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Pollination of *Coffea canephora* in relation to local and regional agroforestry management

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Summary

1. Pollination of crops depends on local agricultural management and the quality of adjacent habitats. Lowland coffee *Coffea canephora*, is an important tropical cash crop. Fruit set depends on cross-pollination by bees, so inadequate pollination leads to reduced yield. In this study we analyse the relationship between bee pollinators, fruit set in coffee, and the local and regional agroforestry systems to identify the optimal conditions for pollinators.

2. We analysed the abundance and species composition of coffee flower-visiting bees in 15 agroforestry systems differing in distance to forest (important for wood-nesting species), light intensity (important for ground-nesting species), blossom cover of coffee and noncoffee-flowering plants, and species richness of flowering plants (as pollen and nectar resources) in Central Sulawesi (Indonesia). We examined which factors were most important for optimal pollination success. We carried out bagged and open pollination experiments in each agroforestry system, to measure the pollination efficiency of 15 bee species.

3. The number of social bee species decreased with distance to forest, whereas the number of solitary bee species increased with light intensity (less shade) and greater quantities of blossoms.

4. Fruit set of open pollinated flowers (as opposed to manually cross-pollinated flowers) increased with the diversity and abundance of flower-visiting bees. In the agroforestry systems studied, a bee community of 20 species or more led to a higher fruit set (95%) than a species-poor bee community of six species (70% fruit set).

5. Pollination activity by members of the species-rich solitary bee assemblage led to higher levels of fruit set than that arising from pollination activity by members of the more abundant social bee assemblage.

6. *Synthesis and applications.* A species-rich and abundant bee assemblage will facilitate high pollination success in lowland coffee. This will increase fruit set and coffee yield. Farmers can encourage different species of bees through simple management measures such as growing coffee in shade beneath a variety of trees; by pruning trees to increase levels of sunlight and numbers of flowering herbs; and by increasing the availability of nesting sites for solitary bees. Weed control and the use of herbicides should be kept to a minimum so that a diverse nectar and pollen resource is available to bees throughout the year. Natural forests and forest fragments should be preserved in the vicinity of coffee agroforestry systems (< 500 m) so that forest-nesting social bees can travel easily to the coffee fields to pollinate the flowers.

Key-words: agroforestry systems, bees, Indonesia, isolation, lowland coffee, pollinator limitation, shade effects.

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Introduction

Traditional agriculture produces a complex landscape mosaic of many different crop and noncrop habitats (Altieri, Merrick & Anderson 1987; Reichhardt *et al*. 1994; Toledo *et al*. 1994). In more intensive agricultural systems there is increasing isolation from natural habitats. This affects species richness, abundance, and community structure (Connor, Courtney & Yoder 2000; Debinski & Holt 2000) and important ecological services may suffer (Naeem *et al*. 1995; Tewksbury *et al*. 2002). The term ecosystem or ecological services is defined as a wide range of conditions and processes within natural ecosystems, and the species that are part of them that help to sustain and fulfil human life (Daily *et al*. 1997), for example predation of pest insects (Moguel & Toledo 1999; Klein, Steffan-Dewenter & Tscharnkte 2002b) and pollination of wild and cultivated plants (Rathcke & Jules 1993; Daily *et al*. 1997; Klein, Steffan-Dewenter & Tscharntke 2003b). The fragmentation and destruction of habitats may lead to the disruption of plant–pollinator interactions (Rathcke & Jules 1993; Renner 1998; Cane 2001; Donaldson *et al*. 2002; Steffan-Dewenter *et al*. 2002). In an isolation experiment with two self-incompatible annuals, Steffan-Dewenter & Tscharntke (1999) found that fruit set decreased with distance to the nearest natural habitat. The quality and connectivity of the agricultural matrix, including the distance to species-rich habitats, appears to be important for species richness and plant–animal interactions, such as pollination and seed dispersal (Steffan-Dewenter *et al*. 2002; Perfecto & Vandermeer 2002; Tewksbury *et al*. 2002). The distance to pollinator habitats may also affect plant–pollinator interactions in economically important crops (Kremen, Williams & Thorp 2002). In the tropics, the distance to the nearest forest is known to affect the diversity of pollinators (Klein *et al*. 2002a; Horner-Devine, Daily & Ehrlich 2003).

