

# Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry

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## Summary

1. Human alteration of natural ecosystems to agroecosystems continues to accelerate in tropical countries. The resulting world-wide decline of rain forest causes a mosaic landscape, comprising simple and complex agroecosystems and patchily distributed rain forest fragments of different quality. Landscape context and agricultural management can be expected to affect both species diversity and ecosystem services by trophic interactions.
2. In Central Sulawesi, Indonesia, 24 agroforestry systems, differing in the distance to the nearest natural forest (0–1415 m), light intensity (37.5–899.6 W/m<sup>2</sup>) and number of vascular plant species (7–40 species) were studied. Ten standardized trap nests for bees and wasps, made from reed and knotweed internodes, were exposed in each study site. Occupied nests were collected every month, over a period totalling 15 months.
3. A total of 13 617 brood cells were reared to produce adults of 14 trap-nesting species and 25 natural enemy species, which were mostly parasitoids. The total number of species was affected negatively by increasing distance from forest and increased with light intensity of agroforestry systems. The parasitoids in particular appeared to benefit from nearby forests. Over a 500-m distance, the number of parasitoid species decreased from eight to five, and parasitism rates from 12% to 4%.
4. The results show that diversity and parasitism, as a higher trophic interaction and ecosystem service, are enhanced by (i) improved connectivity of agroecosystems with natural habitats such as agroforestry adjacent to rain forest and (ii) management practices to increase light availability in agroforestry, which also enhances richness of flowering plants in the understorey.

*Key-words:* bees, parasitism, predation, rain forest conservation, wasps.

*Journal of Animal Ecology* (2006) **75**, 315–323  
doi: 10.1111/j.1365-2656.2006.01042.x

## Introduction

The world-wide expansion of agroecosystems results in the degradation of tropical rain forests and the isolation of these land-use systems from natural habitats (Vitousek *et al.* 1997; Tilman *et al.* 2001). Especially in tropical landscapes natural forest is often patchily distributed between the dominating agroecosystems (Schelhas & Greenberg 1996; Laurance & Bierregaard 1997). Populations within fragmented habitats become isolated from the source populations in large natural

habitats, particularly species using agroecosystems of high isolation from the nearest source habitat such as natural forest. Changes of natural habitats by habitat conversion and the simplification of landscape structure are the main reasons for the world-wide loss of biodiversity (Harrison & Bruna 1999; Dale *et al.* 2000; Davies, Margules & Lawrence 2000), which will increase dramatically in the future, because human alteration of natural ecosystems to agroecosystems continues to accelerate (Bawa *et al.* 2004). As a consequence, ecosystem services provided by natural habitats may disappear (see Kremen *et al.* 2004). Ecosystem services are all the natural services provided by ecosystems that are useful to humans (Daily 1997; Loreau, Naeem & Inchausti 2002; Luck, Daily & Ehrlich 2003; Kremen 2005), such as soil nutrient supply, soil carbon storage

and biodiversity-related services (e.g. decomposition, natural control of pests and invasive species, pollination). Little is known about the manner in which management and the impact of adjacent natural ecosystems affect the properties and services of human-influenced ecosystems. In particular, the importance of trophic levels of agricultural biodiversity, the interactions and the contribution they make to sustainable production require investigation and consideration in agri-environment schemes (van der Putten *et al.* 2004; Tscharnтке *et al.* 2005). Biodiversity loss within a trophic level is likely to impact species at other levels indirectly via changes in ecosystem services (Raffaelli *et al.* 2002) and changes in natural habitats such as habitat fragmentation lead not only to a decline in biodiversity (Hanski 1999), but may also change the relative importance of predation and parasitism in food webs. This occurs because predators find it harder to locate their prey in fragmented habitats compared to continuous habitats (Kruess & Tscharnтке 1994). Isolation from natural habitats does not affect all species equally and specialists of higher trophic levels, such as parasitoids, are more affected than their hosts (Holt *et al.* 1999; Tscharnтке & Kruess 1999; Davies, Marguels & Lawrence 2000; Gibb & Hochuli 2002; Tscharnтке & Brandl 2004). Higher trophic level species are more prone to extinction in more isolated habitats from the natural source habitat because higher levels have more unstable population dynamics, and population size decline for energetic reasons (see Holt *et al.* 1999). After converting natural habitats to agroecosystems, resident populations of parasitoids and predators are typically low (Bosch & Kemp 2002). Because of the low abundance of predators and parasitoids in many types of agroecosystems compared to natural habitats, pest species have an advantage (Gurr, Wratten & Luna 2003). Many agroecosystems, especially intensified monocultures, can be expected to offer usable resources for insects (food resources, nest sites and nesting materials) only when natural habitats are nearby (Steffan-Dewenter 2002; Klein, Steffan-Dewenter & Tscharnтке 2004). Thus, a landscape mosaic with agroecosystems in close proximity to natural habitat fragments is often important for the maintenance of biodiversity (Huston 1999; Ricketts *et al.* 2001; Perfecto & Vandermeer 2002; Steffan-Dewenter 2002; Tscharnтке *et al.* 2002), and only high-diversity agricultural landscapes may guarantee sustainability of the multifunction agroecosystem services (Tscharnтке *et al.* 2005).

