Effects of Land-Use Intensity in Tropical Agroforestry Systems on Coffee Flower-Visiting and Trap-Nesting Bees and Wasps

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Abstract: *Tropical landscapes are dominated by agroecosystems, and most species that survive in forest remnants interact with these agroecosystems. The potential value of agroecosystems for aiding species survival is often ignored. Essential ecosystem services may suffer when functional groups such as pollinators and predators are affected by land use. We used agroforestry systems differing in land-use intensity to examine flower-visiting bees on coffee plants and the community structure of trap-nesting bees and wasps and their natural enemies. The number and abundance of all species of coffee-visiting bees did not show a significant correlation with land-use intensity. The abundance (but not the number of species) of solitary bees increased with land-use intensity, whereas the abundance and number of species of social bees significantly decreased. In a further experiment, abundance and number of trap-nesting species increased with land-use intensity. These results contrast with the common expectation that intensively used agroforestry systems are characterized only by loss of species. Furthermore, they support the idea that many nonpest and beneficial insect species may even profit from agricultural land use. Parasitism and predation of trap-nest inhabitants did not change with land-use intensity, but species diversity (number of enemy species) and ecological function (mortality) were correlated.*

Efectos de la Intensidad del Uso del Suelo en Sistemas Agroforestales Tropicales sobre las Abejas y Avispas que Visitan las Flores del Café

Resumen: *Los sistemas tropicales son dominados por agro-ecosistemas y la mayoría de las especies que sobreviven en los remanentes intactos de bosque interactúan con estos agro-ecosistemas. El valor potencial de los agro-ecosistemas para ayudar a las especies a sobrevivir es frecuentemente ignorado. Los servicios esenciales de los ecosistemas pueden sufrir cuando grupos funcionales, tales como los polinizadores y los depredadores, son afectados por el uso del suelo. Empleamos sistemas agroforestales que difieren en su intensidad de uso para examinar abejas visitadoras de flores en plantas de café y la estructura de la comunidad de abejas que anidan en trampas y avispas y sus enemigos naturales. El número y abundancia de todas las especies de abejas visitadoras de café no mostraron una correlación significativa con la intensidad de uso del suelo. La abundancia (pero no el número de especies) de abejas solitarias incrementó con una baja intensidad de uso del suelo, mientras que el número de especies y la abundancia de abejas sociales disminuyó significativamente. En otro experimento, la abundancia y el número de especies que anidan en trampas incrementó con la intensidad de uso del suelo. Estos resultados se contrastan con lo esperado normalmente que supone que los sistemas agroforestales usados intensivamente se caracterizan únicamente por la pérdida de especies. Más aún, los datos apoyan la idea de que muchas especies de insectos que no son plagas y de insectos benéficos podrían beneficiarse del uso agrícola del suelo. El parasitismo y la depredación de los ocupantes de trampas no cambiaron con la intensidad de uso del suelo, pero la diversidad de especies (número de especies enemigas) y la función ecológica (mortalidad) estaban correlacionados.*

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Introduction

Tropical landscapes are characterized by agroecosystems and expanding land use, so rainforest is often only patchily distributed in them (Schelhas & Greenberg 1996; Laurance & Bierregaard 1997). Efforts to preserve biodiversity have been focused primarily on the remaining areas of natural ecosystems (Tuomisto et al. 1995; Dyer & Letourneau 1999; Moguel & Toledo 1999), but only 5% of the terrestrial environment is unmanaged and uninhabited (Western & Pearl 1989). Thus, most species that survive in forest remnants interact with agricultural systems, but the contribution of management type to species survival is often ignored, as is the potential value of agroecosystems for conservation (Pimentel et al. 1992; Perfecto et al. 1996, 1997; Power 1996; Watt et al. 1997; Power & Flecker 2000). Traditional land-use systems such as agroforestry (Nair 1993) are characterized by high vegetational diversity, and these traditional systems can maintain surprisingly high levels of biodiversity (Pimentel et al. 1992). Traditionally, coffee is grown under a canopy of shade trees. Due to the structural and floristic complexity of the shade trees, such coffee ecosystems may support relatively high biodiversity (Perfecto et al. 1996, 1997; Moguel & Toledo 1999; Greenberg et al. 2000).

The lowland coffee *Coffea canephora* Pierre ex Froehner, syn. *Coffea robusta*, is an important cash crop. Although this species produces lower-quality coffee than *C. arabica*, it is able to grow at lower elevations and has higher resistance to some pests and diseases (Willmer & Stone 1989; Rehm & Espig 1995). Because *C. canephora* is self-sterile and pollinated by bees (Willmer & Stone 1989), the coffee yields depend on pollination (Free 1993). Abundance and diversity of bees are known to be associated with frequency of flower visitation, pollination, and seed set (Free 1993; Rathcke & Jules 1993; Aizen & Feinsinger 1994*a*, 1994*b*; Steffan-Dewenter & Tscharntke 1999). Flower visitation rate is often a good predictor of pollination success, as is the abundance and number of trap-nesting bees (Tscharntke et al. 1998), whereas trap-nesting wasps may be important enemies of pest insects (Harris 1994).

We studied the abundance and number of social and solitary bees and wasps in agroforestry systems of the province Central Sulawesi. We observed flower-visiting bees on coffee and exposed standardized nesting traps for solitary bees and wasps, because trap-nesting bees and wasps are known to be bioindicators sensitive to environmental change (Tscharntke et al. 1998). We tested two hypotheses with respect to the influence of land-use intensity on these insect communities: (1) traditional, extensively managed agroforestry systems support a higher number of bees and wasps than intensively managed agroforestry systems, and (2) land-use intensity does not affect all bee and wasp species equally, and some habitat generalists or species that prefer open habitats may even profit from intensive management.