Coffee is grown traditionally under a canopy of shade trees, which support relatively high insect biodiversity compared with unshaded monocultures (Perfecto & Snelling 1995; Perfecto, Greenberg & Van der Voort 1996; MacVean 1997; Moguel & Toledo 1999; Conservation International 2000; Greenberg *et al*. 2000; Rappole, Kind & Rivera 2003). Accordingly, coffee producers have been encouraged to maintain a variety of shade trees in their agroforestry systems (Soto-Pinto *et al*. 2000). However, we know of no study that has analysed the effects of shade on pollinator communities and the resulting fruit set of lowland coffee.

The lowland coffee bush *Coffea canephora* Pierre ex Froehner, syn. *Coffea robusta* is an important cash crop in many tropical countries (Willmer & Stone 1989). *C. canephora* is reported as a self-sterile, predominantly wind-pollinated crop (Purseglove 1968; Crane & Walker 1983; Free 1993), and insect pollination has been assumed to make only a small contribution to total pollen transfer (McDonald 1930; Purseglove 1968). However, Willmer & Stone (1989) found 57% higher fruit set, and Klein, Steffan-Dewenter & Tscharntke (2003a) found 16% higher fruit set on coffee plants pollinated by wind and insects in contrast to coffee plants pollinated only by wind. The main flower visitors to lowland coffee are bees, and other insects such as ants, butterflies and beetles make only a small contribution in visiting coffee flowers (Willmer & Stone 1989; A.M. Klein, personal observation).

In this study, we analysed the effects of distance to the nearest forest, shade, and pollen and nectar availability (measured as the blossom cover of coffee and of other flowering plants, and the number of plant species) on flower visitation by bees and fruit set of *C. canephora.* We focused on the following questions.

1. Do the numbers of flower-visiting bee species and individuals correlate with distance from forest, light intensity (shade), and pollen and nectar availability?

2. Does fruit set correlate with the number of flower-visiting bee species, and with distance from forest, light intensity (shade) or pollen and nectar availability?

3. Which bee species are the most efficient pollinators of *C. canephora*?

Materials and methods

STUDY REGION AND STUDY SITES

The study was conducted from November 2000 to March 2001 and from June 2001 to October 2001 at the margin of the Lore-Lindu National Park, Central Sulawesi (Indonesia, LAT 01°24′-S; LON 120°20′-E, elevations ranging from about 1224 m to 1299 m), 100 km south-west the city of Palu, in the villages Wuasa, Watumaeta, Alitupu, and Kaduwaa. We focused on 15 agroforestry coffee fields, differing in the amount of shade, distance to forest, and pollen and nectar availability. We measured the light intensity with a luxmeter (Gossen MAVOLUX digital, Wilh. Lambrecht GmbH, Postfach 2654, 37016 Göttingen, Germany, digital light-gauge with four scopes from 0 to 1999 W m^{-2}) under standardized conditions (on the ground, on sunny days, 09.00–15.00 h) and calculated a mean of 20 measurements at each site. The vegetation was mapped between November 2000 and January 2001 in two separated, randomised 25 m^2 plots per study field for herbs and within two separated, randomised 100 m^2 plots for shrubs and trees (see also methodology of Soto-Pinto *et al*. 2000). All four plots were marked with a wooden stake and characterized at the same time per study field, resulting in estimates of the number of total plant species and the percentage of vegetation cover. Percentage cover of flowering coffee plants and percentage cover of all noncoffee flowering plants (all of which were herbs) were recorded for each entire study field to estimate the pollen and nectar availability for flower-visiting bees. The coffee fields were located at different distances from the old-growth rainforest (varying from a position inside the forest margin to a distance of

900 m from the nearest forest). The distance to the forest was measured with GPS (Global Positioning System 12 from Garmin International, Olathe, Kansas, USA).