Bees and wasps using trap nests are used as bioindicators because they are sensitive to environmental changes (Tscharnтке, Gathmann & Steffan-Dewenter 1998). Although trap-nesting bees and wasps make up only a small part of all bee and wasp species which can be found with other trapping or observation methods, the results of this method may be transferred to the whole bee and wasp community visiting the evaluated habitats or landscape because, normally, trap-nesting species richness and species richness of their natural enemies are often highly correlated to other methods,

evaluating the whole bee species of a community, e.g. sweep-netting of flower visitors (Tscharnтке *et al.* 1998; A. M. Klein, data not shown).

The trap-nesting community can be categorized into two ecological groups: (i) pollinating species such as bees (ii) and species of higher trophic levels such as predatory wasps and parasitoids. Bees provide important biodiversity related ecosystem services, the pollination services of crops and non-crop plants (Corbet 1987; Kremen 2005), and isolation of source habitats can lead to pollination limitation which causes losses in crop production (Kremen, Williams & Thorp 2002; Klein, Steffan-Dewenter & Tscharnтке 2003; Kremen *et al.* 2004; Ricketts *et al.* 2004). Predatory wasps may reduce the number of pest caterpillars by using certain pest species as food for their larvae (Harris 1994), but also attack beneficial predators such as spiders (see also Wearing & Harris 1999). The primary trap-nest inhabitants (bees and wasps) are attacked by a range of predators and parasitoids, and thereby may provide little known data on the strength of trophic interactions and its relation to enemy diversity (Tscharnтке *et al.* 1998; Bosch & Kemp 2002).

In this study, local and regional management of agroforestry, which is known to contribute highly to biological and genetic diversity (Atta-Krah *et al.* 2004), were examined. Agroforestry is a collective name for land-use systems where woody perennials are deliberately used on the same land-management units as agricultural crops (see Lundgren & Raintree 1982). Furthermore, woody perennials provide shade for the crops.

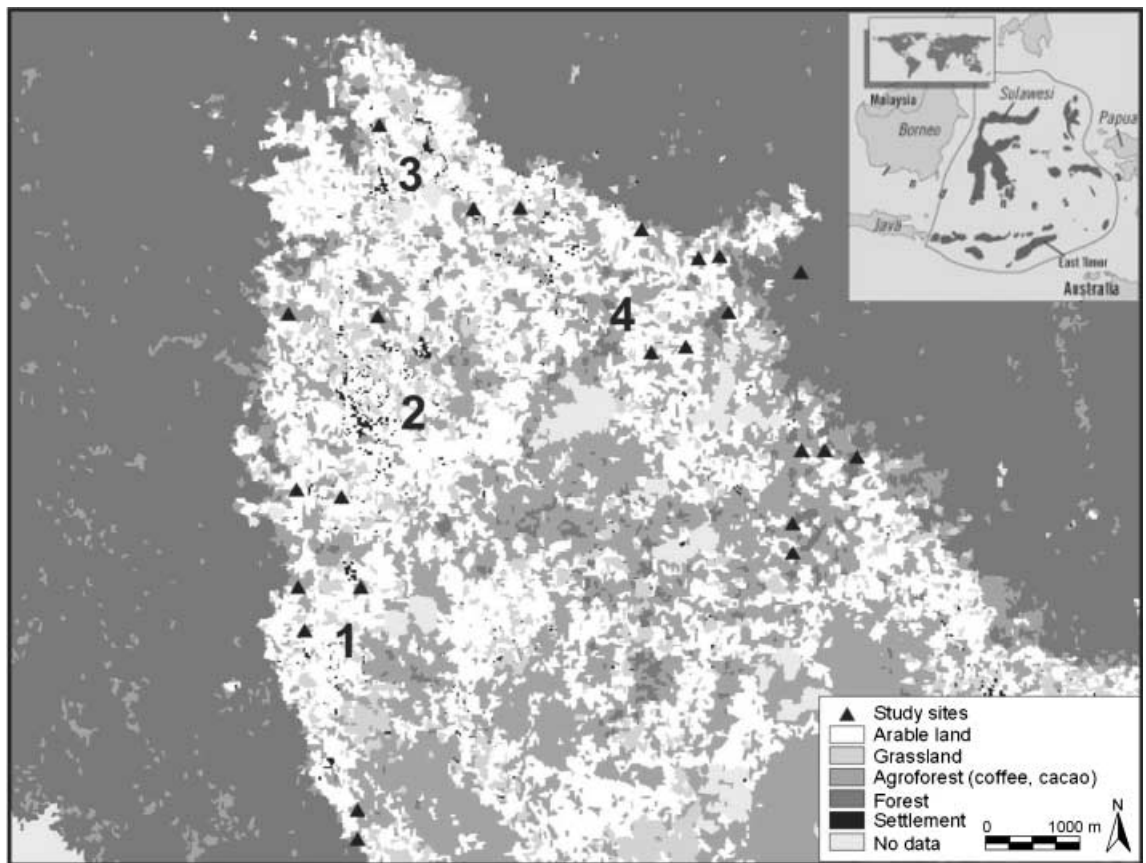
Here, trap nests were exposed over a 15-month period to analyse the community structure of bees and wasps in differently managed agroforestry systems with different distances from the nearest natural forest. The main type of local management is shade management, which is responsible for microclimatic conditions in agroforestry systems, and in combination with a diverse shade tree layer approaches conditions in natural forest (here measured with light intensity). Light influences plant diversity inside the systems, because a dense canopy negatively influences the flowering herb layer, which are the main food resource for many bees and wasps (see Klein *et al.* 2003).