Methods

Study Area and Experimental Sites

Our study was carried out at the border of the Lore-Lindu National Park in Central Sulawesi, 60 km away from the nearest city, Palu, from October 1998 to March 1999. Normally, these months are part of the rainy season, but during the study period they were unusually dry due to the effects of La Niña, which causes unusually cold and dry ocean temperatures in the equatorial Pacific. The Lore-Lindu National Park is characterized by a tropical monsoon climate with an annual rainfall of 2000–3000 mm (World Wildlife Fund 1981). Seasonal temperature ranges from 17° to 35° C and the seasonal relative humidity from 77% to 85% (1998 draft final report of the Central Sulawesi Integrated Area Development and Conservation Project).

The environment of the national park is characterized by extensively managed agroforestry systems (Nair 1993; 1998) dominated by coffee and cocoa. We selected 12 agroforestry systems, six types with two replicates each, on a gradient of land-use intensity with a minimum size of 0.5 ha and a minimum distance of 500 m between each study system. We did not include open sun monocultures as the extreme. Half the systems were located outside the forest (intensively used 2-year-old agroforestry systems, extensively used 4- to 5-year-old agroforestry systems, 8-year-old home gardens) and the other half was located inside the forest (extensively and intensively managed forest gardens and near-natural forest) (Fig. 1).

Habitat Parameters

Abiotic and biotic habitat parameters were characterized for each of the 12 agroforestry systems. The three abiotic parameters were temperature (°C), relative humidity (%), and day-light intensity (lux). Each parameter was measured three times per system under standardized conditions (1.5 m above ground for temperature and humidity, on the ground for the light intensity, on sunny days, 8–10 a.m.). The vegetation was mapped within two different 10-m^2 plots for herbs and two different 100-m^2 plots for shrubs and trees per study system. We estimated the incidence (in percent) of every species inside the plots. We also estimated for each system mean values for the following biotic parameters inside the plots: percent vegetation cover; mean height of vegetation separately for trees, shrubs, and herbs; and percentage of cover of dead organic material on the ground, such as dead branches and leaves. The percent cover of flowering coffee plants was recorded for each study system in one 100-m^2 plot, while we sampled the flower-visiting bees, to quantify the resources available to bees.

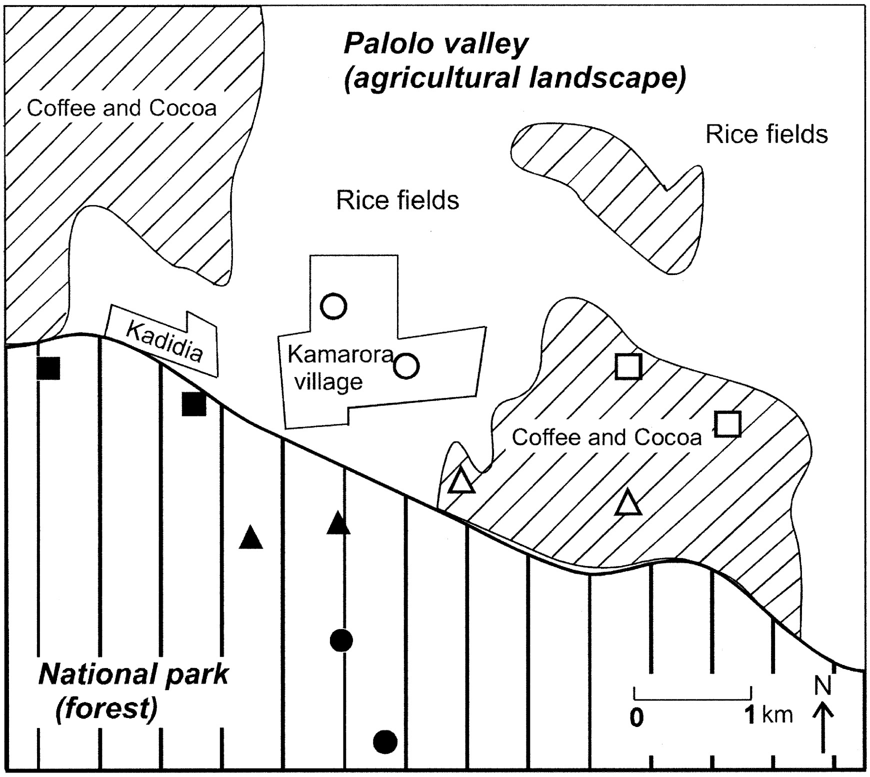


Figure 1. Region where the study was conducted, including the six types of land-use systems and the relative location of each of the 12 sites: ■, extensively managed forest garden; ▲, intensively managed forest garden; ●, near-natural forest; ○, home garden; □, extensively managed agroforestry system; △, intensively managed agroforestry system.

Trap Nests

Trap nests for Hymenoptera (Apidae, Specidae, Eumenidae, Pompilidae) were set up between 26 and 30 October 1998 and removed on 9 February 1999. Six traps for each of the 12 systems were hung with a solid wire in six coffee or cocoa trees at a height of 1.5 m to 2 m. We put sticky glue on each wire and outside the trap nests to deter ants. The standardized traps consisted of about 200 internodes of common reed *Phragmites australis* (Cav.) Trin., with a length of 20 cm, put into plastic tubes 10.5 cm in diameter. The range of internal diameters varied between 2 and 10 mm (Tscharntke et al. 1998). One month after the traps were set up, we replaced all occupied reed internodes every 2 weeks with unoccupied internodes. We opened the reed nests in the laboratory, made a preliminary identification of species, and established the number of brood cells per species. The internal diameters of the internode (mm) and the cell length (cm) were measured with vernier callipers. After the adults had emerged, species were identified and sex ratio and mortality due to parasitism and predation were determined.

Flower Visitation

Although coffee trees bloom throughout the year, flowering is sparse and irregularly distributed. A substantial flush of flowers was restricted to only 1 week in January, during which we made our observations. A few measurements were also taken before and after this period, but these data were not included in our statistical analysis. Each of three randomly chosen coffee trees per agroforestry system was observed for 15 minutes on sunny days between 0800 and 1200 hours to measure the abundance and species composition of flower visitors. Every flower-visiting individual was recorded. After each 15 minutes of observation, we caught bees for 15 minutes with a sweep net and later identified them to species.

