Functional diversity of Hymenoptera along a gradient of agroforestry management in Indonesia

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Chapter 1

General introduction

Forest margin in the study area of Toro, showing the forest border of the Lore Lindu National Park (Sulawesi) in the background and cacao agroforestry in the foreground.

Tropical forests, biodiversity and human well-being

Deforestation accompanies human development since centuries. While in historical times forest reduction occurred especially in the temperate zones of the industrialized Europe, major areas with deforestation are currently tropical rainforests (MEA 2005). Taking into account some uncertainties in estimating deforestation rates, due to a lack of detailed remote sensing data, a net annual loss of primary tropical forest worldwide from 1990 – 2000 of 15.2 million hectares is a realistic estimation (FAO 2001). Particularly Southeast Asia suffers from deforestation, with an annual deforestation rate of 0.91 % between 1990 and 1997, compared to Latin America (0.38 %) and Africa (0.43 %) (Achard *et al.* 2002).

Forests, however, provide essential services for human well-being, comprising social, economic, ecological, cultural and spiritual needs (Forest Principles 1992). Maintenance of the world's biodiversity is a major service provided by forest habitats and because all types of services relate to each other in different ways it is crucial for the maintenance of other services (see Chapter: Biodiversity and pollination). Biodiversity does not just respond to changes in climate, resource availability or disturbance, it also has the potential to influence ecosystem processes. The decline of biodiversity has therefore also focused attention on the implications of species losses for the maintenance of ecosystem functioning (Tilman *et al.* 2006). Provision of these services is at risk, when deforestation is ongoing at the current rate.

However, species richness, as one scale of biodiversity, is under threat due to anthropogenically caused extinctions. Even careful estimations indicate a current species extinction rate several orders of magnitude higher than historical background rates (extinctions per million species per year due to natural processes) (Groombridge 1992, Regan *et al.* 2001). This is mainly a result of species loss in tropical forest, where 50 % or even 90 % of the world's species occur in an area representing 6-7 % of the earth's surface (Groombridge 1992). The main drivers of tropical deforestation are agricultural expansion, wood extraction and infrastructure extension with different agricultural activities consuming most of the primary tropical forest area (MEA 2005). Currently, agricultural land is still expanding in 70 % of the world's countries. One approach in conserving tropical biodiversity is bringing forests under protected status, but as it is difficult to put large enough areas of primary forest under total protection and effective protection particularly in developing countries is often hard to implement, the maintenance of forest species in managed forest areas, such as agroforestry systems is of increasing interest.

Agroforestry systems and conservation

Agroforestry systems involve at least one woody perennial plant species and even in the simplest form they are ecologically and economically more complex, than monocropping systems (Nair 1993, Rice & Greenberg 2000). Management systems range from cacao and coffee agroforestry with diverse shade tree layers to low diverse oil palm plantations (Aratrakorn *et al.* 2006). Tropical cacao and coffee agriculture comprise a variety of differently intense used agroecosystems, integrating agroforestry with a high diversity of shadow tree species protecting especially the young crop plants against solar radiation, or unshaded monocultural plantations (Perfecto *et al.* 1997, Perfecto *et al.* 2007). Agroforestry systems offer several environmental services, such as soil improvement, carbon storage, water quality amelioration, flood prevention and conservation of biodiversity (Nair 2007). The potential of agroforestry systems due to the high diversity of the shadow tree community and the floral complexity of a multiple canopy layer including understorey (coffee and cacao) and overstorey (shadow and fruit trees), has focused scientific attention on agroforestry systems for the conservation of animal (Klein *et al.* 2002, Tylianakis *et al.* 2006, Dietsch *et al.* 2007, Steffan-Dewenter *et al.* 2007) and plant species (Backes 2001). The multiple canopy layers in tropical forests are crucial for species richness in the forests, but the contribution of the forest canopy for species richness depends on the taxon under examination. Most authors show highest diversity in the canopy of forested habitats (Erwin 1982, Dial *et al.* 2006), while a few found equal or more species for certain taxa in the understorey (Schulze *et al.* 2001, Stork & Grimbacher 2006). Agroforestry systems perfectly match the requirements of food production and biodiversity conservation in ecoagriculture, but greater understanding of their conservation potential is necessary (Nair 2007). However, traditional coffee and cacao agroforestry is increasingly converted to sun-grown monocultures, thereby putting environmental services at risk (Perfecto *et al.* 1997, Siebert 2002). This land-use intensification has already been shown to reduce biodiversity (Perfecto *et al.* 1996, Donald 2004).

Biodiversity and pollination

Expansion and intensification of agricultural landscapes on the cost of diverse systems such as agroforestry, do not just put species richness at risk, but also ecosystem functions (Perfecto *et al.* 2007, Priess *et al.* 2007, Steffan-Dewenter *et al.* 2007). The link between biodiversity and ecosystem functioning is of increasing interest, as the maintenance of ecosystem functions is a powerful argument for decision makers in conservation of species richness (Hooper *et al.* 2005, Tilman *et al.* 2006). High species richness is hypothesized to increase a particular function due to niche complementarity from species-specific differences in resource use (Tilman *et al.* 1997, Hooper *et al.* 2005, Cardinale *et al.* 2006). A major ecosystem function in agricultural landscapes is the pollination of cash crops, which has recently been related to declining pollinator diversity (Kremen *et al.* 2002, Klein *et al.* 2003). Animal pollination, particularly via the taxon Apidae is extremely important for human food production (Klein *et al.* 2007), but under threat due to anthropogenic activities, reducing pollinator diversity (e.g. Steffan-Dewenter *et al.* 2002, Tscharntke *et al.* 2005, Biesmeijer *et al.* 2006). The reliance on a diverse native bee community for crop pollination is also increasing because managed colonies of the honeybee decline and wild bees may compensate for this (Kremen *et al.* 2002, Klein *et al.* 2003, Klein *et al.* 2007).

Research objectives

The objectives of the present work ‘Functional diversity of Hymenoptera along a gradient of agroforestry management in Indonesia’ were

(1) to evaluate the contribution of agriculture, in particular agroforestry systems, for Hymenoptera richness
(2) assess the importance of different strata for species richness in primary forests and agroforestry
(3) to test the importance of Hymenoptera diversity for ecosystem functioning and
(4) to assess the influence of habitat quality on temporal density patterns of a pest feeding wasp in agroforestry systems.

The study was part of the subprogramme C3 (Plant-insect interaction and biodiversity on cacao in relation to local and regional land-use management) within the research programme SFB 552 ‘Stability of Rainforest Margins in Indonesia’ (STORMA), in the periphery of the Lore Lindu National Park (Sulawesi).

Study region and study systems

The study took place in Central Sulawesi (Indonesia) on the western margin of the Lore Lindu National Park. Long isolation from the mainland and the location between the Wallace and Weber biogeographic line (Audley-Charles 1983) caused high endemism rates for several taxonomic groups on the island of Sulawesi, making it one focus area for global biodiversity conservation (Kessler *et al.* 2005, Sodhi *et al.* 2005, Veddeler *et al.* 2005).

The National Park covers an area of about 2,290 km^2 and includes lowland and montane forests with an altitude range of 200 – 2,610 m above sea level. In 2005 average annual rainfall in the study area was 2480 mm, temperature 24.2 ^{o}C and humidity 84 %.

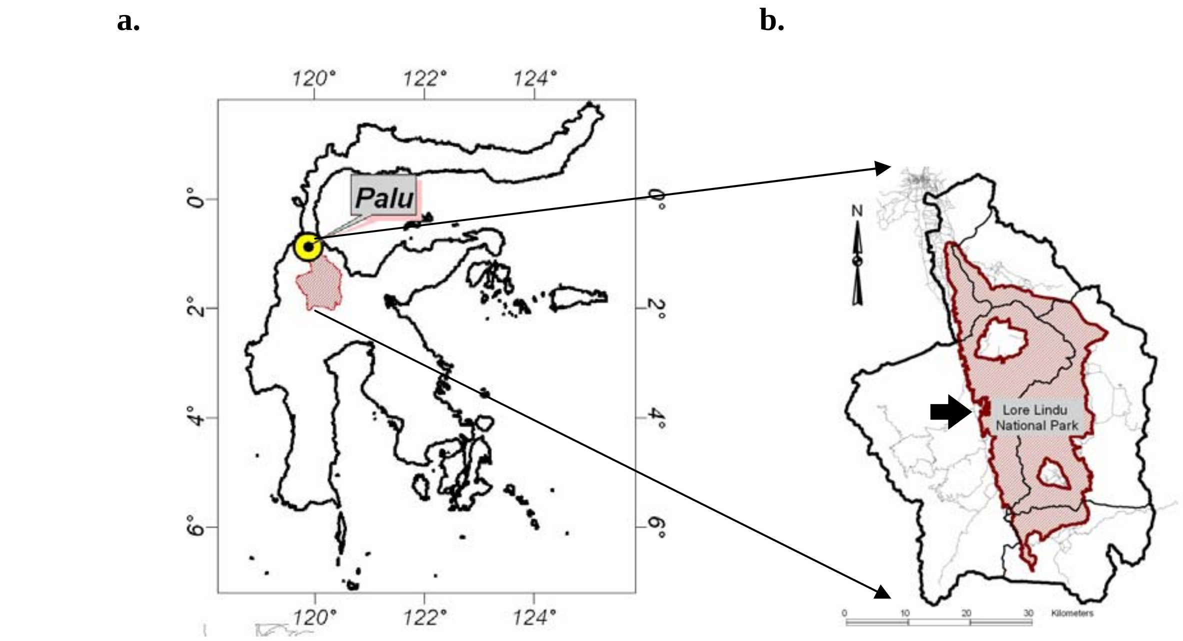

Figure 1: Map of Sulawesi with the whole STORMA research area in pink **a)** and the location of the Lore Lindu National Park in Sulawesi **b)**. The bold arrow is pointing at the exact location of Toro. Maps are provided by Dr. Stefan Erasmi, University of Göttingen.

The Park is surrounded by different land-use systems, comprising agroforestry systems such as cacao (*Coffea* spp.) and coffee (*Theobroma cacao*), irrigated rice fields, slash-and-burn cultivation with annual crops, permanent rainfed cultivation with annual crops, and home gardens with mixed crops. In the 1990s, coffee has been reduced in favour of cacao in Sulawesi and other tropical regions, due to the rising market price of this internationally-traded cash crop, leaving shaded cacao as the major agroforestry system (Belsky & Siebert 2003).

The study sites were situated in the surrounding of the village Toro in the Kulawi Valley (E 120^{o}2’, S 1^{o}30’, 800-1100 masl), 100 km south of Palu, the capitol of the province Central Sulawesi. The landscape is formed by a small scaled mosaic of primary and disturbed submontane forests, agricultural areas, such as cacao agroforestry systems with different land-use intensities and openland, such as pastures, paddy field, fallow land and grasslands. We selected plots comprising primary forests, cacao agroforestry systems and openland.

The primary forest plots were traditionally used for rattan extraction, but no timber extraction occurred and the canopy was closed. The plots were located within the national park and at least 300 m from the forest edge, to avoid edge effects.

The agroforestry systems formed a gradient in land-use intensity, which was according to the composition of shade tree species. We distinguished three different intensities of land-use in the agroforestry systems:

- Low management agroforestry systems include primary forest trees as shade trees, which retained after establishing cacao plantations in the understorey. Cacao is the first cash crop planted in these systems. Large tree density is lower, but the canopy structure resembles that of primary forest more than all other forested habitats.
- Medium intensity agroforestry systems comprise a variety of shade tree species, but they were entirely planted by farmers or regrew after clear cutting. Planted trees include fruit and timber trees. No large trees from primary forests persisted and the canopy cover is less diverse and less dense compared to low intensity systems.
- High intensity agroforestry systems had only a few planted shade tree species, such as *Gliricidia sepium* Jacq. and *Erythrina subumbrans* Hassk.. These legume species were non-native trees, planted to increase soil nitrogen content. The canopy was increasingly open and the duration of the plantation exceeded 20 years.