Three main questions were addressed in this study: (1) does the number of trap-nesting species decrease in agroforestry systems with increasing isolation from natural forest? (2) Are insect populations of higher trophic levels more affected by isolation from natural forest than their hosts? (3) What is the relative importance of forest distance and agroforestry management practices that influence local light regimes and plant diversity?

## Materials and methods

### RESEARCH REGION AND AGROFORESTRY SYSTEMS

The study was carried out from December 2000 to March 2002 in the Napu valley along the forest margin,



**Fig. 1.** Overview of land-use types in the study area in Central Sulawesi (Indonesia) in the Napu-valley close to the boundary of the Lore-Lindu National Park. The numbers show the location of the villages, 1 = Katuwaa, 2 = Wuasa, 3 = Watumaeta, 4 = Alitupu. The map is based on satellite data. We assume that grey patches inside the continuous forest (dark grey) are both logged forest and agroforest.

at the east side of the Lore-Lindu National Park, in Central Sulawesi, Indonesia (for more details about the study area see Klein *et al.* 2003). Twenty-four agroforestry systems were selected with at least 500 m between them (Fig. 1). These agroforestry systems are dominated by coffee, and characterized by different shade levels and vegetational complexity. Often perennial crops such as cacao, bananas, papaya and other common tropical fruit trees are scattered among the coffee plants. The most abundant shade tree species belong to the family Leguminosae (*Gliricidia* sp. and *Erythrina* sp.) providing nitrogen for plant growth, but sometimes old primary trees are retained to provide shade. In systems with an open canopy, plenty of flowering and non-flowering herb species and some vegetables are grown in the understorey. Light-intensity was measured with a luxmeter (Gossen MAVOLUX digital, Wilh. Lambrecht GmbH, digital light-gauge with four scopes from 0 to 1999 W/m<sup>2</sup>) under standardized conditions (on the ground, on sunny days, 0900–1500 h) to calculate the mean of 20 measurements. The vegetation was mapped between November 2000 and January 2001 in two separated, randomized 25 m<sup>2</sup> plots per agroforestry system for herbs and within two separated, randomized 100 m<sup>2</sup> plots for shrubs and trees. All four plots were marked with wooden stakes and character-

ized at the same time per agroforestry system, resulting in estimates of the number of total plant species and the percentage of vegetation cover. Percentage cover of flowering plants was calculated for each system with a mean of eight different estimations, three times in December 2000 to January 2001 and five times between July and September 2001 to estimate the flower resource availability for the trap-nesting species. The agroforestry systems differed in their distance from the nearest natural forest (ranging from inside the forest margin, to a distance of 1415 m from the nearest natural forest, Fig. 1). The distance to the forest was measured using a global positioning system (GPS) from Garmin International, Olathe, KS, USA). Grassland and arable land crops such as maize and rice are grown between the agroforestry systems and the natural forests. Few forest fragments with high logging activities could be found between the agroforestry systems and the natural continuous forest. Because of their small size and high disturbance, these fragments seem to be of low value for the bee and wasp community and were not considered as source habitat for the trap-nesting community. The age of the systems could not be identified, because normally the farmers already use shade trees in the systems and from time to time they replace isolated trees or tree groups with younger or more valuable species,

so systems with coffee of a similar age were selected (5–8 years old).