FLOWER-VISITING BEES AND FRUIT SET OF *C. CANEPHORA*

Observations on coffee flower-visiting bees were carried out over a 7-day period from 26 December 2000 to 1 January 2001. Although coffee plants bloom throughout the year, for most of the time the flowering is sparse and irregularly distributed. In December to January and from June to July there was a substantial flush of flowers after heavy rainfalls. The flowers generally open just before dawn and last two days. During the flowering period, three different coffee plants, with around 100–200 flowers per plant, were observed for 25 min per plant over a 3-day period in sunny weather between 09.00 and 14.00 h at each site. All bees visiting the flowers were counted and preliminarily identified to species or morphospecies within the 75 min observation period. After each 25-min observation period, bees were caught by sweep netting for 5 min to enable identification of these species that could not be identified to species during foraging.

For each of the manual cross pollination (between-plant pollination) and open pollination experiments, we selected four coffee plants per study site (2*4 clustered flowers in one axis of a branch in each of the 15 sites, giving a total of 120 branches). Flowers of the open pollination experiment of four flower-cluster at four branches were labelled and counted. For the hand pollination experiment, four bags per study site of very fine nylon mesh gauze (10 µm) were fixed around several flowers clustered in one axis of four different branches, which were labelled and counted, to exclude wind and insect pollination, following Willmer & Stone (1989). Bags were fixed around the coffee flowers one to six days before flowering. Crawling insects, especially ants, were excluded by sticky glue on the branch beneath the bagged flowers. At time the plants begin to flower, pollen was transferred to stigmas with a brush on the first day of flower opening. Five weeks after the major flowering period ended (after a substantial flush of flowers), bags were removed and the total number of green swollen ovules was counted.

At the beginning of June 2001, 10 coffee plants in one study site (located adjacent to the old-growth natural forest and slightly shaded) were selected to test the pollen transfer efficiency of different bee species. Twenty flower-clusters on one branch with dense and mature buds were enclosed in nylon mesh bags (10 µm) on each of the 10 plants four days before flowering. When the flowers started to open, we removed the bags (one by one), so the bees could visit the still virginal flowers. After one bee visited one or several single flowers, we marked the flowers with bee species-specific colours and enclosed the flowers again in a bag. Five weeks later, we removed the bags from flowers and counted the number of green swollen ovules to measure percentage fruit set. Invariably, two ovules develop into a fruit, so fruit and seed set give almost identical results.

STATISTICS

Statistical analysis was performed using STATGRAPHICS PLUS for WINDOWS 3·0 (Manugistics 1997). All data were tested for normality and transformed if necessary. The independent variable, cover of herb blossom, was always $\log_{10}$ transformed and the independent variable, distance to forest, was always square root transformed (Sokal & Rohlf 1995). After transformation to normality, we tested correlations between the five independent habitat factors. Stepwise multiple linear regression analyses with backward selection examined which independent habitat factors were most important for the dependent variables, social and solitary bee species, bee individuals and fruit set. The habitat factor giving the best fit was shown in a simple linear regression model with the dependent variable. We used *t*-tests to compare the means of fruit set caused by social and solitary bees. To estimate the species saturation in relation to sample size, we calculated the ratio of sampled to expected species richness for flower-visiting bees for each study site using 100 randomisations 5-min samples with the estimator ACE (Abundance-based Coverage Estimator of species richness), within the ESTIMATES program, Version 5. The definition and formula of this method is described at the Estimator homepage, see Colwell (1997). We present the mean value per study site. Arithmetic means ± standard errors are given.