All agroforestry plots underwent frequent agricultural activities, such as mechanical and rarely chemical herb removal, fertilization with litter ash, urea or TSP (Triplesuper-Phosphate) and pruning of the cacao trees. A dense herb layer remained during most time of the year. Besides cacao, farmers grew a variety of other cash crops in the herb layer and the understorey (e.g. *Ananas comosus* L. Merr., *Capsicum annuum* L., *Coffea robusta* Lind., *Cucumis sativus* L., *Curcuma domestica* Vahl., *Cucurbita moschata* Duch. ex Poir, *Manihot esculenta* Crantz., *Solanum* *lycopersicum* L. and *Vanillia planifolia* Andr.) and many shadow trees also serve for fruit production (e.g. *Arenga pinnata* Merr., *Artocarpus hererophyllus* Lamk., *Durio zibethinus* Murr., *Lansium domesticum* Correa., *Musa paradisiaca* L., *Nephelium lappaceum* L. and *Syzygium aromaticum* M. & P.), making diverse and efficient multi crop plantations out of the agroforestry systems. In some high intensity plots, farmers started to remove all remaining shade trees, perpetuating the trend of land-use intensification and simplification in agroforestry systems.

The openland plots had trees of *Gliricidia sepium* used as living fences and were fallow land or sporadically used for cattle grazing and frequently planted with *Arachis hypogaea* L., *Cucurbita moschata*, *Ipomoea batatas* L. and *Zea mays* L. on small patches. They were closest to the village of all plots and located between paddy fields.

We selected four replicates for each habitat type and each plot had a minimum core area of 30 x 50 meters with homogeneous land-use practices of the mentioned habitat type.

Chapter outline

In the second chapter I analyse the relationship between bee species richness and habitat quality in a tropical forested region. I compared tropical primary forests with different intensities of cacao agroforestry systems and openland in terms of bee species composition, using sweep netting along transect walks. I found highest total bee species richness in the openlands and lowest in the primary forests. However, species estimation and the additive partitioning method revealed that agroforestry systems had higher spatial beta diversity than the other habitat types. In addition, multidimensional scaling revealed that bee species communities in openlands were highly clustered, whereas the forested habitats had a much larger variety. The increased total bee species richness of the agroforestry systems compared to primary forests might be due to medium intensity anthropogenic disturbance and the high spatial heterogeneity of agroforestry systems because of high management diversity in the study area. Our findings point out the high potential of agricultural landscapes for the maintenance and even amelioration of a key functional group in the vicinity of the native habitat.

In the third chapter I investigated the importance of the canopy along a management intensity gradient of forested habitats from primary forest to highly intense managed agroforestry. I used standardized nesting possibilities (trap nests) to evaluate species composition of cavity nesting Hymenoptera in three different forest strata. Species richness in primary forests was highest in the canopy compared to intermediate height and understorey. This pattern reversed with land-use intensity, resulting in highest species richness in the understorey of high intensity agroforestry. Furthermore, agroforestry systems showed high spatial beta diversity and therefore significantly contributed to regional species richness. I discuss the influence of microclimate and food resource availability as the main factors shaping the observed patterns and show the uniqueness of primary tropical forests due to the importance of their canopy for species conservation.

Chapter four addresses the contribution of species and functional richness to pollination and final crop yield due to niche partitioning. I observed and recorded the bee pollinator community in standardized pumpkin plantations in different habitats. Bee species showed characteristic spatiotemporal and size-related flower-visiting traits, allowing for classification of each species in distinct functional groups. Species and especially functional group richness were strongly related to seed set, as a surrogate of crop yield. This indicates increased ecosystem function due to complementary in resource use of different functional groups.

In Chapter five I investigate seasonality of the tropical wasp *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera) along a land-use gradient from primary forest to high intensity agroforestry systems. *R. haemorrhoidale* is a solitary and cavity nesting pest predator and even in high intensity cacao agroforestry highly abundant. The species showed strong seasonality, independent of habitat type, in abundance and body size. I discuss a combination of various reasons for the observed patterns, such as climate, food supply and natural enemies (parasitoids, entomopathogenic organisms).

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Chapter 2

Relative contribution of cacao agroforestry, rainforest and openland to local and regional bee diversity

Apis dorsata (Fabr.) visiting *Hyptis capitata* (Jacq.) in a cacao agroforestry system in Toro, Sulawesi.

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(in prep.)

Summary

Due to their potential in species conservation, agricultural landscapes become increasingly important to counteract global species loss, but little is known about the relative importance of natural habitats and different agricultural areas. We investigated tropical primary forest, cacao agroforestry systems of varying land-use intensity and openland in Sulawesi (Indonesia) in terms of their contribution to the native bee community on different spatial scales. Furthermore, we assessed the influence of canopy cover and flowering plants in the herb layer and understorey of the plots on bee diversity, because these characteristics shaped the habitat gradient from close canopy with few flowering plants in primary forests to non-forested, sun exposed habitats with high floral resources.

Local bee density and diversity were highest in openland, followed by agroforestry systems and were lowest in primary forests, revealing the importance of herbaceous food resources, which were negatively correlated with canopy cover. In contrast, estimated numbers of bee species and beta diversity revealed highest regional bee richness in agroforestry systems, because of high community dissimilarity. The multidimensional scaling supported these findings, as the openland habitats showed highly clustered bee species communities.

In conclusion, the bee community profited from the opening of the landscape as a result of agricultural activities, while agroforestry systems increased bee species richness especially on a regional scale due to high management diversity.

***Keywords*:** Apidae, biodiversity, Hymenoptera, land-use gradient, pollinator community.

Introduction

More than 50 % of the world's forests have been lost, mostly due to expanding agricultural land. This trend is ongoing in 70 % of the countries worldwide (MEA 2005). Deforestation is threatening global biodiversity especially in biodiversity hotspots such as tropical Southeast Asia (Groombridge 1992, Castelletta *et al.* 2000, Giri *et al.* 2003). Many species can utilize both native and agricultural habitats, as shown for moths and mammals in the Neotropics (Ricketts *et al.* 2001, Daily *et al.* 2003). Anthropogenic habitats might therefore be considered in conservation planning to reduce biodiversity loss (Daily 2001, Tscharntke *et al.* 2005 a). In particular coffee and cacao agroforestry, two globally important agricultural systems, receive growing attention for their potential in conservation of biodiversity (Perfecto *et al.* 1996, Klein *et al.* 2002, Tylianakis *et al.* 2006, Perfecto *et al.* 2007, Steffan-Dewenter *et al.* 2007). They can provide appropriate surrogate habitats for many forest species, but the composition of these habitats is crucial for the maintenance of a native species community (Dietsch *et al.* 2007). Agroforestry systems include a range of different land-use intensities, from a diverse shade tree community containing primary forest tree species and a dense canopy cover to plantations with only a few planted shade tree species and low canopy cover (Perfecto *et al.* 2007). High biodiversity in agricultural landscapes is particularly important for the maintenance of ecosystem services, such as pollination (Kremen *et al.* 2002, Klein *et al.* 2003 a) and the most important group performing this ecosystem service are the Apiformes (Klein *et al.* 2007). However, the European honeybee is declining world wide, thereby increasing reliance on the diverse wild bee community for pollinating cash crops (Kearns *et al.* 1998, Klein *et al.* 2003 a, Kremen *et al.* 2004, Klein *et al.* 2007).

Studies relating the influence of disturbance and land-use intensity in different habitats to bee species composition apparently arrive to opposed conclusions. Agricultural intensification led to reduced species richness and abundance of the native bee community in North American watermelon fields (Kremen *et al.* 2002), while high anthropogenic disturbance lowered species richness of stingless bees in tropical forest habitats (Cairns *et al.* 2005). In contrast, bee species richness increased with decreasing forest cover in the landscape and was highest in agricultural fields compared to extensive forest, which resemble the natural habitat in a pine oak heath in a study of Winfree *et al.* (2007). Similarly, bee species richness was higher in disturbed forests, compared to primary forest, in tropical Southeast Asia (Liow *et al.* 2001). Comparative studies of a broad range of habitats along a land-use intensification gradient from primary forests, managed agroforestry systems differing in land-use intensity to openland, and their relative contribution for bee species richness are missing. We expect that agroforestry systems increase species richness and density compared to primary forest due to increased floral density of herbs (including cash crops) and high management diversity. Furthermore, agroforestry systems might maintain higher species richness and density compared to openland, because forested habitats with open canopy offer both floral rewards and more suitable nesting sites for wood-nesting bee species (Klein *et al.* 2003 b).

Methods

STUDY REGIONS AND STUDY SITE

The study was conducted in the western margin of the Lore Lindu National Park in Central Sulawesi (Indonesia) 100 km south of the region's capital Palu. Study sites were located in an area of agricultural activity surrounding the village of Toro (E 120°2', S 1°30', 800-1100 m above sea level) and in the primary forest where the village is embedded in. The landscape covers a mosaic of different habitats, from undisturbed primary and disturbed tropical forests to cacao agroforestry systems of differing management intensity and openland such as grasslands, pastures and paddy fields. We surveyed five different habitat types in our study region, comprising a range of environmental conditions. The five habitat types were primary forest (PF), three different management intensities of cacao agroforestry and openland (OL) such as grassland and fallow land with only few trees. We refer to a plot as a site with homogeneous land-use practices of the mentioned habitat type and with a minimum core area of 30 x 50 m. The cacao agroforestry systems formed a gradient according to the composition of shade tree species and associated canopy cover: LIA = low management intensity agroforestry with natural forest trees as shade trees. MIA = medium intensity agroforestry systems with a diverse shade tree community entirely planted by farmers. HIA = high intensity agroforestry plots with few planted shade tree species, mainly *Gliricidia sepium* (Jacq.) and *Erythrina subumbrans* (Hassk.). Forest distance was not significantly different between habitat types ($r^2 = 0.12$, $F_{3,11} = 0.5$, $p = 0.69$; OA: 113.5 ± 8.6, n = 3; HIA: 93.3 ± 9.9, n = 4; MIA: 115.3 ± 10.5, n = 4; LIA: 105.8 ± 18.9, n = 4). Four replicates were chosen for each habitat type, but we were forced to abandon one primary forest plot and one openland plot. Extensive agricultural activities in these two plots, such as clear cutting and corn cultivation, fundamentally changed the habitat character. Canopy cover was measured with a spherical densiometer (Model-C, Robert E. Lemmon, Forest Densiometers, 5733 SE Cornell Dr., Bartlesville, OK 74006) in one meter height (below cacao tree canopy) from two persons independently at twelve positions within each plot and varied between habitats (primary forest plots: 90.9 % ± 5.1 %, n = 3; low intensity plots: 90.5 % ± 1.9 %, n = 4; medium intensity plots: 85.5 % ± 4.7 %, n = 4; high intensity plots: 78.3 % ± 6.5 % , n = 4 and openland: 16.3 % ± 11.2 %, n = 3). Between cacao and shade trees farmers grew a variety of cash crops. Aubergine (*Solanum melongena* L.), chilli (*Capsicum annuum* L.), clove (*Syzygium aromaticum* L.), coffee (*Coffea robusta* Lind.), cucumber (*Cucumis sativus* L.), curcuma (*Curcuma domestica* Vahl.), pineapple (*Ananas comosus* (L.) Merr.), pumpkin (*Cucurbita moschata* Duch. ex Poir.), tapioca (*Manihot esculenta* Crantz.), tomato (*Solanum lycopersicum* L.) and vanilla (*Vanillia planifolia* Andr.) are among the most frequently planted crops contributing to the floral diversity within the plots. Furthermore, agroforestry systems passed a variety of agricultural activities throughout the year and differed in plot history. Both aspects contribute to the management diversity of agroforestry systems.

SAMPLING OF BEE DIVERSITY

Bees (Hymenoptera: Apiformes) were recorded during the morning between 10.30 and 12.00 a. m. in a standardized way along six random transects each 4 m wide and 30 m long. Each bee was caught if possible and the visited plant was noted. We additionally caught slow flying bees, which were searching for flowers, but we did not consider fast passing bees, as they may be ‘tourists’ that do not belong to the plot specific apifauna. To account for temporal species turnover, we conducted five sampling phases with each plot visited once per phase: 1: 22 March 2005 – 20 April 2005, 2: 26 April 2005 – 03 June 2005, 3: 08 June 2005 – 21 July 2005, 4: 10 January 2006 – 09 February 2006 and 5: 28 February 2006 – 17 March 2006. Affirmation and identification of difficult bee species was done by Stephan Risch from Leverkusen, Germany. Voucher specimens are kept at the Bogor Agricultural University (IPB) in Indonesia. Density of each flowering plant species and flower diversity in the herb layer and understorey were recorded subsequent to each transect walk. Flower density of each plant species per transect was estimated, whereby 1 was equivalent to a single flower of one species and 100 to a species that covers the whole area with many flowers. The six transect walks per observation morning and plot covered almost half of the plot core area (720 m^2). Plant species were identified with the help of Dr. Ramadhanil Pitopang from the Herbarium Celebense at the Tadulako University in Palu (Indonesia) using the local collection and library. For standardization we conducted transect walks only on sunny and calm days, but to test for the effect of minor daily climatic differences on bee species composition, we recorded temperature, humidity and light intensity. Measurements were done at the beginning, in the middle and at the end of each observation morning and then averaged. We used a thermo-, hygro- and luxmeter (Mavalux Digital, Gossen) at a height of 2 m in the centre of the plot. Temperature and humidity were measured in the shadow and light intensity in an area receiving full sun. Furthermore, we measured the slope of each plot with a clinometer (Suunto PM-5/360 PC) at four distances within each plot and the four values were averaged.