Identification

Social bees were identified with the help of a bee collection of G. Otis of the University of Guelph. Solitary bees were identified by D. B. Baker of the Oxford University Museum of Natural History. The sphecid wasps were identified based on the work of Turner (1916), Tsuneki (1956, 1970), Bohart and Menke (1976), and Hensen (1987, 1988, 1991). Eumenid wasps were identified based on the work of van der Vecht (1957, 1963), and chrysidid wasps on the work of Linsenmaier (1959) and Kimsey and Bohart (1991). Other nest predators and parasitoids were identified to family level based on the work of Borrer et al. (1981) and Goulet and Huber (1993). Taxonomy follows that of Michener (2000).

Statistical Analysis

Statistical analysis was performed with the software Statgraphics Plus 3.0 (Manugistics 1997). When necessary, logarithmic or square-root-transformed variables were used to achieve a normal distribution. The habitat parameters were closely intercorrelated, so we used a factor analysis to express covariation of the parameters (Sokal & Rohlf 1995). Pearson correlations were used for the analysis of normally distributed data, and Spearman rank correlations were used for non-normal distributed data (Sokal & Rohlf 1995). For further analyses of habitat use, we used general linear models. To estimate the number of bee species based on equal sample size, we calculated for every land-use type the rarefaction algorithm by Hurlbert and Simberloff, as follows (Krebs 1989; Achtziger et al. 1992):

$$E(\hat{S}_n) = \sum_{i-1}^{s}\left[1-\frac{\binom{N-N_i}{n}}{\binom{N}{n}}\right],$$

where $E(\hat{S}_n)$ is the expected number of species in a random sample of n individuals, S is the total number of species in the entire collection, N_i is the number of individuals in species I; N is the total number of individuals in collection (i.e., $E\,N_i$), n is the number of individuals chosen for standardization ($n < N$); and

$$\binom{N}{n}$$

is the number of combinations of n individuals that can be chosen from a set of N individuals ($N!/n!\,(N-n)!$).

Results

Land-use Intensity

The abiotic habitat parameters (relative humidity, daylight intensity, temperature) and the biotic habitat parameters influencing these abiotic parameters (percent canopy cover, average height of the trees, and percent cover of dead organic material) were highly intercorrelated (Table 1). Because of the close correlation between the habitat parameters, multiple regressions or general linear models could not be used to separate the possible effects of single parameters. Therefore, we used factor analysis to condense the biotic and abiotic parameters to only one factor. We called the index that resulted from factor analyses of the six habitat parameters "land-use intensity."

The agroforestry systems outside the forests were obviously characterized by intense land use, because these systems were established after a complete clearing of the forest. It was only afterward that shade trees and crops were planted, whereas in the forest gardens crops were planted beneath primary trees. In completely replanted agroforestry systems, the trees were shorter and less dense, so temperature and day-light intensity were higher and relative humidity lower than in the systems inside the forest. In the intensively managed systems, humans had regularly burned dead organic material, whereas in the forest gardens at most a few dead branches had been collected. Inside the near-natural forest characterized by a high and dense canopy, little burning took place because dead branches usually decayed and human land use was almost absent.

We ordered the following sequence of agroforestry systems and near-natural systems with respect to decreasing land-use intensity: (1) near-natural forest, (2) extensively managed forest garden, (3) intensively managed forest garden, (4) home garden, (5) extensively managed agroforestry system, (6) and intensively managed agroforestry system (Fig. 2). Land-use intensity was negatively correlated with the number of tree species ($r^2 = 0.84$, $n = 12$, $p < 0.001$) but not with total number of plant species. In the following evaluations we used land-use intensity as a predictor variable for the communities of flower-visiting and trap-nesting bees and wasps and their natural enemies.

Trap-Nesting Bees and Wasps and Their Natural Enemies

Altogether 26 species were reared from trap nests, including 2 bee species, 8 wasp species, and 16 species of their natural enemies (Table 2). The eumenid wasps were

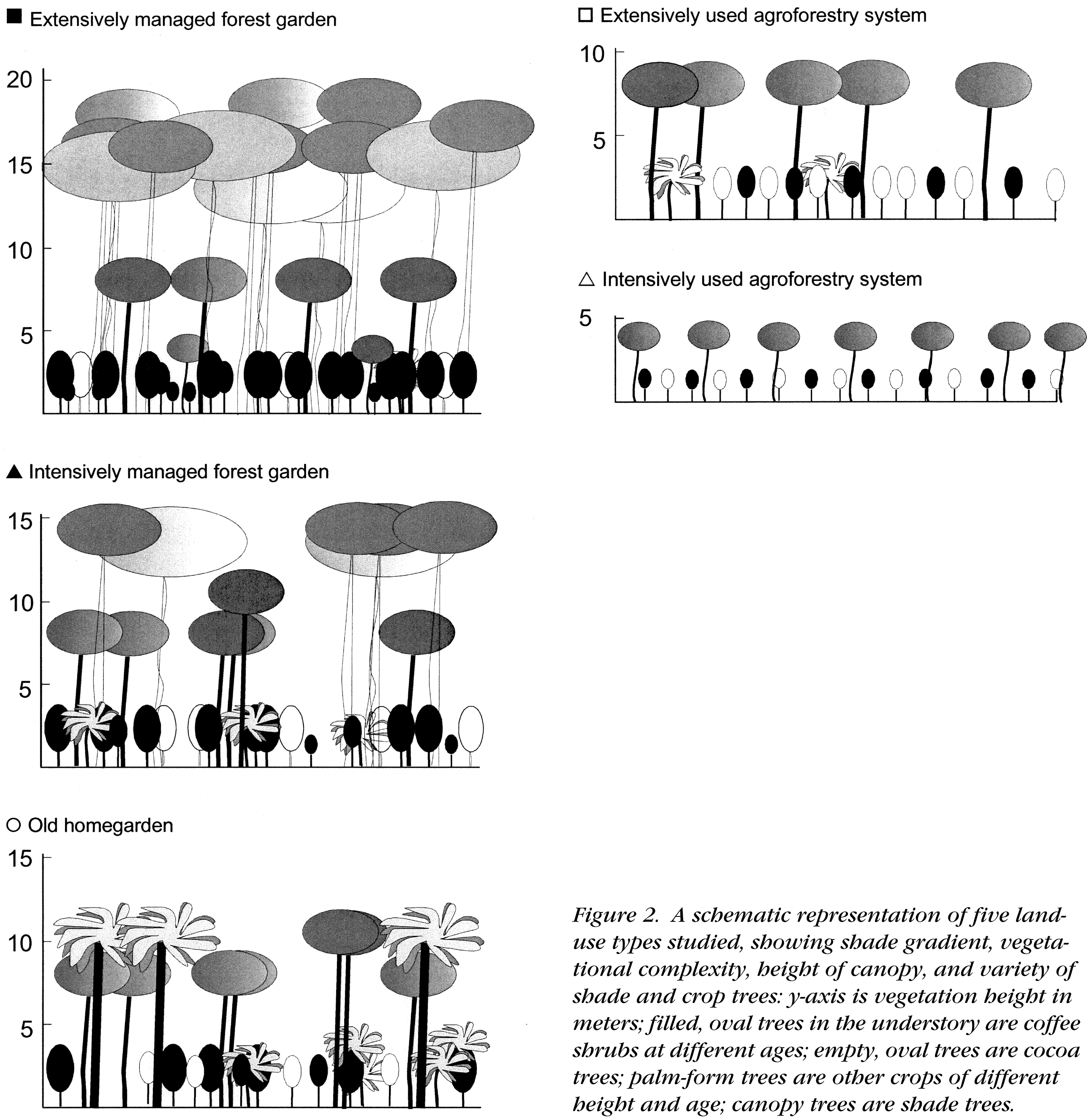
Table 1. Correlation[a] matrix based on simple linear regression between the abiotic and biotic habitat parameters measured in all agroforestry systems.[b]