Results

FLOWER VISITATION

We recorded 1363 social bees from seven species (Hymenoptera: Apidae) and 906 solitary bees from 26 species (Hymenoptera: Apidae, Megachilidae, Halictidae). The average species saturation per study site was 96·8 ± 1·46%, $n = 15$, according to the ACE method (Colwell 1997). We used five independent variables to explain the distribution of the flower-visiting bees and the fruit set of coffee. Effects of local management were characterized by light intensity, blossom cover of coffee, blossom cover of herbs, and numbers of plant species. Regional effects were characterised by the distance to the nearest forest. All these five variables were not independent of one other. In stepwise multiple regressions, we tested which of the five variables were most important for flower-visiting bees. Table 1 shows that the number of all bee species significantly correlated with light intensity, blossom cover of herbs and blossom cover of coffee, and marginally significantly correlated with distance from the nearest forest. The number of all bee individuals was significantly correlated with light intensity and blossom cover of coffee. Separately, we analysed the diversity and abundance of

Table 1. Results of stepwise multiple regression analyses for the dependent variables number of bee species, number of individuals, and fruit set of open pollinated coffee and the independent variables light intensity, forest distance, blossom cover of coffee, blossom cover of herbs, and number of plant species. Only significant relationships are shown

Dependent variables	Habitat factor	T Statistic	*P*-value	r^2
Number of all bee species	Light intensity [W m^{-2}]	3·23	0·001	
	Blossom cover of herbs [%]	3·67	0·004	
	Blossom cover of coffee [%]	–2·49	0·032	
	Forest distance [m]	–2·19	0·054	
	Final model			0·767
Number of all bee individuals	Light intensity [W m^{-2}]	3·58	0·004	
	Blossom cover of coffee [%]	3·05	0·010	
	Final model			0·595
Number of social species	Forest distance [m]	–5·26	< 0·001	0·860
Number of social individuals	Forest distance [m]	–2·95	0·012	
	Blossom cover of coffee [%]	2·30	0·031	
	Final model			0·524
	Final model			0·767
Number of solitary species	Light intensity [W m^{-2}]	4·44	0·001	
	Blossom cover of herbs [%]	3·86	0·003	
	Blossom cover of coffee [%]	–2·92	0·014	
	Final model			0·727
Number of solitary individuals	Number of plant species	–2·18	0·050	
	Blossom cover of herbs [%]	2·01	0·067	
	Final model			0·340
Fruit set of open pollination	Light intensity [W m^{-2}]	3·11	0·009	
	Forest distance [m]	–2·78	0·017	
Final model			0·722	

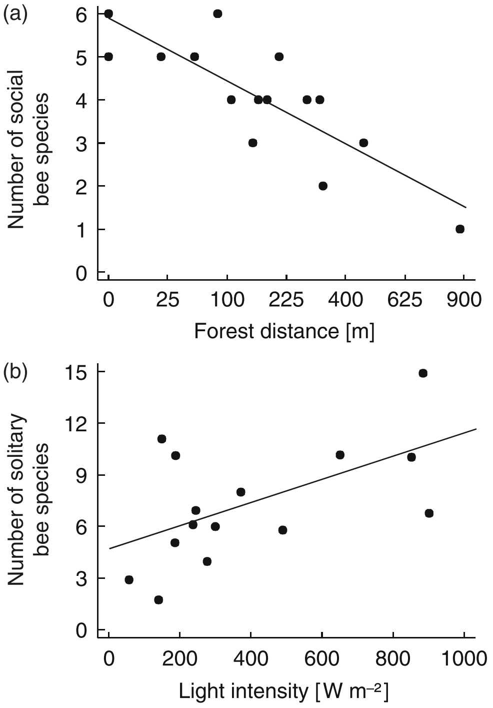

Fig. 1. (a) Relationship between the number of social bee species and the forest distance: $y = 5{\cdot}87 - 0{\cdot}14x^2$, $F = 27{\cdot}63$, $r^2 = 0{\cdot}68$, $n = 15$, $P < 0{\cdot}001$. (b) Relationship between the number of solitary bee species and the light intensity: $y = 4{\cdot}65 + 0{\cdot}01x$, $F = 6{\cdot}26$, $r^2 = 0{\cdot}52$, $n = 15$, $P = 0{\cdot}012$.

social and solitary bees with the five habitat parameters and found that the number of social bee species decreased significantly with increasing distance from the nearest forest (Fig. 1a). The number of social bee individuals decreased with forest distance and increased with blossom cover of coffee (Table 1). The number of solitary bee species was correlated with the light intensity (Fig. 1b), and the blossom cover of herbs and coffee. The number of solitary bee individuals was correlated with the number of plant species and the blossom cover of herbs (Table 1).