STATISTICAL ANALYSIS

In a Spearman's rank correlation matrix, temperature, humidity and light intensity were collinear (temperature & humidity: $N = 86$, $R = -0.86$, $p < 0.001$; temperature & light intensity: $N = 67$, $R = 0.45$, $p < 0.001$; humidity & light intensity: $N = 66$, $R = -0.47$, $p < 0.001$). We therefore used a PCA to reduce the total number of variables and extract one main factor (from now on: "climate"), explaining 75 % of the total variance to be used as a continuous predictor in the following analysis. We conducted two general linear models (GLM) to identify the factors that structure the pollinator community. The models included number of bee species and number of bee individuals as response variables, habitat type and phase as categorical predictors, climate and number and density of flowering plant species as continuous variables. Due to collinearity of density and species richness of flowering plants, we alternated the order of both continuous predictors. Phase was included as random effect. *Post-hoc* tests for differences between habitat types used Tukey's unequal N HSD (Honestly Significant Difference) test. Values per plot and sampling phase of response and predictor variables were used for the statistical analyses. To test whether plant density depends on canopy cover or other plot variables, we conducted a general linear model with plant density as response variable and canopy cover, slope and plot altitude as continuous predictors.

We applied species richness estimation using Michaelis-Menten means (Colwell & Coddington 1994) for each habitat type for a given sample size and calculated the percentage of recorded number of species from estimated number of species. We randomly reduced the number of samples for the agroforestry systems to three, because we had only three replicates for primary forest and openland.

We used the additive partitioning method to test for the contribution of spatial species turnover per habitat type (beta_spatial) and temporal species turnover per habitat type (beta_temporal) to regional gamma diversity (Lande 1996, Crist & Verch 2006, Gabriel *et al.* 2006) such that beta = gamma – alpha diversity. Diversity was partitioned in alpha-diversity (average number of species per plot (= replicate)), spatial beta-diversity (species richness per habitat type minus species richness per plot, averaged per habitat type) and temporal beta-diversity (species richness per habitat type minus species richness per phase, averaged per habitat type). We randomly reduced the number of replicates in the three different agroforestry systems to three. For each alpha, beta_spatial and beta_temporal as response variable, we used one-way ANOVA with habitat type as categorical predictor to test for diversity differences between habitats.

To measure the plant and pollinator community distance between the plots we used the multidimensional scaling method. Each input matrix consisted of a Bray-Curtis similarity index calculated between each plot.

Statistical analyses were carried out in Statistica (StatSoft, Inc. 2004.), version 7. www.statsoft.com.). The Bray-Curtis similarity index and species richness estimation were calculated using EstimateS (Colwell, R.K. 2005, version 7.5. Persistent URL <purl.oclc.org/estimate>). Residuals were tested for a normal distribution and log transformed if necessary. We used type-I (sequential) sum of squares for each model. We give arithmetic mean ± standard error in the text.

Results

In total 1207 bees belonging to 53 species were caught from flowers (86 %) or during search flight for flowers (14 %). We could identify 75 different flowering plant species in all five habitat types, of which 38 species were visited by a bee during transect observations. For the other plant species we can therefore not judge attractiveness for bees and they were not included in the analyses.

The bee community was determined by habitat type and plant density (Table 1a). Bee species richness varied significantly across habitats, with significantly lower bee richness in primary forests (1.54 ± 0.27 species per plot and sampling phase, n = 15) compared to all other habitat types (openland: 9.8 ± 0.92, n = 15; low intensity agroforestry: 4.26 ± 0.53, n = 20; medium intensity agroforestry: 4.85 ± 0.49, n = 20; high intensity agroforestry: 4.45 ± 0.6, n = 20) and significantly higher richness in openland compared to low and high intensity cacao agroforestry systems (Figure 1). Bee richness increased with increasing density of flowering plants (Figure 2), whereas sampling phase, climate and plant richness had no significant influence on bee species richness (Table 1a).

We found similar results for bee density. Habitat significantly influenced bee density. Primary forest habitats had significantly lower and openland has significantly higher bee densities compared to all other habitats (primary forest 2.62 ± 0.64 individuals per plot and sampling phase, n = 15; low intensity 8.58 ± 1.6, n = 20; med intensity 8.4 ± 1.28, n = 20; high intensity 9.3 ± 1.92, n = 20 and openland 43.73 ± 5.58, n = 15). Bee density increased with plant density, whereas sampling phase, climate and plant richness did not influence bee density (Table 1b).

Plant density as the only significant continuous predictor was negatively correlated with canopy cover (Figure 3), but independent of slope and plot height.

Table 1 General linear models for the factors that influence bee species richness a) and density b). Bold letters indicate significant effects.

a)

Bee species richness	Effect	DF	SS	MS	F	P
Habitat	**fixed**	**4**	**15.03**	**3.76**	**14.66**	**< 0.0001**
Phase	random	3	0.04	0.01	0.05	0.99
Climate	fixed	1	0.01	0.01	0.04	0.84
Plant species richness	fixed	1	0.04	0.04	0.16	0.69
Plant density	**fixed**	**1**	**2.16**	**2.16**	**8.42**	**0.006**
Error		50	12.81	0.26		

b)

Bee density	Effect	DF	SS	MS	F	P
Habitat	**fixed**	**4**	**41.46**	**10.36**	**22.91**	**< 0.0001**
Phase	random	3	1.19	0.4	0.87	0.46
Climate	fixed	1	0.04	0.04	0.09	0.77
Plant species richness	fixed	1	0.008	0.008	0.018	0.9
Plant density	**fixed**	**1**	**7.86**	**7.86**	**17.35**	**0.0001**
Error		50	22.64	0.45		

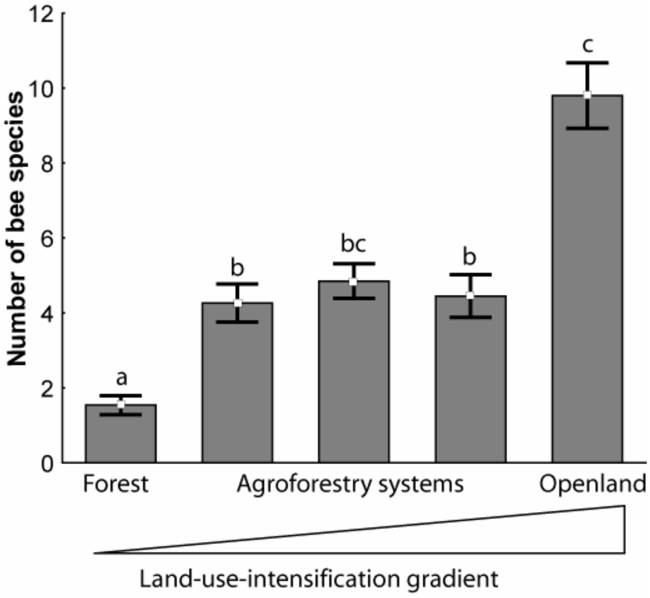

Figure 1 Mean ± standard error of bee species richness along a gradient of land-use intensification per plot and phase. Significant differences between habitat types (p < 0.05) are indicated by different letters.

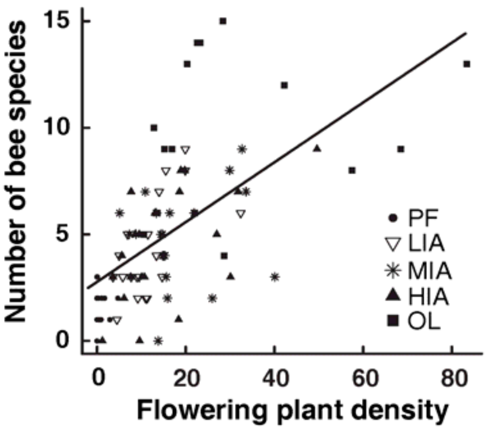

Figure 2 Bee species richness in relation to plant density per plot and phase. Bee species richness increases with increasing plant density. Different habitats are represented by different symbols.

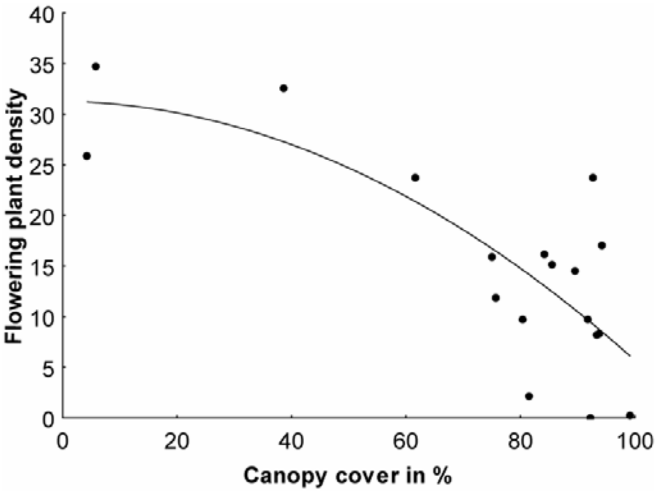

Figure 3 Influence of canopy cover on plant density in the understorey. Plant density, quantified with an index from 1 to 100, is decreasing with increasing canopy cover.

The estimators revealed that all agroforestry systems had higher numbers of species (HIA: 39.1, MIA: 45.4, LIA: 40.8) compared to openland (38.6), when sample size is similar and primary forest had by far the lowest number of species (9.7). Accordingly, the percentage of recorded number of species from estimated number of species was lowest in the agroforestry systems (HIA: 64 %, MIA: 57.3 %, LIA: 53.9) compared to openland (80.2 %) and primary forest (72.2 %).

The additive partitioning showed significant differences between the five habitats in terms of alpha-diversity ($R^2 = 0.58$, $F_{4,66} = 22.74$, $p < 0.0001$). Primary forest plots had a lower alpha-diversity and openland had higher alpha-diversity compared to all other habitat types. Spatial beta-diversity (differences between plots of one habitat type) ($R^2 = 0.75$, $F_{4,10} = 7.52$, $p = 0.0046$) was significantly lower in primary forests compared to all agroforestry systems but not to openland. Temporal beta-diversity (differences between phases of one plot) ($R^2 = 0.79$, $F_{4,20} = 18.53$, $p < 0.0001$) was significantly lower in primary forest plots compared to all other habitat types (Figure 4).

Multidimensional scaling revealed that bee and plant species composition was formed by habitat type, because species communities were ordered along the two dimensions according to land-use intensity (see arrows in Figure 5 a) and b)), whereas low intensity agroforestry (fine rings) was more similar to primary forest plots than medium and high intensity agroforestry. Furthermore, the openland plots were more clustered than all other habitat types and especially the bee community in openland strongly differed from all other habitat types.

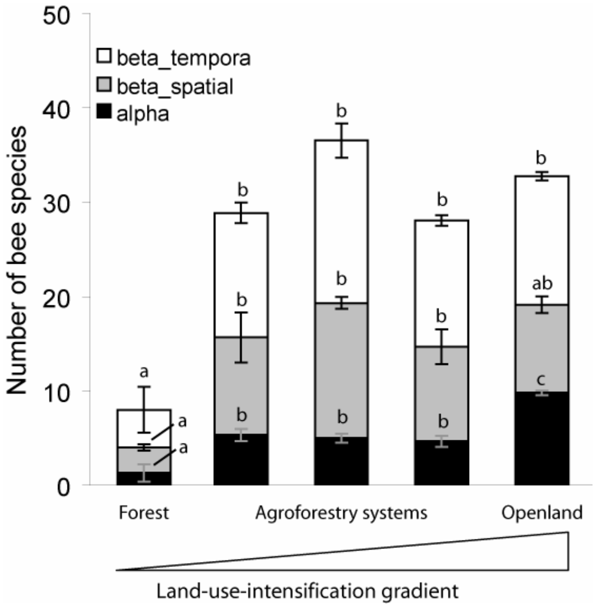

Figure 4 Additive partitioning of species richness along a land-use intensification gradient with the five habitat types. Black bars showing the alpha-diversity fraction, grey bars the spatial beta-diversity (diversity between replicates) and the white bars the temporal beta-diversity fraction (diversity between phases). Different letters indicate significant differences between diversity levels within each habitat type.