	Land-use intensity[c]	*Canopy cover (%)*	*Height of trees (m)*	*Relative humidity (%)*	*Day-light intensity (Lux)*	*Temperature (°C)*
Canopy cover (%)	0.79**	—	—	—	—	—
Height of trees (m)	0.96***	0.63*	—	—	—	—
Relative humidity (%)	−0.95***	0.72**	0.88***	—	—	—
Day-light intensity (Lux)	0.81**	−0.85***	−0.77**	−0.63*	—	—
Temperature (°C)	0.89***	−0.57*	−0.86***	−0.90***	0.62*	—
Dead organic materials (%)	−0.90***	0.49 n.s.	0.93***	0.87***	0.61*	0.83***

[a] *Pearson correlation coefficient* (r_p).

[b] *Significance,* *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; $n = 12$ *study systems.*

[c] *Factor analyses based on six habitat parameters.*


■ Extensively managed forest garden

□ Extensively used agroforestry system

△ Intensively used agroforestry system

▲ Intensively managed forest garden

○ Old homegarden

Figure 2. A schematic representation of five land-use types studied, showing shade gradient, vegetational complexity, height of canopy, and variety of shade and crop trees: y-axis is vegetation height in meters; filled, oval trees in the understory are coffee shrubs at different ages; empty, oval trees are cocoa trees; palm-form trees are other crops of different height and age; canopy trees are shade trees.

most diverse and abundant, with 860 individuals (83% of all) and 5 species. The sphecid wasps included 98 individuals (9%) and 3 species, and the megachilid bees 85 individuals (8%) and 2 species.

The eumenid wasps appeared to prefer nesting sites outside the forest, because we found only 22% of all eumenid individuals in the forest gardens and no nests at all in the natural forest. So the abundance of eumenid wasps was positively correlated with the land-use intensity ($r^2 = 0.67$, $n = 12$, $p = 0.001$). Nests of the sphecid wasps and megachilid bees were found in all study systems inside and outside the forest, and abundance did not change with land use. The number of all species was closely correlated with the number of occupied nests ($r^2 = 0.75$, $n = 12$, $p < 0.001$). Due to the dominance of the eumenid wasps, the correlation of land-use intensity and abundance (number of brood cells) held for all species (Fig. 3a). The number of species in the trap nests increased with land-use intensity (Fig. 3b).

Sixteen natural enemies, including parasitoids such as ichneumonid and chalcid wasps and predators such as chrysidid wasps, drosophilid flies, and mordellid beetles, were found in the trap nests (Table 2). The chrysidid wasps were found only and abundantly in the inten-

Table 2. The trap-nesting bees and wasps found in all 12 agroforestry systems and number of brood cells, predators, parasitoid species, and percent parasitism for each species.

Species	*No. of brood cells*	*Predators and parasitoids*	*Parasitism (%)*
Rhynchium haemorrhoidale umeroatrum (Eumenidae)	543	*Stilbum chrysocephalum* (Chrysididae), *Chrysis smaragdula* (Chrysididae), *Chrysis* sp. 2 (Chrysididae), Ichneumonidae gen. sp. 1, Braconidae gen. sp. 1, Eulophidae gen. sp. 1, Drosophilidae gen. sp. 1, Tachinidae gen. sp. 1 & 2, Mordellidae gen. sp. 1	14.5
Rhynchium atrum (Eumenidae)	101	*Chrysis smaragdula* s.l. (Chrysididae), *Chrysis* sp. 2 (Chrysididae), Ichneumonidae gen. sp. 1, Drosophilidae gen. sp. 1	16
Antherhynchium fulvipenne (Eumenidae)	62	*Chrysis smaragdula* s.l. (Chrysididae), *Chrysis* sp. 2 (Chrysididae), Braconidae gen. sp. 1	17
Epsilon manifestum crassipunctatum (Eumenidae)	45	*Chrysis smaragdula* s.l. (Chrysididae), Eulophidae gen. sp. 1	13
Subancistrocerus clavicornis (Eumenidae)	109	*Chrysis* sp. 1 (Chrysididae), *Chrysis ignita* s.l. (Chrysididae), Mordellidae gen. sp. 1	2.7
Chalybion bengalense (Sphecidae)	4	*Chrysis* sp. 2 (Chrysididae)	25
Trypoxylon sp. (Sphecidae)	66	*Chrysis* sp. 2, *Trichrysis* sp. (Chrysididae), *Leucospis* sp. 1 (Chalcididae)	3
Pison sp. (Sphecidae)	28	Drosophilidae gen. sp. 1, Tachinidae gen. sp. 1	13
Chalicodoma (*Callomegachile*) *terminale* (Megachilidae)	78	*Leucospis* sp. 2, Eulophidae gen. sp. 2 (Chalcididae*)*, *Chrysis* sp. 2 (Chrysididae)	18.3
Megachile (*Paracella*) sp. (Megachilidae)	7	—	0