FRUIT SET

In stepwise multiple linear regression analysis with the independent variables mentioned above, fruit set after open pollination was correlated with light intensity (Fig. 2a) and with forest distance (Fig. 2b, Table 1). The difference between fruit set after open pollination and manual cross pollination was, with marginal significance, positively correlated with the number of bee species ($F = 4{\cdot}29$, $r^2 = 0{\cdot}49$, $n = 15$, $P = 0{\cdot}058$), and significantly positively correlated with the number of bee individuals ($F = 9{\cdot}06$, $r^2 = 0{\cdot}41$, $n = 15$, $P = 0{\cdot}010$). Fruit set after open pollination was positively correlated with the number of flower-visiting bee species (Fig. 3a), and with the number of flower-visiting bee individuals (Fig. 3b). Testing social and solitary bees separately in the multiple model, fruit set was positively correlated with the number of flower-visiting social bee species ($F = 15{\cdot}30$, $r^2 = 0{\cdot}54$, $n = 15$, $P = 0{\cdot}002$), and also with the number of flower-visiting social bee individuals ($F = 7{\cdot}79$, $r^2 = 0{\cdot}37$, $n = 15$, $P = 0{\cdot}015$). In contrast, fruit set was correlated neither with the number of flower-visiting solitary bee species ($F = 2{\cdot}02$, $r^2 = 0{\cdot}13$, $n = 15$, $P = 0{\cdot}179$), nor with the number of flower-visiting solitary bee individuals ($F = 0{\cdot}09$, $r^2 = 0{\cdot}07$, $n = 15$, $P = 0{\cdot}770$).

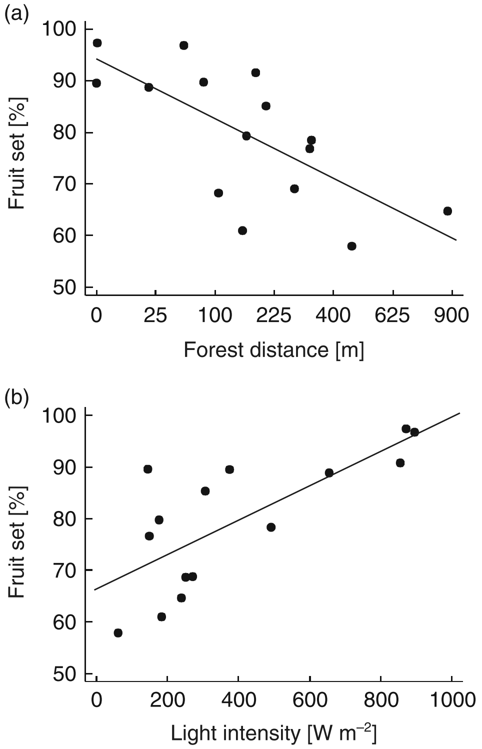

Fig. 2. (a) Relationship between fruit set after open-pollination and forest distance: $y = 94{\cdot}11 - 1{\cdot}15x^2$, $F = 12{\cdot}92$, $r^2 = 0{\cdot}49$, $n = 15$, $P = 0{\cdot}003$. (b) Relationship between fruit set after open-pollination and light intensity: $y = 66{\cdot}60 + 0{\cdot}03x$, $F = 15{\cdot}48$, $r^2 = 0{\cdot}74$, $n = 15$, $P = 0{\cdot}002$.