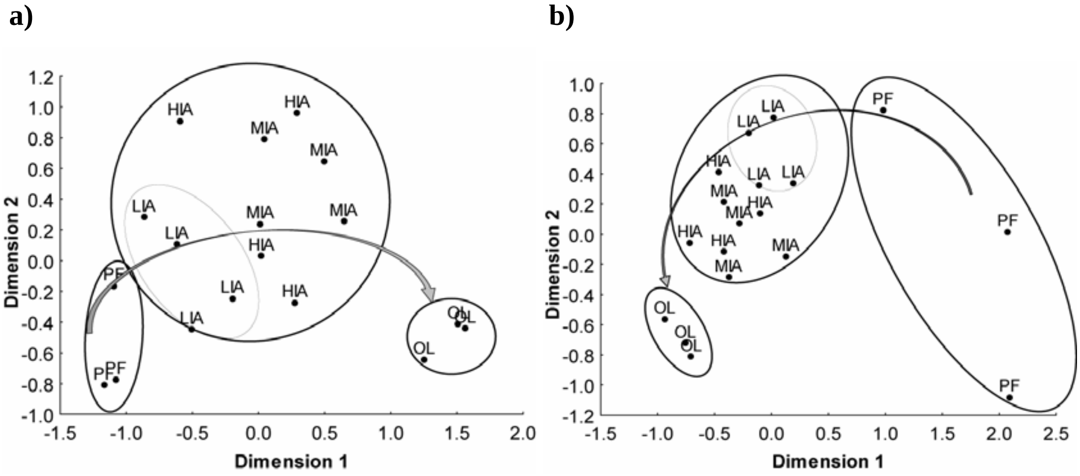

Figure 5 Multidimensional scaling of **a)** bee and **b)** plant species community. Points represent the species composition of a certain habitat (PF – primary forest, LIA – low intensity agroforestry, MIA – medium intensity agroforestry, HIA – high intensity agroforestry, OL – openland) with four and three replicates, respectively, shown by numbers. Larger distances between the points indicate larger distances in species compositions. Rings were used to group primary forests, agroforestry systems and openland. Fine rings comprise the low intensity agroforestry plots to visualize the vicinity of species composition to primary forest. Changes in community composition from forest to low, medium and high agroforestry and up to openland follow the direction of the arrow.

Discussion

Openland plots had highest bee species richness and abundance compared to agroforestry and forest plots, whereas agroforestry management type did not affect bee species richness and abundance. Even though forested habitats are closer to the natural vegetation type than un-forested habitats they do not appear to be major habitats maintaining high species richness (Liow *et al.* 2001, Winfree *et al.* 2007). We show that semi-natural habitats provided better food supply in the understorey due to high flower density (Potts *et al.* 2006), which was negatively correlated with canopy cover (Bruna & Ribeiro 2005, Lindh 2005), resulting in higher bee richness and density. Canopy cover in low intensity agroforestry systems was very similar to primary forests, but flowering plant density was higher and thus bee richness and abundance. However, we sampled the herb layer and the understorey of the forested plots, and sampling the canopy, in particular in the primary forest, may change the picture (Hoehn *et al.* submitted).

Due to the high species richness in tropical regions only a small fraction of the total number of species can be sampled especially in hyperdiverse insect communities (Summerville & Crist 2005). Therefore, we estimated real bee species richness within our habitats and found that all three agroforestry systems had higher numbers of species not just compared to the species poor primary forest, but also openland at a given sample size, contradicting the findings of our first model. The low percentages of recorded numbers of species from estimated numbers of species indicate underestimation of real bee species richness in agroforestry systems, when the increased beta diversity is disregarded. Openland had a significantly higher alpha but not beta diversity compared to all other habitat types. Agroforestry systems had a higher spatial beta diversity compared to primary forests, but not openland. High spatial heterogeneity appeared to be responsible for increased beta diversity in agroforestry systems compared to what may have been expected from the high alpha diversity in openland. The multidimensional scaling supports the positive effect of spatial heterogeneity on bee species richness. Bee communities of openland plots were highly clustered comprising a smaller area compared to forested habitats, which appeared to cover a larger variety of species compositions. Hence, agroforestry systems may maintain high regional bee species richness due to high management diversity and medium intensity disturbance as shown by Winfree *et al.* (2006), enhancing floral abundance and spatiotemporal habitat heterogeneity. Canopy disturbances in primary forests occur frequently due to tree fall gaps, resulting in increased vegetation density and insect richness and compared to interior forest (Dirzo *et al.* 1992, Bruna & Ribeiro 2005, Horn *et al.* 2005, Wunderle *et al.* 2005). Anthropogenic disturbances in agroforestry systems, such as opening of the canopy, appeared to simulate and promote the positive effect of natural tree fall on the plant and thereby the bee community in our study. Therefore, we would have obtained a different picture, if we did not sample the closed primary forest, but forest gaps or edges.

Forested habitats offer nesting sites for many bee species (Klein *et al.* 2003 b, Brosi *et al.* 2007), while openland provides better food resources in the herb layer and bees are known to often bridge different habitats providing different resources (Tscharntke *et al.* 2005 b). Therefore, bee diversity of human-dominated habitats may often depend on large areas of natural habitats providing nesting resources (Steffan-Dewenter *et al.* 2002), but floral resources may be similar or even more important (Westphal *et al.* 2003).

In conclusion, the different habitat types strongly differed in their relative contribution to the bee community. The land-use systems in our human dominated tropical landscape strongly increased local and regional pollinator species richness increasing heterogeneity of the landscape. Local species richness was highest in openland, but the high beta diversity of agroforestry systems levelled off this difference, resulting in similar gamma diversity. However, farmers tend to remove shade trees in coffee and cacao agroforestry, thereby simplifying these systems (Perfecto *et al.* 1996, Steffan-Dewenter *et al.* 2007).

Such reduction of heterogeneity in tropical landscapes will further reduce overall biodiversity and associated ecological function such as pollination service of wild and crop plants provided by the bee communities.

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Chapter 3

Rainforest conversion and agroforestry intensification reverse vertical distribution of Hymenoptera diversity


Cacao agroforestry canopy in Toro, Sulawesi.


Primary forest canopy in the Lore Lindu National Park, Sulawesi.

Patrick Höhn, Ingolf Steffan-Dewenter and Teja Tscharntke

(submitted)

Summary

1. High species richness in tree canopies, compared to understorey, is often assumed to be a clue in understanding tropical biodiversity, while experimental evidence is mixed. Here, we tested the hypothesis that vertical diversity patterns reverse in a gradient from natural rainforest to intensified agroforestry.

2. We studied the variability in vertical distribution patterns of species richness, community composition and trophic interactions of cavity-nesting Hymenoptera along a land-use gradient of tropical forests. We experimentally exposed standardized trap nests in four different habitat types from primary forest to high intensity cacao agroforestry and in three different heights from understorey to tree canopy. We collected 7450 trap-nesting individuals from 32 species and 269 individuals from four parasitoid species attacking *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera).

3. Vertical changes in diversity were contingent on land-use intensity. Forest canopy harboured more species than the understorey, whereas low and medium intensity agroforestry systems showed no stratification and high intensity plots had highest species richness in the understorey. Species composition in primary forests differed from that in agroforestry systems. Agroforestry systems showed similar species compositions within one stratum, indicating vertical preferences of agroforestry species independent of land-use intensity.

4. In contrast to expectations, forest plots showed similar alpha and beta diversity, whereas beta diversity (between sites) was higher in high and medium intensity plots. Apparently, management heterogeneity increased this regional turnover in Hymenoptera richness. Further, forest and high intensity plots did not show higher beta (between strata) than alpha diversity, due to only one high-diversity stratum, i.e. the forest canopy and the understorey in high-intensity agroforestry plots.

5. The observed pattern in species richness and composition from tree canopy to understorey reversed across the management gradient from primary forest to high intensity agroforestry. The changes may be due to vertical food resource distribution. In primary forests, the canopy and in high-intensity agroforests, the herb layer appeared to provide greater resources. In addition high heterogeneity in land-use practices and thereby, high beta diversity of agroforestry systems, contributed to regional biodiversity and should be taken into account in conservation plans, complementing the preservation of primary forest with its unique species composition.

***Keywords*: ** Additive partitioning of biodiversity, agricultural management, bee and wasp diversity, land-use gradient, multidimensional scaling.

Introduction

Conversion of tropical rainforests to agriculture is ongoing at an unprecedented rate, particularly in Southeast Asia (Achard *et al.* 2002, Giri *et al.* 2003). Destruction of natural habitats and human land-use intensification are the most important drivers for biodiversity loss, especially in regions with high proportions of endemic species (Brooks *et al.* 2002). Conservation planning should therefore include low-intensity agroforestry systems as one strategy to reduce biodiversity loss in managed tropical landscapes, since these systems have been shown to provide suitable habitats for numerous forest species (Dietsch *et al.* 2007, Steffan-Dewenter *et al.* 2007). Two globally important agroforestry systems receiving growing attention for their conservation potential, coffee and cacao agroforestry, include shade tree diversity that ranges from highly shaded, highly diverse forest gardens containing primary forest tree species to plantations with only a few planted shade tree species and low canopy cover (Perfecto *et al.* 2007).

The importance of the forest canopy for insect diversity is of increasing interest (Le Corff & Marquis 1999, Schulze *et al.* 2001, Dial 2006, Roisin *et al.* 2006, Stork & Grimbacher 2006), as this vertical component of the habitat appears to be partly responsible for the high species richness of tropical rainforests (Erwin 1982, Fermon *et al.* 2005, Dial *et al.* 2006). In contrast, Stork & Grimbacher (2006) found that beetle diversity does not significantly differ between rainforest canopy and ground in the Australian rainforest. Consequently, variation in the vertical distribution patterns of different taxa may have important implications for management recommendations to improve conservation benefits from agroforestry systems. For example, flower availability in the forest canopy can be expected to result in higher species richness of flower visitors such as bees and wasps (e.g. Apiformes, Eumenidae, Pompilidae and Sphecidae) in the canopy compared to the ground. However, in managed agroforestry systems with a less dense canopy, herbaceous ground vegetation may also support diverse Hymenoptera assemblages (Klein *et al.* 2003). Therefore, we hypothesize that vertical diversity patterns reverse from natural rainforest to disturbed forested land-use habitats, although comparative studies of primary forests and managed agroforestry are lacking. Altered habitat structure might also change species composition in different strata and thus modify biotic interactions such as parasitism and predation, as shown by Tscharntke (1992) and Kaneko (2004). Parasitism might cause hosts to seek enemy free spatial (Scheirs & De Bruyn 2002, Stireman & Singer 2003, Singer *et al.* 2004, Zvereva & Kozlov 2006) or temporal (Strohm *et al.* 2001) refuges.

We investigated whether assemblages of trap-nesting Hymenoptera change in species richness and composition in different vertical forest layers along a land-use gradient from primary tropical forest to agroforestry systems of increasing management intensity. We expected food resource availability to be responsible for the vertical patterns. Collecting and rearing Hymenoptera from standardized traps has proven to be a valuable research technique in landscape ecology (e.g. Gathmann *et al.* 1994, Steffan-Dewenter 2002, Tylianakis *et al.* 2005, 2007), allowing a systematic comparison of habitat and stratum type with respect to community structure and trophic interactions. Parasitism rates were used to test whether enemy free space (forest height, habitat type) was important, or whether parasitism was related to host density (e. g. Tscharntke 1992, Teder & Tammaru 2003).

Methods

STUDY AREA

We conducted sampling in the surroundings of the village of Toro (E 120°2’, S 1°30’, 800-1100 m above sea level) about 100 km south of the region’s capital Palu, on the western margin of the Lore Lindu National Park in Central Sulawesi, Indonesia. Annual rainfall in the study area in 2005 was 2480 mm, average temperature was 24.2 °C and humidity 84 %. The landscape in this area is dominated by primary and disturbed tropical mountain forests, cacao agroforestry systems of differing intensity, and openland such as grassland and paddy fields.

