). The corolla of coffee flowers is small and deep, so the long-tongued bees may have touched the stigma more often.

(iv) We observed that some social stingless bees often bite holes at the base of the flower to reach the nectar. Stingless bees are known to damage flowers, so fruit or seed set may be negatively influenced (McDade & Kinsman 1980; Maloof & Inouye 2000; Irwin *et al.* 2001).

Although our pollination experiments showed that single visits of solitary bees resulted in a significantly higher percentage fruit set, the more abundant social bee community visited about twice as many flowers, so all bee species (social bees, because of their high frequency, and solitary bees, because of their high pollination efficiency) were important for coffee pollination.

Further mechanisms in this diversity–function relationship could include spatial and temporal complementarities of different bee species (Cambell & Halama 1993). In our study, the CV of fruit set was negatively correlated with bee diversity, indicating that a species-rich pollinator community reduces the spatial variability of fruit set and conserves a high constant fruit set. Other explanations seem not to be appropriate as regards our results. Species-specific preferences are known for low- and high-placed flowers (Hambäck 2001), but in our study only terminal flowers at similar heights were analysed. Some species prefer small flower groups; others prefer large flower groups (Willmer & Stone 1989), but our observations were carried out in a blooming period with only large flower groups. Activity patterns of bee species are also known to differ temporally, within days and between seasons (Stone *et al.* 1999). Variation in daily activity patterns between species may have contributed to the diversity effect, whereas seasonal variation of pollinator assemblages could not have played a part in our study, because we focused on one of the short flowering periods of coffee. Although coffee flowers three or four times in 1 year, with a substantial flush of flowers, during the rest of the year flowering is sparse and irregularly distributed. In such a situation solitary bees become even more important, because social bees are often completely absent when only a few flowers are open (Willmer & Stone 1989; Klein *et al.* 2002).

Our pollination experiments were carried out in 24 agroforestry coffee fields, differing in shade and distance to the nearest forest, so we could also analyse the response of the two bee guilds to these two habitat factors. The diversity of social bees decreased with increasing forest distance, whereas the diversity of solitary bees was best explained in terms of light intensity and species numbers of plants. Forest distance is known to affect social bees greatly in the tropics, because forests offer a wealth of suitable nesting sites for colonies of stingless bees and honeybees (Liow *et al.* 2001; Klein *et al.* 2002). When foraging distances into the adjacent land-use systems were too long, coffee had a reduced fruit set in our study. Kremen *et al.* (2002) found that isolation from natural habitat affects pollination services to watermelons, and this effect appeared to be more important than the local management (organic versus conventional). Only a few publications show that the seed set of wild plants in isolated habitats is reduced as a result of pollinator limitation (Steffan-Dewenter & Tscharntke 1999; Cunningham 2000). In addition, the quality of the agricultural matrix may affect ant diversity (Perfecto & Vandermeer 2002) and bee diversity (Steffan-Dewenter *et al.* 2002) and these insect groups could serve as pollinators. Most of the solitary bees observed usually build nests outside the dark for-

ests and prefer less shaded and less humid agroecosystems offering open ground for the many ground-nesting species (with the exception of some leaf-cutting and carpenter bees, which nest above ground) (Michener 1979; Liow *et al.* 2001; Klein *et al.* 2002). Because diverse communities of herbaceous plants provide a diverse pollen food resource, they are generally expected to promote a diverse bee community (Siemann *et al.* 1999; Steffan-Dewenter & Tscharntke 2001). This is mainly important for the solitary bees, because social bees are known to prefer mass-flowering plants (Steffan-Dewenter & Tscharntke 2000).

In conclusion, pollination of highland coffee can no longer be considered to be an ecological service available everywhere (Allen-Wardell *et al.* 1998; Kevan & Phillips 2001); it depends on a diverse bee community. The results show that the enhancement of bee diversity from three to 20 species may increase fruit set from 60% to 90%. At least in our study region (Indonesia), improved land-use management should include close proximity of agroforestry systems to forests (for the enhancement of social bees) and reduced shading (for solitary bees, because of the bees' nesting requirements). Farmers should conserve bee diversity to improve their coffee production.

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