#### TRAP NESTS

Trap-nesting bees (Megachilidae) and wasps (Eumenidae, Sphecidae, Pompilidae) use holes of suitable diameter for nesting. A nest consists of one to several brood cells, and the females provide the cells with food for the larvae. In this study, bees used a nectar–pollen mixture, pompilid- and sphecid wasps used spiders, and eumenid wasps used caterpillars as larval food. Parasitoids (mainly ectoparasitic Hymenoptera) lay their eggs in the cells and the larvae feed on their host's larvae and often also on their host's food. Predators lay their eggs in the cells and the larvae primarily feed on their host's food, so the egg of the trap-nesting species does not develop into an adult (A. M. Klein, personal observation).

Trap nests were set up in December 2000 and removed in March 2002. Ten traps were hung in each of the 24 agroforestry systems in coffee or cacao shrubs, or legume shade tree, each with a solid wire, at a height of 1.5–2 m. Sticky glue was put around each wire outside the trap nests to deter ants. The standardized traps consisted of about 120 internodes of a mixture of common reed *Phragmites australis* (Cav.) Trin. and Japanese knotweed *Reynoutria japonica* Houtt, cut to a length of 20 cm and inserted into plastic tubes of 10.5 cm diameter and a length of 25 cm. The range of internal diameters of the reed internodes varied between 2 mm and 20 mm. In each trap at least five internodes with large diameters (around 20 mm), and 10 with small diameters (around 2 mm) were inserted. The other internodes showed diameters between 2 and 20 mm, and the distribution of the diameters was similar in each study site. All occupied internodes were replaced monthly with unoccupied new internodes of a similar diameter. Nests were opened in the laboratory to make a preliminary identification of species and to establish the number of brood cells per species. After the adults had emerged, species were identified and mortality due to parasitism and predation, and unknown mortality was established.

#### STATISTICAL ANALYSES

A pre-analysis was carried out, testing for spatial autocorrelation by relating the number of bee and wasp species and individuals and the number of natural enemy species and individuals to geographical distance between sites with the Mantel statistics based on Spearman's rank correlation with 1000 permutations, and Euclidian distances as similarity indices (Legendre & Legendre 1998), using the statistical program R (R Development Core Team 2004). No spatial autocorrelations were found for the bee- and wasp community ( $r = 0.03$ ,  $P = 0.299$ ) and the natural enemy community ( $r = -0.09$ ,  $P = 0.916$ ).

All data were tested for normality and transformed if necessary to achieve a normal distribution. The predic-

tor variable forest distance was always square-root transformed (Sokal & Rohlf 1995). The habitat factor light intensity was highly intercorrelated with most of the vegetation parameters in the 24 agroforestry systems. The number of plant species was only slightly correlated with light intensity ( $r = 0.44$ ,  $P = 0.03$ ), in contrast to the other vegetation parameters such as the percentage cover of all plants ( $r = -0.82$ ,  $P < 0.001$ ), the number of herb species ( $r = 0.62$ ,  $P < 0.001$ ) and the percentage cover of trees ( $r = -0.96$ ,  $P < 0.001$ ), which were highly intercorrelated and therefore reflected by the parameter light intensity. Therefore, light intensity was used in multiple regression analyses and the number of plant species to test for relations with bees, wasps and natural enemies. The species were divided into three groups: bees, wasps and natural enemies. In stepwise multiple regression analyses with backward elimination we examined which predictor habitat factor (forest distance, light intensity, number of plant species) was the best predictor for the number of bee and wasp species and individuals (together and divided into the two groups of bees and wasps) and the number of natural enemy species, and the percentage mortality due to natural enemies. For the latter two response variables, host density was included as additional predictor variable in the model. The number of bee and wasp individuals was related closely to the number of nests, tested in a linear regression using nest numbers and brood cell numbers of the living progeny separately for all species and agroforestry systems ( $F = 460.43$ ,  $r = 0.98$ ;  $n = 147$ ,  $P > 0.001$ ). Multiple and linear regressions were performed using the software Statgraphics plus for Windows version 5.1. (Anonymous 2001). The analyses were also conducted for the Shannon–Wiener index calculated for each site using the formula  $H = [-(\sum P_i / \sum P) \times \ln(\sum P_i / \sum P)]$  where  $P_i$  is the number of brood cells established by each species or the number of parasitized brood cells and  $P$  is the number of all brood cells or the number of parasitized brood cells calculated for each site for the hosts and the parasitoids separately.

Additional analyses were carried out to test which habitat factor is most important for count data (the number of species and individuals, separately for bees and wasps and parasitoids) using generalized linear model analyses assuming Poisson distribution, and for the percentage mortality due to natural enemies assuming binominal distribution using the statistical program R (Crawley 2002). The same patterns were found with these analyses as in the multiple regression analyses assuming normal distribution (results not shown).