STUDY DESIGN

We selected plots representing a gradient in land-use intensity, ranging from closed and diverse primary forests with high buffering abilities for microclimatic conditions, to high intensity agroforestry systems. The habitat types were (A) primary forest and (B, C, D) three different intensities of cacao agroforestry. Trap nest were placed within an area of 30 x 50 m of each habitat plot. The cacao agroforestry systems formed a gradient according to the composition of shade tree species: B = Low management intensity agroforestry with primary forest trees as shade trees. C = Medium management intensity systems with a diverse shade tree community planted by farmers. D = High management intensity plots with only a few planted shade tree species (mostly the legume trees *Gliricidia sepium* (Jacq.) and *Erythrina subumbrans* (Hassk.)). Land-use practices within the agroforestry plots comprised mechanical and chemical herb removal and fertilization (Appendix Table 1), whereas a dense herb layer persists during most of the year. Four replicates were chosen for each habitat type. To test whether the density of flowering plants influenced the vertical species distribution of Hymenoptera, we estimated density of flowers in the herb layer along six transects, each 4 m wide and 30 m long in the core area of the study plot. The scale ranged from one (a single flower of one species) to 100 (a species that covered the whole area with many flowers). Estimation of flower density was accomplished on three visits per plot (except for one B plot with only two visits), with each visit covering almost half of the plot's core area (720 m^2).

TRAP NESTS

Trap nests offer standardized nesting sites for above-ground nesting bees and wasps and can therefore be used to experimentally study these insects (Figure 1). They were constructed from PVC tubes with a length of 28 cm and a diameter of 14 cm. Internodes of the reed *Saccharum spontaneum* (L.) (Poaceae) with varying diameter (3 – 25 mm) and a length of 20 cm were inserted into these tubes to provide nesting sites (following Tscharntke *et al.* 1998). Twelve trap nests per plot (four in each stratum) were installed from October 2004 till September 2005 in three different heights from understorey (U) and intermediate tree height (I) to the canopy (C), where we placed the trap nests with a crossbow and a line. Trap nests were checked every month and bee and wasp larvae were reared for later identification. Understorey was defined as below the cacao tree canopy and trap nests were placed 1.5 m above ground. Intermediate height trap nests were placed above the cacao tree canopy and below the shade tree canopy (four meters above the ground in high intensity plots and seven meters in primary forest, depending on canopy structure).

Due to technical constraints we placed the canopy trap nests in the lower part of the shade tree canopy. Here, trap nest heights varied between habitat type due to different canopy heights, with higher nests in primary forests (19.13 ± 0.44 m, n = 16) and low intensity agroforestry systems (20.89 ± 0.75 m, n = 16) and lower nests in medium (16.36 ± 0.62 m, n = 16) and high intensity agroforestry systems (15.29 ± 0.84 m, n = 16). Sticky glue was applied every month to the edge of the PVC tube to deter ants from colonizing the trap nests. Individuals from the four trap nests per plot and stratum and the whole year were pooled for analysis.

Figure1 Understorey trap nest in a cacao agroforestry system.

STATISTICAL ANALYSIS

Stratification within habitats: To test for differences between strata and habitat type we used mixed effects models for each habitat type with species richness as response variable and plot (random factor) and stratum (fixed factor) as categorical predictors. We use the term "abundance" for the number of brood cells in the trap nests. We fitted a mixed-effects model with flower density as dependent variable, and habitat type (fixed effect), plot (random effect nested in habitat type) and plot visit (fixed) as categorical predictors.

Community distance between habitats and strata: We used multidimensional scaling to measure community similarities between habitats and strata. The Bray-Curtis similarity index between each height in each habitat type was used for the input matrix.

Additive partitioning of diversity within region and habitat type: We used the additive partitioning method such that beta = gamma – alpha diversity, to test the contribution of stratification and replicate to the overall diversity per habitat type (Lande 1996, Crist & Veech 2006, Gabriel *et al.* 2006). We partitioned diversity per habitat type in alpha-diversity (average number of species per plot (= replicate) and height), between-plot-diversity (beta-plot) and between-strata-diversity (beta-strat) to test the contribution of stratification to species richness in different habitat types. For each alpha, beta-strat and beta-plot diversity, we used one-way ANOVA with habitat type as categorical predictor to test for diversity differences within habitat.

Parasitism rate: To analyze whether parasitism rates changed between different heights and habitats we fitted a mixed effects model with parasitism rate of the most abundant eumenid wasp host *Rhynchium haemorrhoidale* (F.) as the dependent variable, and habitat type (fixed effect), plot (random effect nested in habitat type) and strata (fixed) as categorical predictors. We considered only parasitoid species which actively entered the nests (e.g. *Chrysis* sp.) and did not consider the few species which got into the nests via phoresis (transportation into the nest on the body of the nest building adult e.g. Trigonalyidae, Ripiphoridae). We used Spearman’s rank correlation to test whether parasitism rate depended on host density.

ANOVA, GLM and multidimensional scaling were carried out in Statistica (StatSoft, Inc. 2004, version 7. www.statsoft.com.). The Bray-Curtis similarity index was calculated using EstimateS (Colwell, R.K. 2005, version 7.5. Persistent URL <purl.oclc.org/estimate>). All residuals were tested for a normal distribution and transformed if necessary. We used type-I (sequential) sum of squares for each model. We give arithmetic mean ± standard error in the text.

Results

In total we found 7,450 brood cells of 33 species including Apiformes, Eumenidae, Pompilidae and Sphecidae. The eumenid wasp *Rhynchium h.* (with the two subspecies *R. h. haemorrhoidale* (Fabricius) and *R. h. umeroatrum* (Gusenleitner)) accounted for 72 % of all trap-nesting individuals (Appendix Table 2). We also found 269 parasitoids of *R. haemorrhoidale* coming from four species (*Chrysis* sp. 1 (*smaragdula* group), *Chrysis* sp. 2 (*angolensis* group), one ichneumonid wasp species and *Leucospis* sp.).

STRATIFICATION OF SPECIES RICHNESS WITHIN HABITAT TYPES

Species richness in primary habitats was strongly determined by stratum ($r^2 = 0.67$, $F_{2,6} = 10.5$, $p = 0.01$). Tree canopies had significantly more species per site (4.5 ± 0.65, n = 4) compared to the understorey (1.5 ± 0.5, n = 4) (Figure 2). In contrast, species richness in high intensity plots was higher in the understorey (7.5 ± 0.87, n = 4) compared to the higher canopy (4.5 ± 0.29, n = 4; $r^2 = 0.53$, $F_{2,6} = 11.57$, $p = 0.009$). There was no significant stratification in species richness in low ($r^2 = 0.21$,

$F_{2,6}$ = 0.92, p = 0.45) and medium intensity (r^2 = 0.19, $F_{2,6}$ = 0.74, p = 0.52) agroforestry systems. Density of flowering plants in the understorey was significantly lower in primary forests (3.13 ± 1.1 %, n = 4) compared to the three agroforestry systems (B: 12.24 ± 1.43 %, C: 14.21 ± 1.18 %, D: 13.24 ± 1.96 %, n = 4 respectively; r^2 = 0.47, $F_{3,29}$ = 6.7, p = 0.007).

COMMUNITY SIMILARITY OF HABITAT TYPES AND STRATA

Multidimensional scaling showed distinct species compositions between agroforestry systems and primary forests (Figure 3a)). Agroforestry systems were found to cluster independent of stratum, whereas primary forest had a different species composition with higher values along the dimension 1 axis. Within primary forests, species composition in the understorey was very different to composition at intermediate and canopy heights along the dimension 2 axis. We also analysed stratification within agroforestry systems separately after removing primary forest sites from the data set. Strata in agroforestry systems were ordered along the dimension 1 axis (Figure 3b)). Especially high and medium intensity plots showed similar species compositions within the same stratum (bold rings Figure 3b)).

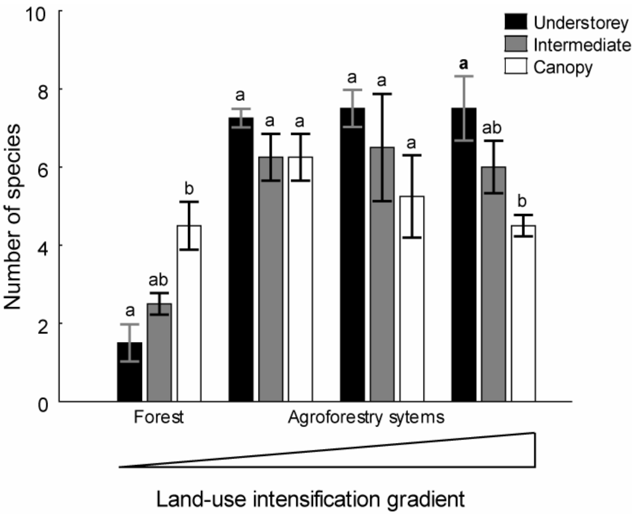

Figure 2 Mean ± standard error of species richness depending on habitat type and vertical stratum. Significant differences between strata within each habitat type ($p < 0.05$) are indicated by different letters. Black bars stand for understorey, grey bars for intermediate height and white bars for canopy.

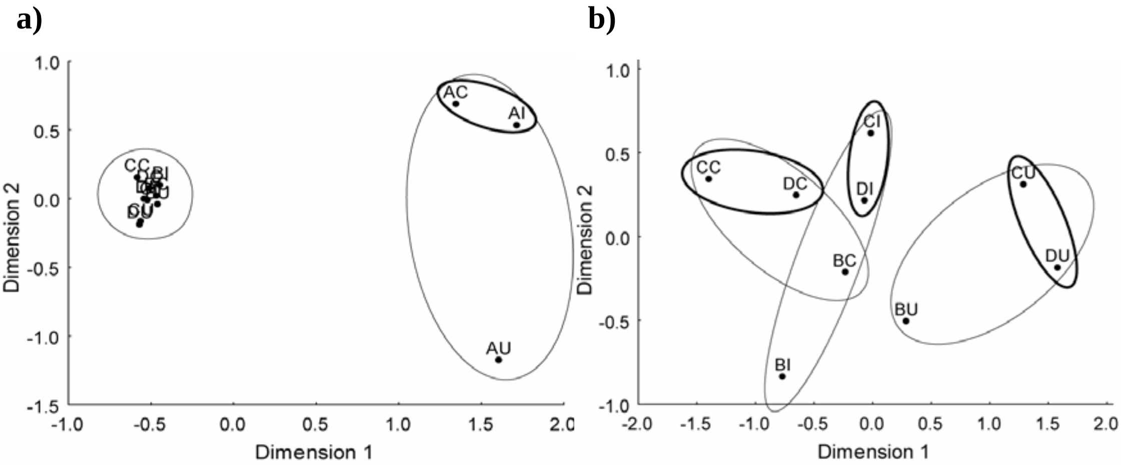

Figure 3 Multidimensional scaling of trap-nesting species with points representing the species composition of a certain stratum (U - understorey, I - intermediate height, C - canopy) in each habitat type (A – primary forest, B - low intensity agroforestry, C – medium intensity agroforestry, D – high intensity agroforestry). Higher distances between the points indicate higher distances in species compositions. **a)** All four habitat types are illustrated. Fine rings comprise primary forest and agroforestry systems respectively. The bold ring comprises the more similar intermediate and canopy strata of the primary forests. **b)** Only agroforestry systems are illustrated. Fine rings comprise one stratum of the three agroforestry system types. Bold rings comprise the more similar high and low intensity plots of one stratum.

ADDITIVE PARTITIONING OF SPECIES RICHNESS WITHIN REGION AND HABITAT TYPE

Primary forest and low intensity plots did not show differences in alpha and beta diversity (Primary forest: $r^2 = 0.28$, $F_{2,16} = 3.13$, $p = 0.07$; low intensity plots: $r^2 = 0.12$, $F_{2,16} = 1.1$, $p = 0.35$). Alpha diversity was significantly lower than between plot diversity in medium (alpha diversity: 6.4 ± 0.51, n = 12; between plot diversity: 12 ± 0.87, n = 4; $r^2 = 0.63$, $F_{2,16} = 13.79$, $p = 0.0003$) and high intensity agroforestry plots (alpha diversity: 6 ± 0.46, n = 12; between plot diversity: 10.5 ± 0.65, n = 4; $r^2 = 0.52$, $F_{2,16} = 8.75$, $p = 0.003$). Further, alpha diversity was significantly lower compared to between strata diversity only in medium intensity plots (between strata diversity: 10.3 ± 1.45, n = 3) (Figure 4).