sively managed systems outside the forest and not in the forest systems. Likewise, the parasitoid wasps from the family Braconidae were found only in the intensively managed study systems outside the forest. In contrast, the parasitoid wasps from the family Chalcididae were found only inside the forest in less intensively managed systems. The drosophilid flies were more abundant in the forest gardens than outside the forest. All other predators and parasitoids, such as the Ichneumonidae, Tachinidae, and Mordellidae, did not exhibit such a pattern of being more abundant in the land-use types inside or outside the forest. The percent mortality due to parasitism and predation of trap-nest inhabitants was not correlated with land-use intensity but increased with number of species of predators and parasitoids ($r^2 = 0.34$, $n = 12$, $p = 0.04$). Accordingly, number of species and ecological function (predation) covaried.

Performance of the Flower-Visiting Bees

Only 10 agroforestry systems were sampled, because coffee trees were extremely sparse or even absent in the natural forest. Altogether, 22 bee species with 510 individuals were observed on coffee flowers, 7 social species with 312 individuals and 15 solitary species with 198 individuals. Stingless bees of the subfamily Meliponinae were the most abundant social bees, with 204 individuals, and the Apinae in the genus *Apis* were second, with 108 individuals and 3 species observed. The most abundant solitary bees were the Apidae (only the solitary species included), with 157 individuals. There were 23 Megachilidae individuals and 18 Halictidae individuals. Several species were found both in the forest gardens and in the agroforestry systems, but most species were restricted to either the forest gardens or to the agroforestry systems outside the forest (Table 3).

We also calculated the number of species with the rarefaction method for every land-use type with equal sample size (61 individuals) because this was the smallest sample size. The rarefaction value for species number was on average 8% lower than the actual value, but both values were highly correlated ($r^2 = 0.95$, $n = 5$ types of agroforesty, $p = 0.005$). In addition, we tested how reliable our estimation of actual species richness was. We

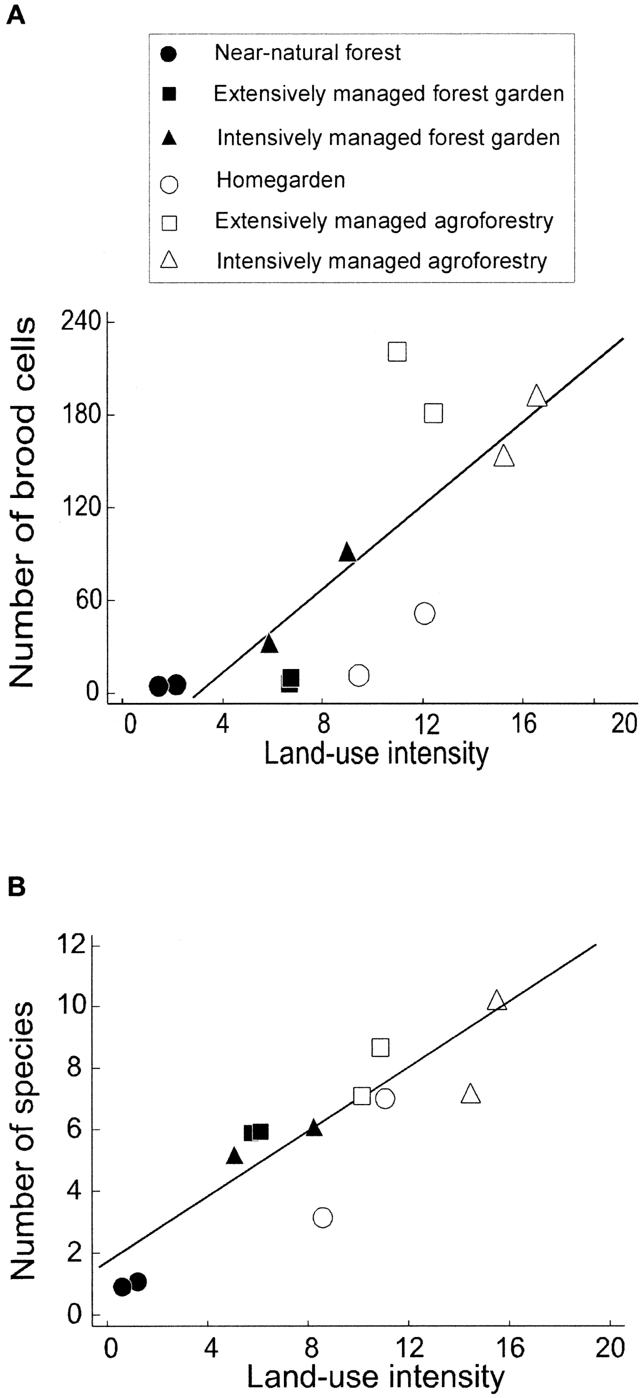


Figure 3. Land-use intensity in relation to trap-nesting bees and wasps: (a) the number of brood cells ($y = -30.23 + 13.56x$*,* $F = 14.03$*,* $r^2 = 0.58$*,* $n = 12$*,* $p = 0.004$*) and (b) the number of trap-nesting species (*$y = 1.31 + 0.54x$*,* $F = 28.45$*,* $r^2 = 0.74$*,* $n = 12$*,* $p < 0.001$*).*

found on average 61.8% of all species in the first sample and 84.2% in the second sample. For three study sites, we tested the reliability of our estimation of species richness with three, four, and five samples. We did not find new species in the additional samples. These results suggest that (1) the actual species numbers were good estimates, as shown by the rarefaction computation, and (2) three samples gave a reliable estimation of species richness, which could not be improved by a fourth or fifth sample.