To estimate the species saturation in relation to sample size, the ratio of sampled to expected species richness were calculated for trap-nesting species and separately for their natural enemies for each agroforestry system using 100 randomizations per month with the estimator ACE (Abundance-based Coverage Estimator of species richness), within the EstimateS program, version 5 (Colwell 1997).



**Table 1.** Bees (Megachilidae), wasps (Sphecidae, Eumenidae, Pompilidae) and their natural enemies (Braconidae, Chrysididae, Chalcidoidea, Dermestidae, Eulophidae, Ichneumonidae, Megachilidae, Pompilidae, Tachinidae) reared from trap nests

Species	Occupied brood cells (%)	Colonized sites (of 24)	Unknown Parasitized brood cells (%)	Mortality per brood cell (%)	No. of natural enemy species
<b>Megachilidae</b>					
<i>Chalicodoma (Callomegachile) incisum</i>	0.09	2	0	50	0
<i>Chalicodoma (Callomegachile) terminale</i>	0.88	12	1.67	6.67	2
<i>Chalicodoma (Callomegachile) tuberculatum clotho</i>	0.09	4	8.33	50	1
<i>Heriades (Michenerella) sp. aff. fulvescens</i>	20.23	22	0	4.79	0
<i>Megachile (Paracella) sp.</i>	1.21	13	0.61	14.54	1
<b>Eumenidae</b>					
<i>Antherhynchium fulvipenne</i>	0.01	1	0	0	0
<i>Epsilon manifestum crassipunctatum</i>	0.15	4	4.76	4.76	1
<i>Rhynchium atrum</i>	0.93	9	27.56	17.32	6
<i>Rhynchium haemorrhoidale umeroatrum</i>	17.08	24	18.14	20.94	11
<i>Subancistrocerus clavicornis</i>	0.35	10	4.26	42.55	2
<i>Zethus celebensis</i>	3.22	15	0.68	10.03	1
<b>Sphecidae</b>					
<i>Chalybion bengalense</i>	0.05	2	28.57	0	1
<i>Pison sp.</i>	0.14	5	5.26	36.84	1
<b>Pompilidae</b>					
<i>Auplopus levicarinatus</i>	55.57	24	2.84	15.37	7

## Results

### COMMUNITY STRUCTURE

Altogether, 13 617 brood cells of five leaf-cutting bee species (Megachilidae), six mason wasp species (Eumenidae), two mud wasp species (Sphecidae) and one spider wasp species (Pompilidae) were found in 240 exposed trap nests within the 15 months. This is an average saturation of  $96.4 \pm 0.88\%$  ( $n = 24$  agroforestry systems) of the estimated bee and wasp species richness using our trap nests. The most abundant and widespread species were the spider wasp *Auplopus levicarinatus* Wahis, which made up 55.6% of all brood cells, the megachilid bee species *Heriades (Michenerella) sp. aff. fulvescens* Cockerell with 20.2% and the eumenid wasp species *Rhynchium haemorrhoidale umeroatrum* Gusenleitner with 17.1%. The remaining 11 species were relatively rare and made up in total only 7.1% of the brood cells (Table 1). Twenty-five species of natural enemies were found – including all agroforestry systems and months, an average saturation of  $91.4 \pm 0.82\%$ ,  $n = 24$ , of the estimated natural enemy species; Appendix S1 (see Supplementary material) – which attacked a mean of 5.0% of all brood cells: 2.1% of bees, 9.2% of eumenid wasps, 16.9% of sphecid wasps and 2.8% of pompilid wasps, respectively. The mortality inside all brood cells for which no cause could be assigned was 14.1% (Table 1).

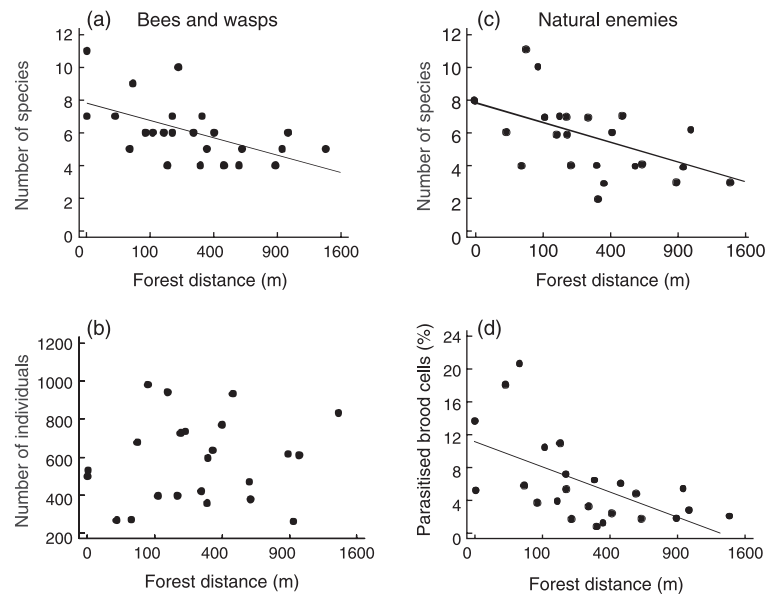
The number of trap-nesting species was correlated only marginally with the number of natural enemy species ( $F = 3.57$ ,  $r = 0.14$ ,  $n = 24$ ,  $P = 0.072$ ), and the number of trap-nesting individuals (number of brood cells) was not correlated with the number of natural enemy individuals ( $F = 0.64$ ,  $r = 0.03$ ,  $n = 24$ ,  $P = 0.433$ ).