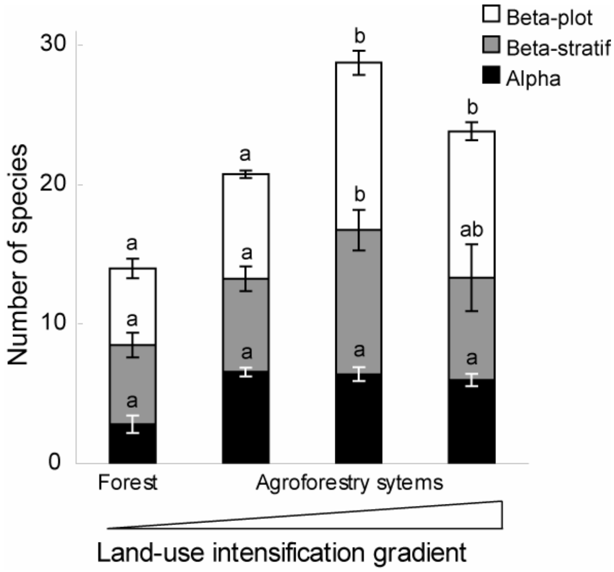

Figure 4 Additive partitioning of species richness within the four habitat types, with the black bar showing the alpha- diversity partition, grey bar the beta-diversity partition of between strata diversity and the white bar the beta-diversity partition of between plots (replicates) diversity. Different letters indicate significant differences between diversity levels within each habitat type.

PARASITISM RATE

Parasitism rate of the most abundant eumenid wasp *R. haemorrhoidale* was not influenced by habitat ($r^2 = 0.17$, $F_{3,21} = 2.16$, $p = 0.14$) nor by height ($r^2 = 0.068$, $F_{2,21} = 1.64$, $p = 0.217$) or plot ($r^2 = 0.32$, $F_{12,21} = 1.3$, $p = 0.288$), but Spearman's rank correlation showed a strong positive correlation between parasitism rate and host density ($R = 0.42$, $p = 0.007$). We found similar results when we included all hosts and parasitoids (16 species) in the mixed effects model (habitat: $r^2 = 0.01$, $F_{3,30} = 0.138$, $p = 0.94$; height: $r^2 = 0.04$, $F_{2,30} = 1.12$, $p = 0.34$, plot: $r^2 = 0.39$, $F_{12,30} = 1.79$, $p = 0.01$).

Discussion

Our results showed that the vertical changes of Hymenoptera richness from the canopy to the understorey reversed from primary forests to high intensity agroforests. Hence, vertical biodiversity patterns can be mixed depending on the habitat type studied. This may be why published evidence reports findings from taxa showing highest diversity in the canopy (Erwin 1982, Fermon *et al.* 2005, Dial *et al.* 2006), whereas others found equally or even more species on the ground, for example in Coleoptera (Stork & Grimbacher 2006), fruit-feeding nymphalids (Schulze *et al.* 2001) and termites (Roisin *et al.* 2006). In agroforestry systems with high land-use intensity species richness was highest in the understorey, presumably due to the thin canopy allowing a rich herb layer, while low and medium intensity habitats were intermediate with no stratification of species richness. In terms of species community composition, primary forest plots differed in all three strata from agroforestry systems, due to changing species identity and abundance (total numbers of individuals: A - 182, B - 2021, C - 2550, D - 2697). However, vertical stratification in species composition of agroforestry systems was much more pronounced than the effect of agroforestry type, especially when only medium and high intensity plots were considered (Figure 3b). Consistency in species occurrence within agroforestry strata is well shown by species like *Sceliphron rufopictum* (Sm.) and *Subancistrocerus clavicornis* (Sm.), which have highest abundances in the canopy independent of agroforestry type, while species like *Chalybion* sp. and *Pison* sp.1 were consistently concentrated in the understorey (Appendix Table 2). Thus, differences in shade tree species composition appeared to be less decisive than the effect of strata in agroforestry systems. Following Stork & Grimbacher (2006), Rader & Krockenberger (2006) and Schulze *et al.* (2001), we suggest that changes in vertical species richness and composition are due to vertical shifts in resource availability. Food resource availability for pollen and nectar feeding insects is highest in the sun-exposed and flower rich canopy of a primary forest (Schulze *et al.* 2001), whereas in high intensity plots the understorey receives more sunlight allowing the development of a dense flowering herb layer. The canopy in high intensity plots consists of a few rarely flowering tree species and therefore provides only temporary food sources, whereas high tree diversity can assure a continuous nectar supply in a natural tropical forest or agroforest canopy. Several cavity-nesting species, for example *R. haemorrhoidale*, *Auplopus levicarinatus* (Wahis) and *Epsilon manifestatum crassipunctatum* (Gus.), occurred mainly in the canopy of the primary forests, while they had highest abundances in the understorey of agroforestry systems (Appendix Table 2). For the same reason, stratification might have been weaker in medium and low intensity plots, where nectar sources can be assumed to be more similarly distributed among strata. Food supply also appeared to be responsible for differences in species composition between understorey and the canopy in primary forests (Figure 3a), as many species appeared to depend on easy nectar supply in strata (see above), and few to the shaded primary forest understorey (*Megachile* sp.2). In addition to food resource distribution, nesting site availability and changes in microclimate such as wind and temperature may have influenced vertical preferences (Szarzynski & Anhuf 2001, Potts 2005). Solar radiation and temperature are known to influence Vespidae in terms of nest building and foraging activity (Ishay & Lior 1990, Elisei *et al.* 2005). A relation between strata and diversity might therefore be due to the influence of canopy cover on climatic conditions.

In contrast to our expectation, beta-diversity values per stratum were not higher in primary forest plots. The relatively low beta diversity in primary forest plots might be due to the dominance of the canopy, where most species occurred. In contrast, medium intensity plots showed significant higher beta than alpha diversity values, presumably because of similar dominance of each vertical stratum and a corresponding high vertical species turnover. In high intensity plots understorey becomes increasingly dominant with a similar effect like for primary forests and decreasing beta diversity values. In a comparison across habitat type, primary forest plots and low intensity agroforestry systems did not show higher beta diversity than medium and high intensity plots. Natural tropical forests are known to show patchy distribution of species (trees: He *et al.* 1997, carabids: Lucky *et al.* 2002), so our unexpected results indicate that agricultural habitats can contribute to high regional species turnover. The heterogeneity of historical (antecedent crops) and recent management (fertilizing, partial herb removal within the plots) of the medium and high intensity plots might be responsible for community dissimilarity among plots of the same habitat type (Appendix Table 1). However, primary forests are known to often act as a species source for agroforestry systems (Duelli & Obrist 2003, Floren & Deeleman-Reinhold 2005, Klein *et al.* 2006). Insect species that require primary habitats or late successional stages (Yu *et al.* 2006) and habitats with low disturbance levels (Tovar-Sanchez *et al.* 2004) may spillover across habitat edges to nearby agroecosystems (Bianchi *et al.* 2006, Rand & Louda 2006).

Parasitism rate of *R. haemorrhoidale* was not influenced by habitat type or stratum. Hosts in primary forests and agroforests as well as in the canopy and understorey were similarly attacked by parasitoids, so that an enemy free space could not be found for this predaceous wasp, as found for phytopagous arthropods (Scheirs & De Bruyn 2002, Rossbach *et al.* 2006). The parasitoids were highly mobile (personal observation), actively searching for kairomones (Hoffmeister *et al.* 2000) and appeared to have easy access to all habitats and heights. Host density proved to be the only predictor of parasitism rate, supporting for example, findings in Lepidoptera (Costamagna *et al.* 2004, White & Andow 2005, Xuereb & Thiery 2006).

In conclusion, primary forest canopy was far more important for Hymenoptera richness than the understorey, contrasting with the vertical distribution in high intensity agroforestry. The relative importance of canopy richness decreased along the studied gradient in land-use intensity. Food resource availability appeared likely to be an important factor forming vertical pattern of species richness across this gradient of forested habitats, but also microclimatic conditions and nesting site availability might differ between strata. In addition, agroforestry habitats due to their varying history and land-use practices, greatly contributed to beta diversity, so the diversity of management practices should therefore be considered in regional conservation programs.

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Appendix

Table 1 Plot history and land-use practices of each replicate per habitat type according to a census of the plot owners in 2005.

Habitat /Replicate	Antecedent crop planted	Fertilizing method	Removal of the herb layer (times per year)
B1	Coffee and sugar palm	Litter ash	mechanical (3 x)
B2	Coffee	Nothing	mechanical (4 x)
B3	Coffee	Nothing	mechanical (1 x)
B4	Coffee	Nothing	mechanical (n. s.)
C1	unknown	Litter ash	mechanical (25 x)
C2	Primary forest	Nothing	mechanical (4 x)
C3	Clove	Rotting litter	mechanical (4 x)
C4	Coffee, clove, peanut, corn and others	KCL and Urea	mechanical and chemical (3 x)
D1	Coffee	Nothing	mechanical (4 x)
D2	Corn	Urea and TSP*	mechanical and chemical (3 x)
D3	Paddy	Nothing	mechanical (4 x)
D4	Homegarden	Urea and TSP*	mechanical (3 x)

*Triplesuper-Phosphate

Table 2 Trap nest species, trophic level (Poll - pollinator, Pred 1 - first order predator, Pred 2 - second order predator, Paras - parasitoid) and number of individuals per habitat type (A - primary forest, B - low intensity agroforestry, C - medium intensity agroforestry, D - high intensity agroforestry) and stratum (C - canopy, I - intermediate height, U - understorey).

Species	**Troph. level**	**AC**	**AI**	**AU**	**BC**	**BI**	**BU**	**CC**	**CI**	**CU**	**DC**	**DI**	**DU**
Anthidiellum smithi	Poll							3					
Auplopus humilis	Pred 2					3							6
Auplopus levicarinatus	Pred 2	10	11		5	17	23		16	99	7	3	53
Auplopus wallacei	Pred 2	7	9	4	15		16		2	3		2	
Chalicodoma aterrima	Poll	8	2		25	19	8	7	14	10	9	15	12
Chalicodoma **sp.**	Poll										4		
Chalicodoma terminalis	Poll	2			7	13	22	1		1	5	9	15
Chalicodoma tuberculata	Poll					3	3	1		1			
Chalybion	Pred 2	2		1	76	101	127		19	48	19	19	87
Chrysis **sp. 1 (*angolensis* group)**	Paras				12	18	33	3	14	30	12	26	51
Chrysis **sp. 2 (*smaragdula* group)**	Paras					1		12	14	4	7	4	24
Delta campaniforme gracilior	Pred 1							3					
Epsilon manifestatum crassipunctatum	Pred 1	12			11	30		48	94	119	10	16	78
Epsilon vechti	Pred 1									1			
Heriades **sp.**	Poll							38					
Hylaeus **sp. (Subgenus: *Hoploprosopis*)**	Poll						15		2				
Ichneumonidae	Paras				2						1		
Isodontia aurifrons	Pred 1	1										1	
Isodontia cestra	Pred 1				4		10	9	8	16		7	13
Isodontia **sp.**	Pred 1												1
Leucospis **sp.**	Paras						1						
Megachile **sp. 2 (Subgenus: *Megachile*)**	Poll	8	11	58			5						
Megachile **sp. 1**	Poll	4				13	11		1	7	6	6	1
Pepsis **sp.**	Pred 2												1
Phimenes fulvipenne	Pred 1							1					1
Pison **sp. 1**	Pred 2					22	42			6			41
Pison **sp. 2**	Pred 2				3								
Rhynchium atrum atrum	Pred 1							1				27	2
Rhynchium haemorrhoidale	Pred 1	24			478	307	555	319	509	1013	419	556	1187
Sceliphron rufopictum rufopictum	Pred 2				12		3	12		7	18	17	1
Subancistrocerus clavicornis	Pred 1	4			5			16	21		14		
Trypoxylon **sp. 1**	Pred 2					3	7						
Trypoxylon **sp. 2**	Pred 2							5				8	
Trypoxylon **sp. 3**	Pred 2					1		8					
Trypoxylon **sp. 4**	Pred 2		4										
Trypoxylon **sp. 5**	Pred 2								55	1			
Zethus celebensis	Pred 1								3				

Chapter 4

Spatiotemporal complementarity of a pollinator community increases crop yield

Lasioglossum halictoides (Smith) visiting a flower of *Cucurbita moschata* (Duch. ex Poir.) in a pumpkin plantation.