The percent cover of coffee flowers was negatively correlated with land-use intensity ($r^2 = -0.81$, $n = 10$, $p < 0.001$). Number of bee species and total abundance were significantly correlated with neither land-use intensity nor the percent cover of coffee flowers, but the abundance of solitary bees increased significantly with increasing land-use intensity (Fig. 4a), explaining 65% of the variance, and correlated negatively with the cover of coffee flowers, explaining 58% of the variance. The abundance of social bees declined significantly with increasing land-use intensity (Fig. 4b) and with the cover of coffee flowers, explaining 81% of the variance. The number of solitary bee species did not depend on land-use intensity (Fig. 4c) or percent cover of coffee flowers. The number of social bee species declined significantly with increasing land-use intensity (Fig. 4d) and was also related to the percent cover of coffee flowers, which explained 70% of the variance.

The negative correlation between land-use intensity and the percent cover of coffee flowers was due to the high density of coffee trees in the forest gardens (more than 60% of the area covered by coffee) in comparison with the few trees outside the forest (5% of the intensively managed agroforestry systems were covered by coffee). We calculated analyses of variance for all 30 coffee trees we observed in the 10 land-use systems with a general linear model to analyze the relative importance of coffee-flower abundance and land-use management, including the number of flowering branches per tree and the percent cover of coffee flowers per system. For solitary bees, the model showed a highly significant influence of land-use intensity, but not of the number of flowering branches or percent cover of flowers. For social bees, land-use intensity also had the strongest influence and the number of flowering branches had a much weaker but significant influence. Percent cover of flowers could not be related to the abundance and number of social bee species (Table 4).

Abundances of social and solitary bees were negatively correlated ($r^2 = 0.58$, $n = 10$, $p = 0.001$). Several times we observed the solitary bees visiting flowering plants of the herb layer on the ground, and social bees visited the coffee trees with high abundance. We also checked habitats for potential and actual nesting sites. Almost all nesting sites of social bees were found in the forest gardens or inside the forest in hollow trees or in the canopy. In contrast, all nesting sites of solitary bees, typically in the vegetation-free ground, were found outside the forest in the home gardens or agroforestry systems. Only the nests of the wood-boring carpenter bee,

Table 3. The number of flower-visiting bee species on *C. canephora*, based on 45 minutes observation time per agroforestry system.

	*Agroforestry system**									
	EMFG		*IMFG*		*HG*		*EMAS*		*IMAS*	
Social bees										
Apis cerana	.	.	.	.	26	9	8	.	.	.
Apis dorsata binghami	9	30	7	3	3	.	.	.	.	.
Apis nigrocinta	3	5	.	3	1	.	.	.	1	.
Trigona (*Lepidotrigona*) *terminata*	12	15	15	21	.	1	.	.	4	.
Trigona (*Heterotrigona*) sp.1	18	35	34	27	4	5	.	.	.	.
Trigona (*Heterotrigona*) sp.1	5	4	.	.	.	.	.	.	.	.
Trigona ssp.	.	.	4	.	.	.	.	.	.	.
Solitary bees										
Xylocopa (Zonohirsuta) dejeanii nigrocaerulea	4	7	3	6	7	.	6	10	7	9
Thyreus nitidulus quartinae	.	1	1	1	.	1	2	.	.	.
Amegilla sp. aff. *samarensis*	1	1	.	.	.	.	10	6	17	20
Chalicodoma (*Callomegachile*) *terminale*	2	5	.	.	.	.	.	.	.	.
Creightonella frontalis atrata	.	.	.	.	.	.	4	2	2	4
Lipotriches sp.	.	.	1	2	.	.	3	4	.	.
Ceratina (*Ceratinidia*) sp. nom. nud.	.	.	.	.	.	.	2	1	3	2
Ceratina (*Ceratinidia*) *rugifrons*	.	.	.	1	.	.	1	7	9	3
Coelioxys smithii	.	.	.	1	.	.	1	1	.	.
Pithitis unimaculata	.	.	.	.	1	2	1	2	.	.
Patellapis (*Pachyhalictus*) sp.	.	.	.	.	.	.	1	.	.	.
Nomia thoracica	.	.	.	.	.	1	3	1	.	1
Nomia (*Curvinomia*) *fulvata*	.	.	.	.	.	.	.	1	.	.
Pithitis sp. 2	.	.	.	.	.	.	.	2	.	.
Euaspis sp.	.	.	.	.	.	.	.	1	.	.

**Abbreviations: EMFG, extensively managed forest garden; IMFG, intensively managed forest garden; HG, home garden; EMAS, extensively managed agroforestry system; IMAS, intensively managed agroforestry system.*

Xylocopa (*Zonohirsuta*) *dejeanii nigrocaerulea*, were found everywhere. We also tested the hypothesis that the abundance and the number of species of bees are correlated with the number of total plant species, but there was no significant relationship.

Discussion

Our results show that the transformation of traditional coffee agroecosystems, from the near-natural forest to intensively managed agroforestry systems, was associated with changes in abiotic and biotic habitat parameters and corresponding changes in the bee and wasp communities. The case of coffee is particularly important because in many countries it is the only forested habitat left at mid-elevation (Perfecto et al. 1996), and in the study area it is one of the most important cash crops. The results of our studies support our initial hypothesis: land-use intensity does not affect all bee and wasp species equally. The trap-nesting eumenid wasps and the flower-visiting solitary bees appeared to profit from intensive management, whereas the social bees were put at a disadvantage by increasing land use.