### RELATION OF LOCAL AND REGIONAL HABITAT PARAMETERS TO THE TRAP-NESTING COMMUNITY

In stepwise multiple regression with forest distance, light intensity and number of plant species as predictor variables and the number of trap-nesting bee and wasp species (excluding natural enemies) as the response variable, forest distance and light intensity explained most of the variation (Table 2, Fig. 2a). The number of wasp species showed the same tendency, whereas the number of bee species was not related to any of the three predictor variables in the regressions (Table 2). The number of bee and wasp individuals was not related to the three habitat variables (Fig. 2b). The number of wasp individuals alone, however, decreased with light intensity, whereas the number of bee individuals increased with light intensity and decreased with forest distance (Table 2). Diversity of natural enemies was related only to forest distance, but not to light intensity, plant diversity or number of host individuals (Table 2, Fig. 2c). In contrast to the relationship of bee and wasp density to forest distance, the percentage of parasitized brood cells decreased with forest distance and was not related to light intensity, plant diversity or host density (Table 2, Fig. 2b). This indicates that natural enemies are more positively influenced by forest vicinity than their hosts. The Shannon–Wiener index calculated for the bees and wasps and separately for the natural enemies decreased with increasing forest distance (bees and wasps:  $F = 5.18$ ,  $r = -0.44$ ,  $n = 24$ ,  $P = 0.033$ ; natural enemies:  $F = 6.81$ ,  $r = -0.49$ ,  $n = 24$ ,  $P = 0.016$ ). A comparison of regression lines indicated higher intercepts for the parasitoids ( $P < 0.001$ ), but slopes were not significantly different ( $P = 0.938$ ).

**Table 2.** Results of stepwise multiple regression analyses to explain species richness. The three predictor habitat factors were light intensity, forest distance and number of plant species on species richness and abundance of bees and wasps (excluding natural enemies) on bees and wasps separately. Species richness of natural enemies and percentage of parasitized brood cells were also related to the host density as predictor variable. Only significant results ( $P < 0.05$ ) are shown

Response variables	Explanatory variables	t Statistic	P-value	$r^2$
Number of bee and wasp species	Forest distance (m)	-2.45	0.023	0.348
	Light intensity ( $W/m^2$ )	2.26	0.035	
	Final model			
Number of wasp species	Light intensity ( $W/m^2$ )	3.18	0.004	0.537
	Forest distance (m)	-2.55	0.019	
	Final model			
Number of bee species	Final model			NS
Number of natural enemy species	Forest distance	-3.42	0.002	0.347
Number of all individuals	Final model			NS
Number of wasp individuals	Light intensity ( $W/m^2$ )	-2.92	0.008	0.281
Number of bee individuals	Light intensity ( $W/m^2$ )	5.04	< 0.001	0.552
	Forest distance (m)	-2.27	0.034	
	Final model			
Percentage of parasitized and predated brood cells	Forest distance	-3.28	0.003	0.328



**Fig. 2.** Distance to the nearest natural forest in relation to (a) the number of trap-nesting bee and wasp species per agroforestry systems (without natural enemies):  $y = 7.74 - 0.10\sqrt{x}$ ,  $r = -0.55$ ,  $n = 24$ ,  $P = 0.006$ ; (b) the number of trap-nesting bee and wasp species per agroforestry systems (without natural enemies):  $y = 520.65 + 3.04\sqrt{x}$ ,  $r = 0.14$ ,  $n = 24$ ,  $P = 0.523$ ; (c) the number parasitoid species per agroforestry systems:  $y = 7.96 - 0.14\sqrt{x}$ ,  $r = -0.59$ ,  $n = 24$ ,  $P = 0.002$ ; (d) percentage of parasitized brood cells per agroforestry systems:  $y = 73.17 - 1.96\sqrt{x}$ ,  $r = -0.58$ ,  $n = 24$ ,  $P = 0.003$ , see also Table 3.