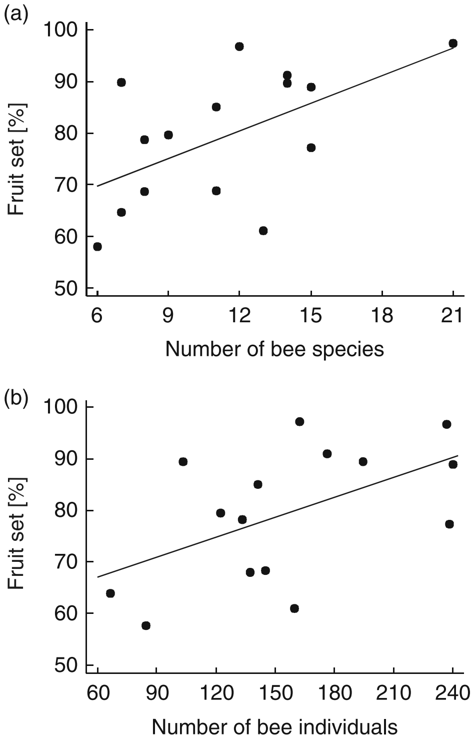

Fig. 3. (a) Relationship between fruit set after open-pollination and the number of flower-visiting bee species: $y = 59{\cdot}48 + 1{\cdot}77x$, $F = 5{\cdot}89$, $r^2 = 0{\cdot}31$, $n = 15$, $P = 0{\cdot}031$. (b) Relationship between fruit set after open-pollination and the number of flower-visiting bee individuals: $y = 59{\cdot}38 + 0{\cdot}13x$, F = 5·40, $r^2 = 0{\cdot}29$, $n = 15$, $P = 0{\cdot}037$.

Table 2. Pollination success of single social and solitary bee visits. Results from experimentally bagged coffee flowers allowed a single visit from a single individual of a specific bee species to a single, virginal coffee flower. We show the single-visit experiments for each species with the resulting mean fruit set and the frequency of flower visitation within 75 min

Bee species	Number of replicates	Fruit set %	Frequency of flower-visitors
Social bees			
Apis nigrocinta	72	72·22	404
Apis dorsata binghami	60	71·66	271
Apis cerana	16	68·75	156
Trigona (Lepidotrigona) terminata	25	84	224
Trigona sp.	17	74·71	27
Trigona (Heterotrigona) sp. 1	15	66·66	83
Trigona (Heterotrigona) sp. 2	38	55·26	198
	Sum 243	Mean 70·40	Sum 1363
Solitary bees			
Amegilla sp.	12	83·33	89
Megachile sp.	10	63·33	62
Ceratina sp.	13	84·61	56
Creightonella frontalis	28	89·29	115
Halictidae	14	87·57	161
Heriades sp.	34	94·12	50
Xylocopa (Koptotorsoma) aestuans	4	100	22
Xylocopa (Zonohirsuta) dejeanii nigrocerulea	10	90	45
	Sum 125	Mean 86·53	Sum 553

POLLINATION EFFICIENCY

Species-specific pollination efficiency was tested experimentally with a number of bee species. We observed individual flower visits of 368 bees of 15 species (seven social and eight solitary bees, which frequently visited coffee plants) to virginal (previously bagged) coffee flowers. The most frequent flower-visitors were three honeybee species of the genus *Apis*. The stingless bees of the genus *Trigona* were also abundant (Table 2). On average, flower visitation by solitary bees resulted in a significantly higher fruit set (86·5%) as compared with social bees (70·4% fruit set, $t = -3{\cdot}19$, $n = 7$ social plus 8 solitary bees, $P = 0{\cdot}007$, see Table 2).

Discussion

Our study shows that both local and regional characteristics of agroforestry systems affect the diversity and abundance of flower-visiting bees and the fruit set of lowland coffee, an important tropical crop. The diversity of social bees decreased with distance to forest, whereas the diversity of solitary bees was correlated with increasing light intensity and increasing percentage of flowering herbs within an agroforestry system. We found higher densities of social bees within and near the forest than at greater distances from forest, presumably because forests offer a wealth of suitable nesting sites for the colonies of stingless bees and honeybees foraging into the adjacent land-use systems (Heard & Exley 1994; Klein *et al*. 2002a). In contrast, most of the solitary bees observed in this study built nests outside the dense forest, preferring less shaded and less humid agroecosystems that offered open areas for the many ground-nesting species and herbaceous plants for pollen and nectar resources (Michener 1979; Liow, Sodhi & Elmqvist 2001; Klein *et al*. 2002a).