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(submitted)

Abstract

Functional complementarity is one of the central mechanistic explanations provided for positive biodiversity-ecosystem functioning relationships, but little empirical evidence for complementarity within functional animal groups exists. This study related differences in functional traits of pollinating bees to the seed set of obligately cross-pollinated pumpkin across a land-use intensity gradient from tropical rainforest and agroforests to grassland. Pollinator diversity, but not abundance, was positively related to seed set of pumpkin. Diversity of functional groups (based on species-specific differences in flower visitation traits: height and time of flower visitation, body size-related behaviour) explained even more of the variance in seed set (r^2 = 45 %) than did species richness (r^2 = 32 %) highlighting the importance of complementarity. These results provide the first empirical evidence for spatiotemporal and behavioural mechanisms via which high natural pollinator diversity can increase pollination success in natural ecosystems.

***Keywords*:** Biodiversity, complementary resource use, crop pollination, ecosystem services, functional diversity, habitat modification, Hymenoptera, Indonesia, land-use management.

Introduction

Global biodiversity decline has focused attention on the implications of species losses for the maintenance of ecosystem functioning (Hooper *et al.* 2005, Balvanera *et al.* 2006, Tilman *et al.* 2006). Animal pollination contributes to 35 % of global food production (Klein *et al.* 2007), but anthropogenic activities such as habitat loss, habitat fragmentation, land-use intensification and use of agrochemicals have adverse effects on pollinator diversity (e.g. Steffan-Dewenter *et al.* 2002, Tylianakis *et al.* 2005, Biesmeijer *et al.* 2006), putting crop pollination services at risk (Kearns *et al.* 1998, Kremen *et al.* 2002, Steffan-Dewenter *et al.* 2005, Tscharntke *et al.* 2005). The most important group performing this service are the Apiformes (Klein *et al.* 2007), but a world-wide decline in the number of managed colonies of the European honeybee has increased reliance on diverse communities of wild bees for supplying crop pollination services (Kearns *et al.* 1998, Klein *et al.* 2003 (b), Kremen *et al.* 2004, Ricketts 2004, Shuler *et al.* 2005, Klein *et al.* 2007).

Recent studies have related declining pollinator diversity to the ecosystem function of pollination (Kremen *et al.* 2002, Klein *et al.* 2003 (b)). The literature about the biodiversity-ecosystem functioning relationship suggests that diverse assemblages might function better due to niche complementarity (Hooper *et al.* 2005, Balvanera *et al.* 2006, Cardinale *et al.* 2006), whereby a combination of many different species can extract more resources in space and time than a species-poor community (Cardinale *et al.* 2004, Fargione & Tilman 2005, Hooper *et al.* 2005, Cardinale *et al.* 2006, Fontaine *et al.* 2006). The importance of this mechanism in natural pollinator communities is unknown. Pollinator communities might be structured by behavioural niche differentiation, but little is known about the pollinating habits of individual bee species. However, Larsen *et al.* 2005 used pollen deposition as a surrogate for pollination efficiency, and suggested that the presence of a single but effective species may be more important than niche complementarity. In most cases, pollinator abundance and flower visitation frequency have often been related to pollination success (Klein *et al.* 2003 (a), Morandin & Winston 2005, Vázquez *et al.* 2005, Degrandi-Hoffman & Chambers 2006, Morandin & Winston 2006). Therefore, the effect of pollinator diversity on pollination rates needs to control for possible covariation between diversity and abundance.

Functional diversity has been suggested to be the most important component of diversity (e.g. Tilman *et al.* 1997, Hulot *et al.* 2000, Lavorel & Garnier 2002) and a common approach to test the effects of biodiversity on ecosystem functioning is experimental manipulation of functional guild diversity (e.g. Lanta & Leps 2006, Moretti *et al.* 2006, Scherber *et al.* 2006). Species are often assigned to functional guilds based on a priori expectations of complementarity due to taxonomic, physiological or morphological traits. This approach has been mostly used for plant species (e.g. Tilman *et al.* 1997, Hooper & Dukes 2004, Roscher *et al.* 2004, Fargione & Tilman 2005) but also for pollinators (Fontaine *et al.* 2006). Here we test the effect of pollinating bee species richness and functional diversity on the number of seeds per fruit of a crop plant, pumpkin *Cucurbita moschata* Duch. ex Poir., in different agricultural habitats (grassland, agroforest and forest). We compare the bee species in terms of their behaviour (Chagnon *et al.* 1993), and quantify preferred pollinating height, the time of day at which they are active, and body size, which is strongly related to behaviour within and between pumpkin flowers (Table 1). We then use statistically significant differences in these parameters to group species into post-hoc functional guilds, and relate the effect of pollinator species and functional guild diversity to pollination success.

We show that habitat modification affects species richness of pollinators, which in turn promotes pollination success of pumpkin. More importantly, however, we show for the first time that quantitative species-specific differences in pollinator traits, such as spatiotemporal species turnover and behavioral differences during flower visitation, underlie this positive effect of biodiversity on ecosystem functioning.

Methods

The study was conducted on the western margin of the Lore Lindu National Park in Central Sulawesi (Indonesia) in the surroundings of the village Toro (E 120°2’, S 1°30’, 800-1100 m above sea level) about 100 km south of the region’s capital Palu. The land-use in this area is small scaled and dominated by natural and disturbed tropical forests, cacao agroforestry systems of differing management intensity, grasslands and paddy fields. As no honey bees are managed in this region, farmers completely rely on pollination services provided by the diverse native bee community.

We selected 18 study plots in five different habitat types, which covered a range of environmental conditions and differed in the diversity of pollinator assemblages. The five habitat types were natural forest, three different management intensities of cacao agroforestry and openland with few trees. We refer to a plot as a site with homogeneous land-use practices of the mentioned habitat type and a minimum core area of 30 x 50 m. The cacao agroforestry systems formed a gradient according to the composition of shade tree species: - low management intensity agroforestry with natural forest trees as shade trees (low-intensity). - Medium intensity systems with a diverse shade tree community planted by farmers (medium-intensity). - High intensity plots with few planted shade tree species (*Gliricidia sepium* (Jacq.) and *Erythrina subumbrans* (Hassk.)) (high-intensity). The number of shade tree species was strongly correlated with canopy cover (Spearman: R = 0.609, n = 18, p = 0.0073) and corresponding microclimatic conditions such as temperature (Spearman: R = -0.489, p = 0.0001) and humidity (Spearman: R = 0.705, p < 0.0001). Four replicates were chosen for each habitat type, but we were forced to abandon one plot in the natural forest and one plot in the openland, as experimental pumpkin plants failed to grow. In our study plots, farmers grew a variety of field crops between the cacao and shade trees. Pumpkin, vanilla (*Vanillia planifolia* Andr.), chilli (*Capsicum annuum* L.), tapioca (*Manihot esculenta* Crantz.) and coffee (*Coffea robusta* Lind.) are among the most frequently planted crops contributing to the floral diversity within the plots.

Pumpkin (*Cucurbita moschata*, Fam.: Cucurbitaceae) is a common cash crop in the research area, with several advantages for studies of plant-pollinator interactions. It is cultivated in all habitat types, has local economic value and it is a fast growing plant with highly attractive flowers for bees. The plant only sets seed after cross-pollination and seed set is pollen limited so that pollination success can be directly measured (Walters & Taylor 2006). Pumpkin is a crawling and climbing plant, which allowed us to use twines to expose flowers at different heights. This three dimensional growth allows testing for niche differentiation in space. Finally, the opening time of flowers is restricted to approximately four hours in the morning which makes it possible to record almost the entire temporal pollinator turnover during this receptive phase of flowering. We planted experimental pumpkin patches of 2 x 5 m in each plot for observations of the pollinator community and measurement of the resulting seed set. We used liquid fertilizer to prevent soil nutrient availability from limiting fruit production.

Pumpkin observations were conducted in three phases: 1: 26 April 2005 – 01 June 2005, 2: 10 June 2005 – 21 July 2005 and 3: 10 January 2006 – 03 February 2006, with each plot visited once per phase. Bee abundances in the openland plots were higher compared with the other habitat types, so in order to classify all occurring bee species according to body size-related flower visitation behaviour we visited grassland plots an additional one or two times. The specimens from this fourth and fifth phase were used only for the classification of bee species into functional groups, and were not included in the calculations of seed set, pollinator richness and abundance per plot. Pollinators were recorded in a standardized way for three and a half hours from 07:00 until 10:30 a.m. which encompassed most of the opening time of flowers each day (203 plot observation hours in total). We adjusted the number of flowers for each observation and removed excess flowers or added missing flowers in small jars to keep a constant number of five flowers across replicate pumpkin patches (Ishii 2006), which resembles the approximate number of large and ephemeral pumpkin flowers on an area of ten square meters per day. To add or remove flowers also allows standardization of the sex ratio per plot and control of flower height, which ranges form 0.1 to 1 meter in each plot. Analysis of flower preferences refers to single pumpkin flowers, characterized by their length of the corolla (cm), diameter of corolla edge (cm), height (m above ground) and sex (male/female). Observed bees were caught for identification and to avoid counting the same individual twice. The time of flower visitation and the body size-related behaviour of the pollinator species, such as within-flower movements, were noted (Table 1). We measured the diameter of the largest pollen transporting leg part (femur, tibia or first tarsi), including hair structures and noted other pollen transporting body parts to estimate a hierarchy between species in terms of the amount of pollen transferred. Stephan Risch (Leverkusen, Germany) supported bee species identification. Voucher specimens are kept at the Bogor Agricultural University (IPB) in Indonesia.

Subsequent to the observation of pumpkin pollinators, the diversity and density of flowers in the herb layer and understorey were measured along six transects each 4 m wide and 30 m long. Flower density of each plant species on the transect was estimated, whereby 1 was equivalent to a single flower of one species and 100 a species that covers the whole area with many flowers. The transect walks per observation day and plot covered almost half of the plot core area (720 m^2). Conspecific flowers act as a pollen source and may therefore enhance seed set in the experimental plot, particularly because pollinators often specialize temporarily on a single or a few plant species (Ishii 2006). To allow for this, farmer-sown pumpkin flowers in the plot were counted in a radius of approximately 50 m around the experimental pumpkin patch. Temperature, humidity and light intensity were measured every 30 min from 7.00 to 11.00 a.m. on each observation day at a height of 2 m using a thermo-, hygro- and luxmeter (Mavalux Digital, Gossen) in an area receiving full sun. Ripe pumpkin fruits were collected throughout the entire time the plants grew. The size of pumpkins was measured (girth in cm) and seeds were counted. We used mesh bags for eleven female flowers to test the effect of pollinator exclusion for fruit development. Nine flowers, each from a different plot, were hand-pollinated by rubbing the dry anthers of at least three male flowers from different plots against the pistil of the female flower to estimate the maximum possible seed set when pollination is not limiting. We performed only eleven pollen exclusions and nine hand-pollinations in total, because pumpkin did not set fruits without cross pollination and there were no notable differences between hand-pollinated fruits from different habitat types in seed set (419 ± 17 SE seeds per fruit, n = 9).

STATISTICAL ANALYSIS AND CLASSIFICATION SCHEME

To identify the factors that structure the pollinator community, a general linear model (GLM) was used. The model included number of bee species and number of bee individuals as response variables (multivariate response), season (observation phase), habitat type and plot as categorical predictors and temperature, humidity, light intensity, density and diversity of flowering plant species and number of pumpkin flowers in the plot surrounding the pumpkin plantation as continuous variables. Because samples from the same plot in different seasons (phases) were non-independent, plot and season were included as random effects and plot was nested in habitat type. Post-hoc tests for differences between habitat types used Tukey's unequal N HSD (Honestly Significant Difference) test. Values per plot per sampling phase of response and continuous variables were used for the statistical analyses.

To analyze the effects of variables that we hypothesized to have an influence on seed set, a GLM with seeds per fruit as the dependent variable was conducted. Bee abundance and richness were used as continuous predictors of seed set per fruit. In addition, the number of pumpkin flowers surrounding the plantation, humus thickness (nutrient supply), slope (water supply) and canopy cover (light availability) were added as covariates because they are likely to affect plant growth and thereby, affect seed set. Habitat type was used as a categorical predictor. Mean values of bee observations, pumpkin flowers in the plot and measured abiotic variables per plot were used, because seed set data are available only at a plot level and not for each observation day. Due to a lack of female flowers in four plots (natural forest, low-intensity, medium-intensity and high-intensity), the number of plots was reduced to n = 14.