Parasitism rate of the highly parasitized, common trap-nesting species *R. haemorrhoidale*, which was found in all sites and which was the predominant species in a trap-nesting study of Klein *et al.* (2002a), were tested for correlation with forest distance. Parasitism decreased significantly with increasing forest distance testing only this highly parasitized species ( $F = 11.8$ ,  $r = -0.59$ ,  $n = 24$ ,  $P = 0.002$ ). Additionally, the correlation of percentage of brood cells parasitized of the three most abundant trap-nesting species was tested with distance to forest. Only parasitism of *R. haemorrhoidale* was correlated with forest distance ( $F = 11.87$ ,  $r = 0.32$ ,  $n = 24$ ,  $P = 0.002$ ), but not parasitism of *A. levicarinatus* ( $F = 0.20$ ,  $r = 0.09$ ,  $n = 24$ ,  $P = 0.659$ ).

Although *H. fulvescens* occupied 2754 brood cells, no parasitoid or predator of this species was found.

The negative relationship between the number of wasp individuals and light intensity was based on the very abundant spider-hunting wasp species *A. levicarinatus*, which occupied more than 50% of all brood cells (Table 1). Further, wasp species were divided into spider-hunting wasps (all species of the family Pompilidae and Sphecidae of this study foraged on spiders) and caterpillar-hunting wasps (all species of the family Eumenidae foraged on caterpillars). The number of spider-hunting wasp individuals was correlated negatively with light intensity ( $F = 8.40$ ,  $r = 0.28$ ,  $n = 24$ ,  $P = 0.008$ ), whereas the caterpillar-hunting wasp individuals

showed no correlation with light intensity, and the species richness of caterpillar-hunting wasps even increased with light intensity of agroforestry systems ( $F = 13.15$ ,  $r = 0.37$ ,  $n = 24$ ,  $P = 0.001$ ). Consequently, the spider-hunting species determined the relationship between the number of all wasp species and light intensity (Table 2).

## Discussion

### ISOLATION OF AGROFORESTRY SYSTEMS FROM NATURAL FOREST

In this study, the highest trophic level of the trap-nesting community, the parasitoids, was affected more strongly by distance of nests from the forest than were its hosts. The percentage of parasitism was related to forest distance, but not host density (bee and wasp abundance). Species richness of bees and wasps and of natural enemies was affected by forest isolation. In natural forests, higher trophic levels may build up large populations over a long period without disturbance. This supports the idea that higher trophic levels show a greater susceptibility to habitat disturbance and isolation than their hosts (Kruess & Tschardtke 1994; Holt *et al.* 1999; Tschardtke & Kruess 1999). Accordingly, parasitoids should generally be more affected by isolation than predators, as they show greater host (or prey) specificity. The density of high trophic level populations is often lower and more variable than those of lower trophic levels (van Nouhuys & Hanski 2002). Both rarity and population variability are well-known predictors of local extinction (Schoener & Spiller 1992; Gaston 1994; Fagan *et al.* 2001), and trophic position, rarity and population variability often may be correlated closely (Kruess & Tschardtke 1994).

Similar effects were found in temperate landscapes. When traps were exposed in the cleared agricultural landscape at a large distance from the nearest species-rich grassland, mortality of trap-nesting bees and wasps induced by natural enemy significantly decreased (Tschardtke *et al.* 1998). Forest fragmentation affects parasitoids such that pest outbreaks last longer in fragmented than in continuous forests (Roland & Taylor 1997; Roland 2000).

The number of wasp species, but not individuals, was correlated negatively with distance to forest. The most abundant wasp species presumably profit from the abundant food resource for their larvae inside the agroforestry systems (Klein *et al.* 2002a, 2004). Unlike wasps, the number of bee individuals, but not bee diversity, was affected by forest distance, probably because there were only five trap-nesting bee species collected. In tropical landscapes moth species richness has been shown to decrease with increasing distance to natural forest (Ricketts *et al.* 2001), and diversity of coffee flower-visiting bees was negatively correlated with forest distance (Klein *et al.* 2003). Populations of trap-nesting bees and wasps depend mainly on the availability of cavities for nesting sites (Potts *et al.* 2005), so colonization of the exposed traps should be enhanced by the

presence of nearby old trees which provide many nesting cavities. Similarly, an isolation experiment on meadows in Germany showed that trap nests associated with few trees were colonized less than traps with many trees providing source populations (Tschardtke *et al.* 1998).