Local management strategies that improve the availability of pollinating bees in coffee agroforestry systems are still unknown in Indonesia. The most important factor at a local scale is shade as this influences the yield of most plantation crops (Amoah, Osei-Bonsu & Oppong 1997). Shade trees affect the moisture and nutrient relations of crops, and the chemical and physical properties of the soil through deposition of leaf litter and root growth. Shade can also influence populations of insect pests, prevalence of disease, and weeds (Perfecto *et al*. 1996; Beer *et al*. 1998). Although shade improves the growth and production of coffee, several authors argue that more than 50% shade depresses yield (Escalante 1995; Amoah, Osei-Bonsu & Oppong 1997; Muschler & Bonnemann 1997; Soto-Pinto *et al*. 2000).

Bee community structure changes with light intensity and temperature (Klein *et al*. 2002a), but shade effects on flower-visiting bee communities on coffee and the resulting fruit set are poorly studied. Willmer & Stone (1989) recommended that populations of a certain solitary bee species (the ground-nesting *Creightonella frontalis*) should be encouraged, because this species seems to be a better pollinator than social honeybees on lowland coffee. They suggest two management strategies to improve coffee yield in Papua New Guinea. First, creation of more nesting sites for ground-nesting bees, e.g. open soil on embankments, and secondly, increase the availability of alternative flower resources such as weeds and hedgerow plants. In the light of our findings in Central Sulawesi, we suggest similar local management strategies. To encourage solitary bees we recommend a reduction of shade and less intensive weed control, thereby maintaining a diverse herbaceous ground vegetation.

At the regional scale, species diversity and abundance of social bees could be enhanced if agroforestry coffee systems were located close to natural forest. Even small, isolated forest fragments may help to retain diversity and increase the conservation value of agricultural landscapes (Horner-Devine, Ehrlich & Boggs 2003). The mosaic structure of landscapes with traditionally managed agroecosystems has been shown to maintain or improve biodiversity (Altieri, Merrick & Anderson 1987; Reichhardt *et al*. 1994; Toledo, Ortiz & Medellin 1994; Perfecto & Vandermeer 2002). A change to crop monoculture leading to habitat isolation may influence the structure of bee communities, change the foraging behaviour of flower-visiting bees, and reduce fruit set and gene flow of isolated plant populations (Aizen & Feinsinger 1994; Didham *et al*. 1996; Steffan-Dewenter & Tscharntke 1999; Cunningham 2000; Kremen, Williams & Thorp 2002). In this study, we have shown that increasing distance from agroforestry systems to natural forest discouraged social bees, presumably because social bees prefer to nest in cavities of tall trees (all honey bees except *Apis cerana*) or in fallen dead trees (all stingless bees, A.M. Klein, pers. observ., Heard & Exley 1994). In a recent study in California, habitat isolation appeared to have a greater effect on pollinating bees than local management (Kremen, Williams & Thorp 2002). Another factor influencing pollinators is the availability of flower resources. Social bees are known to prefer mass-flowering crops (Waddington *et al*. 1994). Coffee was mass-flowering during our observation period and the number of social bees showed a positive correlation with blossom cover of coffee. By contrast, the abundance of solitary bees correlated negatively with blossom cover of coffee, but positively with the blossom cover of herbs. Most solitary bees foraged on coffee, but at mass-flowering time of coffee, social bees were attracted in large numbers whereas solitary bees often appeared to switch to ground vegetation (Willmer & Stone 1989; Klein *et al*. 2002a). Light intensity is often correlated with the number of flowering herbs, so most solitary bees prefer open habitats (Klein *et al*. 2002a). Outside the mass-flowering period, there was some blossom on the coffee plants for three to seven days every month. At this time social bees were often absent and solitary bees were the main flower visitors (A.M. Klein. pers. obs.). Thus, populations of solitary bees should be encouraged via appropriate management strategies to ensure year-round fruit set of single flowers.