Two hypotheses may explain why the solitary bees profited from land-use intensity. First, increasing land-use intensity led to more nesting sites for ground-nesting solitary bees (Michener 1979; Roubik 1995). Second, the close negative correlation between the abundance of social and solitary bees may have been due to interspecific competition. The first hypothesis was strongly supported by our observation. Almost all solitary bee nests could be found only outside the forest in little-shaded, intensively managed systems that offered open ground for nesting (with the exception of the leaf-cutting bees and the carpenter bees, which are aboveground-nesting species). According to Michener (1979), nests of solitary bees are not adapted to the high humidity of the tropics, except some Halictidae and Andrenidae, and the humidity decreased with increasing land use from the intensively managed agroforestry systems outside the forest to the extensively managed forest gardens. Open ground for nests was almost absent in forested areas but was characteristic of managed systems, and ground-nesting bees are known to profit from open ground, shown experimentally by Wesserling and Tscharntke (1995). The second explanation for the increasing abundance of the solitary bees—the interspecific competition with social bees—has been discussed often (Schaffer et al. 1979; Sudgen et al. 1996; Steffan-Dewenter & Tscharntke 2000). We found a negative correlation between the abundance of social and solitary bees and observed solitary bees visiting flowers of the ground cover, whereas coffee flowers were visited by social bees. Social bees are

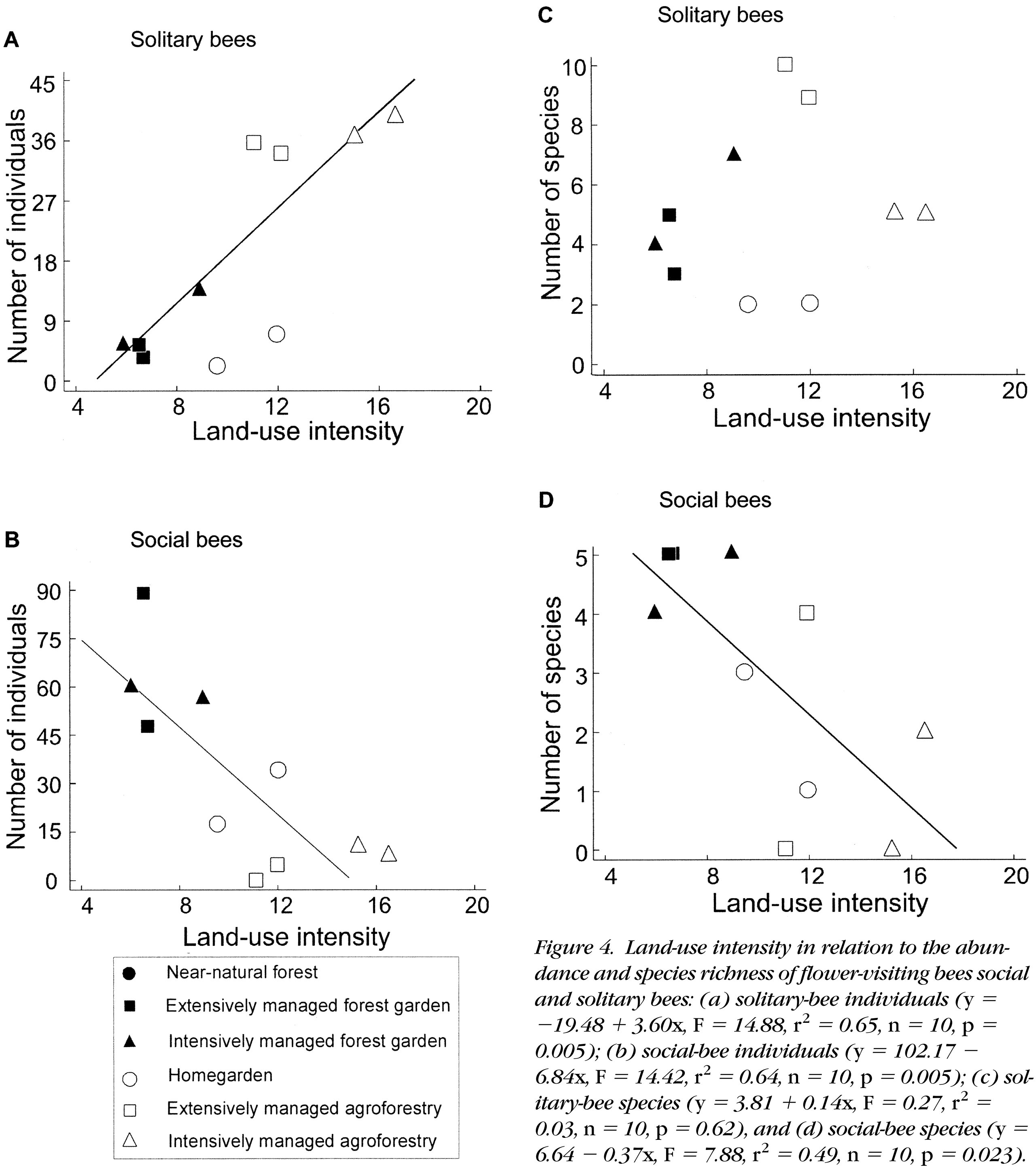


Figure 4. Land-use intensity in relation to the abundance and species richness of flower-visiting bees social and solitary bees: (a) solitary-bee individuals ($y = -19.48 + 3.60x$*,* $F = 14.88$*,* $r^2 = 0.65$*,* $n = 10$*,* $p = 0.005$*); (b) social-bee individuals (*$y = 102.17 - 6.84x$*,* $F = 14.42$*,* $r^2 = 0.64$*,* $n = 10$*,* $p = 0.005$*); (c) solitary-bee species (*$y = 3.81 + 0.14x$*,* $F = 0.27$*,* $r^2 = 0.03$*,* $n = 10$*,* $p = 0.62$*), and (d) social-bee species (*$y = 6.64 - 0.37x$*,* $F = 7.88$*,* $r^2 = 0.49$*,* $n = 10$*,* $p = 0.023$*).*

known to prefer mass-flowering crops (Waddington et al. 1994; Sudgen et al. 1996; Steffan-Dewenter & Tscharntke 2000). At times when coffee flowers are abundant, social bees are attracted in large numbers (Willmer & Stone 1989). We observed this also and that the solitary bees were more abundant at times when only single flowers were blooming, with a correspondent decline of social bees. These observations are in agreement with the idea of possible competition between social and solitary bees, but more experiments need to be done to clarify this hypothesis. Accordingly, both the nesting-site and the competition hypothesis are supported by our findings.