### HABITAT MANAGEMENT

The number of natural enemy species and the percentage of mortality caused by them were related neither to light intensity nor to the number of plant species, but both response variables greatly decreased with increasing distance to the nearest forest. Wilby & Thomas (2002) showed, with simulation models, that increasing intensification in agricultural systems should decrease the natural enemy diversity, thereby supporting general expectations. Sperber *et al.* (2004) found that richness of parasitized families increased significantly with increasing tree diversity in cacao agroforestry. Forests and near-forest habitats offer a wealth of nesting sites in an undisturbed environment, so populations of natural enemies appear to build up over many years, whereas the highly disturbed environment of agroecosystems may inhibit the build-up of populations of higher trophic levels, because of the lack of nest sites (Tschardtke 2000; Klein *et al.* 2002b).

The number of wasp species was correlated positively with light intensity in the agroforestry systems, whereas the number of wasp individuals was correlated negatively with light intensity. Light inside the agroforestry systems should generally favour nesting activity, and early in the morning and during or shortly after rain, when there is no or little sunshine, the wasp species did not forage (A. M. Klein, personal observation). This negative correlation with light intensity was found, because numbers of the spider wasp *A. levicarinatus*, which inhabited more than 50% of all brood cells, decreased significantly with light intensity. *A. levicarinatus* is a spider-hunting species, and spiders are more abundant in the shaded systems with dense trees and high structural diversity (Klein *et al.* 2002b). The abundance of spiders could be related to the density of branches (Rinaldi & Sanches Rui 2002), which should be also correlated negatively with light intensity. The eumenid wasps, which showed high diversity in our study, are caterpillar-hunters and most of the caterpillars found in their nests feed on cacao leaves and are pests of this species. Some of the eumenid wasp species seem to be adapted to anthropogenic land-use systems, even nesting inside human houses (Klein *et al.* 2002a). Eumenids often profit from increasing land-use intensity (Klein *et al.* 2002a), which usually means increasing pest caterpillar populations, combined with high light intensity (Risch, Andow & Altieri 1983; van Emden 1990; Wilby & Thomas 2002).

The positive relationship between the number of bee individuals and light-intensity could be explained as follows: (1) light intensity is highly correlated with air temperature (see Klein *et al.* 2002a), and bees prefer to

nest in warm and dry sites (Potts & Willmer 1997); and (2) high light intensity favours the growth of herbs, offering flowers during the whole year, whereas perennial crops such as coffee flower for a only short time. Therefore, herbs are important pollen and nectar resources for the bees and, for example, the abundant megachilid bee *H. fulvescens* often foraged on a common herbaceous plant in the family Asteraceae (A. M. Klein, personal observation). In this study, the number of bee individuals was correlated with the number of herb species and the density of herbs, and also with light intensity. The species richness and abundance of trap-nesting bees are often related closely to plant species richness, because heterogeneous pollen and nectar resources usually attract a diverse community of flower visitors (Tschamtkke *et al.* 1998).

In conclusion, the trap-nesting bees and wasps were affected by isolation from natural forest. Populations of higher trophic levels, the parasitoids, responded more sensitively to forest distance than their hosts, as expected for species at higher trophic levels. Parasitoid abundance and richness was not related to abundance and richness of their hosts. Within a 500-m distance the number of parasitoid species decreased from eight to five, and percentage of parasitism from 12% to 4%. These results suggest higher trophic level interactions and indicate a higher diversity of bees and wasps in agroecosystems close to rain forest. With respect to local management, increasing light intensity favoured the number of bee individuals and the number of caterpillar-hunting wasp individuals, but decreased the number of spider-hunting individuals. Therefore, the cutting of branches or trees when the understorey is strongly shaded may enhance diversity and biotic interactions.

### Acknowledgements

Funding for this work was provided by the Deutsche Akademische Austauschdienst (German Academic Exchange Programme) and the Deutsche Forschungsgemeinschaft (German Science Foundation). We thank S. A. Kaisang and S. D. G. Massiri for their careful and laborious analyses of the trap nests, D. Buchori, V. Fuest, G. Gerold, D. Ratnadewi, E. Somba and S. Werner of the German-Indonesian Research Project STORMA (Stability of Tropical Rainforest Margins) for their great support and help, S. Erasmi for providing the satellite data and D. Gabriel and C. Bürger for helping with the view of the land-use map, I. Perfecto, S. van Nouhuys, J. Krauss, J. Tylianakis and three anonymous referees for helpful comments on the manuscript and J. Gusenleitner (Eumenidae), M. Ohl (Sphecidae), K. Horstmann (Ichneumonidae), O. Niehuis (Chrysididae), R. Wahis (Pompilidae) and D. B. Baker (Megachilidae) for species identification.

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Received 19 November 2004; accepted 9 September 2005

### Supplementary material

The following supplementary material is available as part of the full-text online article from <http://www.blackwell-synergy.com>

**Appendix S1.** Natural enemy species and the number of brood cells that were parasitized by the species in 24 agroforestry systems differing in light intensity and forest distance.