We report some experimental evidence for a higher pollination efficiency by solitary bee species, compared to the more abundant social species. Earlier studies have shown that solitary wild bees are more efficient pollinators for certain crops than social bees (Corbet *et al*. 1991). The difference in pollination success between these two pollinator guilds could be explained by the following findings: (1) solitary bees switch between plants more often than social bees, thereby offering a higher enhance of cross pollination (Willmer & Stone 1989). (2) Social bees collect less pollen and more nectar than solitary bees and contact the stigma less often (Corbet 1987; Freitas & Paxton 1998). (3) Most solitary bees have longer tongues and therefore make contact with the stigma more often (Corbet 1996). (4) Social, stingless bees often damage flowers, so fruit set may be reduced (Maloof & Inouye 2000; Irwin, Brody & Waser 2001). Reduced pollination is known to be one major reason for low fruit set in some plant species, for example *Acacia brachybotry*, *Centaurea scabiosa*, *Coffea arabica*, *Coffea canephora*, *Eremophila glabra*, *Lythrum salicaria* (Ågren 1996; Ehlers 1999; Cunningham 2000; Roubik 2002; Klein, Steffan-Dewenter & Tscharnkte 2003a). Both the number of species and the number of individuals in the bee community on lowland coffee appeared to be important for overall pollination success. In contrast, fruit set of highland coffee *Coffea arabica* L. was found to be related to bee diversity, but not abundance (Klein, Steffan-Dewenter & Tscharntke 2003b). The flowers of lowland coffee are much bigger, have a more intense smell and produce more flowers than highland coffee. This appeared to enhance the frequency of flower-visitors (Klein, Steffan-Dewenter & Tscharntke 2003a) and encourage the abundant social bees. However, in Panama, fruit set increased more than 50% through pollination by primarily non-native honeybees (Roubik 2002).

We recorded the flower visitors in one large blooming period during one week of 2269 bee individuals. Note that the main flowering periods of coffee are always extremely short and light intensity will not change greatly over the year, because the trees and shrubs in the agroforestry systems are all evergreen. Nevertheless, farmers should trim the trees and shrubs if the canopy will become too close over the years. The herb species flowered throughout the year providing a continuous source of nectar and pollen for flower-visiting bees. In contrast, the shade trees flower for only a short time in the year.

Klein, Steffan-Dewenter & Tscharntke (2003a) show in a parallel study that wind pollination leads on average to 16% lower fruit set than open pollination in *C. canephora*, using pollination experiments that excluded insects with coarse mesh gauze and with very fine openings to exclude wind and insect pollination. In agroforestry systems with few pollinators (strongly shaded, plant species poor, and far from natural forest margin), fruit set of open pollination was not higher than that of wind pollination. In agroforestry systems with a species-rich bee community (medium shaded, plant species rich, located inside the margin of the natural forest), wind pollination lead to 35·5% lower fruit set than open pollination (unpublished data). Overall, species-rich agroforestry systems with 20 bee species led to a higher fruit set (95%) than a system with a species-poor bee community (six species and only 70% fruit set; see Fig. 3a). Willmer & Stone (1989) found 57% higher fruit set on coffee plants pollinated by wind and insects in contrast to coffee plants pollinated only by wind. A possible reason for the different degree in wind pollination could be different weather conditions. Dry weather should enhance the pollen transportation through wind.

In conclusion, this study provides new insights into the importance of habitat management at local and regional scales. Isolation from forests and too much shade affected the flower-visiting bee community of lowland coffee, an important cash crop in the tropics. The results indicate that a diverse and abundant bee community plays a significant role in fruit set in this system. Coffee farmers should aim to increase the abundance and diversity of flower-visiting bees in their agroforestry systems to improve their yield. According to our results, coffee agroforestry systems should be established near the margin of natural forests. Alternatively landscape management should aim to preserve scattered forest patches, at best within a range of 500 m of coffee fields, to enable social bees to bridge the distance between their main nesting habitats (forests) and the crop. Local management should promote a flower-rich ground layer of herbs as well as sparse covering of shade trees, to provide dry ground as nesting habitat for the species rich ground-nesting solitary bees and to encourage populations of flowering herbs that offer important nectar and pollen resources for solitary bees during the whole year.

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