The negative correlation between land-use intensity and abundance and number of social bees was paralleled by the negative correlation between land-use intensity and percent cover of coffee flowers. This was caused by the high abundance of coffee trees in the forest gardens in comparison with the few trees outside the forest. In an

Table 4. Effects of land-use intensity, flowering branches per observed tree, and percent cover of coffee flowers per agroforestry system on the abundance of social and solitary bees.*

Source of variation	*df*	*MS*	F	p
Social bees				
land-use intensity	4	1.93	7.63	<0.001
number of flowering branches	1	1.43	5.64	0.026
cover of coffee flowers per study site (%)	1	0.16	0.65	0.43
residuals	24	0.25		
model with all variables	6	4.06	16.01	<0.001
Solitary bees				
land-use intensity	4	108.88	7.26	<0.001
number of flowering branches	1	23.61	1.58	0.221
cover of coffee flowers per study site (%)	1	5.82	0.39	0.539
residuals	26	14.99		
model with all variables	6	117.81	7.86	<0.001

**Results of a general linear model analysis for all sources of variation and the complete model are given. We included all 30 coffee trees we observed in 10 sites (*n = 30*).*

analysis of variance including all 30 coffee trees in the 10 sites, however, the abundance and number of social bees was best explained by the intensity of land use. Cover of coffee flowers did not contribute to the explanation, and the number of flowering branches was of only minor importance. These results suggest that the abundance of social bees depends primarily on land-use intensity and only secondarily on the local performance of the coffee trees. Distance from forest may also be an important factor influencing bee communities (Aizen & Feinsinger 1994*b*). Because some of our study systems were located within and some outside the forest, the distance from forest might have been a confounding factor influencing the bee communities. But outside the forest, the intensively managed agroforestry systems were located nearer the forest than the house gardens and extensively managed agroforestry systems. This suggests that land-use intensity was most important.

With respect to pollination success, it would be interesting to know which species of coffee pollinators were most responsible for seed set. Willmer and Stone (1989) found in Papua New Guinea that only a single solitary species was responsible for a high seed set, whereas pollen transfer between trees is probably rather poor in social bees. In a study of 24 agroforestry systems (A.-M.K. et al., unpublished data), we found that the abundance of bees was related to fruit set of *C. canephora* and that social bees had an important influence on pollination success.

The availability of suitable nesting sites and resources (pollen or prey insects) was related to the abiotic conditions of the study systems, and shade inside the habitats appeared to be a major parameter influencing bees, wasps, and their natural enemies (Heithaus 1979; Roubik 1995). Our characterization of land-use intensity was based on abiotic parameters such as relative humidity, day-light intensity, and temperature, and on biotic parameters such as percent canopy cover, height of trees, and percent cover of dead organic material. Systems with many shade trees provide a more diverse layer of decaying wood and leaf litter (Power 1996) and protection from rain and wind (Beer 1987). Canopy density is an important factor in the microclimate of the coffee understory (Perfecto et al. 1996; Perfecto & Vandermeer 1996) and is often used for indirect measurement of moisture and temperature (Beer 1987). Microclimatic conditions are some of the most important factors in habitat changes (Lovejoy et al. 1986; Bierregaard et al. 1992; Didham et al. 1996; Turner 1996). The type of coffee system, determined by different degrees of ecosystem manipulation, affects biological diversity (Moguel & Toledo 1999).

The strong correlation of the number of individuals of all trap-nesting species with land-use intensity was caused by the dominance of the eumenid wasps in the intensively managed agroforestry systems. The eumenids were frequent: 83% of all specimens and more than half of all eumenid individuals came from one species, ***Rhynchium haemorrhoidale umeroatrum***. We often observed this seemingly synanthropic species nesting inside houses in small holes between or in the wooden structures. Therefore, the high abundance of trap-nesting species was presumably due to the availability of suitable nesting sites. Because the abundance and number of common pests, including harmful caterpillars, increases with land-use intensity (Klein et al. 2002), the eumenids should have also found large numbers of prey in these anthropogenic habitats.

In contrast to common hypotheses that species numbers decline with increasing land use, the number of species of the trap-nest community increased with intensity of land use. The species richness of insects and plants is often found to correlate closely (Siemann et al. 1999) and does so in trap-nesting communities (Tscharntke et al. 1998), but we could not find a correlation between the species richness of trap-nesting insects or flower-visiting bees and plants. This may be due to the use of herbicides in the study systems. Only the number of species of the woody plants showed the expected correlation with the number of species of the trap-nesting inhabitants and the flower-visiting bee species.

One might expect an increasing percentage of parasitism and predation with increasing habitat complexity and decreasing land-use intensity (Roland & Taylor 1997; Lawton et al. 1998; Menalled et al. 1999; Thies & Tscharntke 1999). In our experiments, the mortality of the trap-nesting bees and wasps due to parasitoids and predators was neither correlated with the species richness of plants nor with land-use intensity, so increasing prey abundance (bees and wasps) and decreasing land-use intensity appeared to have contrasting effects on predation rates. In a parallel study with phytophagous and entomophagous insects on cocoa, predator-prey ratios showed the expected decrease with land-use intensity (Klein et al. 2002).

Studies show that land-use intensity does not affect all insects equally, which supports conclusions from insect studies in forested ecosystems in Sulawesi (Stork & Brendell 1990; Holloway & Stork 1991). Lawton et al. (1998) also found that the number of species does not generally decline with increasing habitat modification through land use. With respect to biodiversity, the increasing abundance of eumenid wasps and solitary bees with land-use intensity suggests that tropical agroecosystems may be more important for nature conservation than previously thought.

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