To test whether the stability of seed set was influenced by the bee community, the coefficient of variation (CV) for seeds per fruit was calculated (standard deviation/mean) for each plot. The CV was used as a dependent variable in a GLM, with habitat type as a categorical predictor and number of bee species and number of individuals of pollinators as continuous predictors. There were only one or two fruits produced in four plots, so an accurate CV could not be calculated and the data set was reduced to n = 10 for this part of the analysis.

We tested whether species-specific spatial and temporal foraging preferences and body size-related behaviour within flowers differed significantly among species, such that this may lead to complementarity. We fitted two mixed-effects models, one with flower visiting height and one with flower visiting time as dependent variables, and habitat type (fixed effect), plot (random effect nested in habitat type) and species identity (fixed) as categorical predictors. We used Spearman's rank correlation to test whether flower height and time of flower visitation were correlated, in both within and between species analyses. The twelve most abundant species were compared because they were abundant enough to allow statistical analyses.

To test whether different bee species prefer a certain flower size, we used flower volume as a dependent variable and habitat type (fixed effect), plot (random effect nested in habitat type) and species identity (fixed) as categorical predictors. We calculated flower volume from the diameter (2r) and length (h) of the corolla with the formula for a cone as a close approximation for flower volume:

$$\mathbf{V} = \frac{h \times \pi \times r^2}{3}$$

We also sorted species into body size classes, as there was evidence that within- and between-flower behaviour is strongly influenced by body size (Stout 2000). Table 1 shows four exemplary within- and between-flower pollinating traits which we could easily observe in the field and which characterize different size classes. We used the same twelve species as for the spatiotemporal differences, to ensure comparability.

We measured intertegular span of the pronotum and obtained five size classes (very small (VS): less than 1.5 mm, small (S): 1.5-2 mm, medium sized (M): 2.1-3 mm, large (L): 3.1-5 mm, and very large (VL): > 5 mm) (Table 1).

To test differences in behaviour within flowers that may depend on body size, we conducted a GLM with duration of flower visitation at a single flower (in seconds) as the response variable and habitat type (fixed) and size class (fixed) as categorical predictors. We measured duration of flower visitation for *Lasioglossum* sp., *Lasioglossum halictoides*, *Xylocopa dejeani* and *Xylocopa confusa*. We described each species in terms of other behavioural traits within flowers that depend on body size by dividing them into categories. We recorded the number of visited pumpkin flowers and pollen distribution on the anther or pistil (due to bee movement on reproductive plant parts) during the field observations.

We used a GLM with flower visiting height and flower visiting time respectively as dependent variables and habitat type (fixed effect), plot (random effect nested in habitat type) and body size class (fixed) as categorical predictors to test whether bee body size influences spatiotemporal flower visiting traits. Social bees played only a minor role in pumpkin pollination, thus social status was not included as a classification criterion. For a classification into functional guilds we used differences in the spatiotemporal and body size-dependent within-flower behavioural characteristics above. Species were assigned to the same guild if they did not differ significantly in any of these variables.

Table 1: Bee behaviour within flowers and pollen deposition in relation to body size (size classes: VS–very small, S–small, M–medium, L–large and VL–very large). Duration of flower visitation (Mean ± SE in seconds) of four bee species. Pollen deposition: diameter of the pollen transporting leg part (fe = femur, ti = tibia, ta = first tarsi, in mm), remarks are additive pollen transporting body parts.

Body size class	**Duration of flower visitation**	**Number of visited flowers**	**Pollen deposition**	**Pollen distribution on the stigma**
VS	52 ± 1.8^b (n = 19) (*Lasioglossum* sp.)	few	Very low; 0.2-0.3 (*Lasioglossum*: fe, *Trigona*: ti); *Lasioglossum*: ventral abdomen, *Trigona*: none	high
S	214 ± 6.7^a (n = 27) (*Lasioglossum halictoides*)	few	Low; 0.5 (*Ceratina*: ti, *Lasioglossum*: fe), ventral abdomen	very high
M	unknown	unknown	Medium; 0.9-1.3 (*Apis*: ta, *Nomia*: fe), *Apis*: pronotum, *Nomia*: propodeum	medium
L	unknown	unknown	High; 2.1 (*Apis*: ta, *Amegilla*: ti), pronotum	low
VL	21 ± 0.6^b (n = 23) (*Xylocopa confusa/dejeani*)	many	Very high; 2.5-2.8 (ta), pronotum and abdominal tip	low

We conducted a multiple regression model with seed per fruit as the response variable and bee species richness and number of functional guilds as covariates, to have a direct comparison of explanatory strength of the two approaches. To factor out abundance we regressed seed set against abundance and used the residuals from this model as the response variable. As functional diversity and species richness covary (Naeem 2002), we conducted two models (Table 3) with sequential Type I sums of squares. In the first model species richness was included ahead of functional diversity and vice versa in the second model.

Statistical analyses were carried out in Statistica (StatSoft, Inc. 2004.), version 7. www.statsoft.com.). All residuals were tested for a normal distribution and transformed if necessary. We used type-I (sequential) sum of squares for each model. We give arithmetic mean ± standard error in the text.

Results

Pollinator exclusion by bagging female flowers caused plants to abort the fruit. In contrast, all hand-pollinated female flowers matured to seed bearing fruits. We found on average 2.72 ± 0.33 pumpkin flowers in the surrounding of each pumpkin plot (n = 14). In total 633 bee individuals from 25 species and nine genera were caught.

The pumpkin pollinator community was strongly determined by habitat type. Both bee richness and abundance varied significantly across habitats (Richness: $r^2 = 0.252$, $F_{4,52} = 4.03$, $p = 0.025$; Abundance: $r^2 = 0.376$, $F_{4,52} = 4.99$, $p = 0.012$). Bee species richness was significantly higher in openland (on average 4.9 ± 0.512 species per plot, n = 9) than in natural forests (2 ± 0.471 species, n = 9), but was not different from cacao agroforestry systems (low-intensity: 3 ± 0.618, medium-intensity: 3.16 ± 0.297, high-intensity: 3.8 ± 0.534 species per plot per sampling phase, n = 12). Bee abundance was significantly higher in openland (21.3 ± 4.793 individuals, n = 9) compared to all other habitat types (natural forest: 3.6 ± 1.029, n = 9; low-intensity: 6.273 ± 1.465, medium-intensity: 6.083 ± 0.957, high-intensity: 10.6 ± 2.718 individuals on average, n = 12). Temperature showed significant positive correlations with number of bee species ($r^2 = 0.08$, $F_{1,52} = 7.8$, $p = 0.021$) but not with number of individuals ($r^2 = 0.034$, $F_{1,52} = 3.17$, $p = 0.086$).

Bee species richness was the only significant predictor variable in the model for seed set per fruit ($r^2 = 0.452$, $F_{1,13} = 19.24$, $p = 0.022$; Figure 1) whereas bee abundance did not significantly correlate with seed set. Mean number of seeds per fruit from plots with high species richness (10 bee species) almost reached that of hand-pollinated control flowers (Figure1), whereas low richness (4 species) led to just 50 % of control seed set. Number of seeds per fruit was correlated with fruit size (Spearman: $R^2 = 0.635$, $p = 0.015$), which is the economically most important trait.

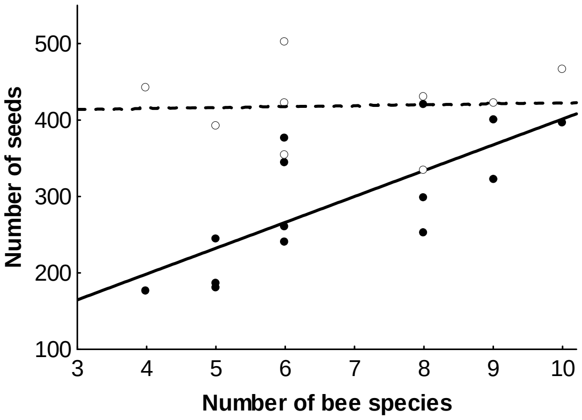

Figure 1: Mean number of seeds per fruit, per pumpkin patch in relation to the number of bee species per pumpkin patch. Results for open-pollinated flowers are shown with black dots and continuous line and results for hand-pollinated bagged control flowers in 9 plots are shown with black circles and dashed line.

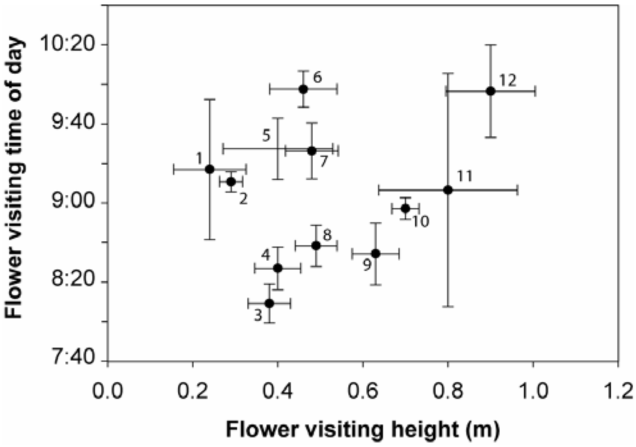

Figure 2: Height and time of flowers preferred by each bee species. Arithmetic means and ± standard error are given. For mean values, standard error and significance levels see table 2. Numbers represent species identity: 1 - *Nomia concinna*, 2 - *Lasioglossum* sp., 3 - *Apis cerana*, 4 - *Xylocopa dejeani*, 5 - *Nomia fulvata*, 6 - *Ceratina cognata*, 7 - *Trigona* sp. 8 - *Amegilla* sp., 9 - *Xylocopa confusa*, 10 - *Lasioglossum halictoides*, 11 - *Apis dorsata*, 12 - *Xylocopa nobilis*.

Stability (within-plot CV) in seed set was not affected by bee richness ($r^2 = 0.032$, $F_{1,7} = 0.25$, $p = 0.63$), abundance ($r^2 = 0.036$, $F_{1,7} = 0.28$, $p = 0.614$) or plot type ($r^2 = 0.036$, $F_{4,7} = 0.071$, $p = 0.989$).

Species differed in their spatial resource use (height of flowers: $r^2 = 0.142$, $F_{11,575} = 9.712$, $p < 0.001$), with *Nomia concinna* preferring the lowest, and *Xylocopa nobilis* preferring the highest flowers (Table 2, Figure 2). Pollinating height in one high-intensity plot was significantly lower compared to two openland plots ($r^2 = 0.05$, $F_{13,575} = 3.2$, $p = 0.0001$), while habitat had no influence ($r^2 = 0.04$, $F_{4,575} = 1.9$, $p = 0.177$) on pollinating height. Temporal species turnover showed even stronger differences, as almost all species differed significantly from each other in their preferred time of visitation ($r^2 = 0.2$, $F_{11,567} = 14.845$, $p < 0.001$). The species that visited flowers earliest were *Apis cerana*, *Xylocopa dejeani* and *Xylocopa confusa*, whereas *Xylocopa nobilis* and *Ceratina cognata* appeared significantly later (Table 2, Figure 2). Flower visitation in one low-intensity cacao plot was on average earlier compared to one medium-intensity, high-intensity and openland plot ($r^2 = 0.08$, $F_{13,567} = 5.123$, $p < 0.001$) and habitat had no influence ($r^2 = 0.03$, $F_{4,567} = 0.91$, $p = 0.49$). Species identity explained minor variance of the overall model for flower size ($r^2 = 0.04$, $F_{8,430} = 2.82$, $p = 0.0047$), and as only *Apis cerana* (233 ± 37 cm^3, n = 18) differed from *Ceratina cognata* (134 ± 20 cm^3, n = 17) and *Lasioglossum* sp. (157 ± 8 cm^3, n = 137) in preferred flower size, we did not include flower size for further analyses.

Body size was closely related to pollinating behaviour and each size class showed consistent patterns. Duration of a single flower visitation was significantly longer for small bees compared to very small and very large bees ($r^2 = 0.38$, $F_{2,65} = 20.11$, $p < 0.001$) (Table 1). Body size classes also differed in the number of flowers they visited. Very large bees checked two or three flowers mostly in their preferred height range, whereas small bees fed for a very long time but only on one flower. The amount of pollen transferred per flower visit was a consequence of species-specific anatomical characteristics, because larger bees had larger pollen-transporting surfaces such as the plumose ventral section of the abdomen and the dorsal part of the thorax or femur (Table 1). The within-flower movements are responsible for pollen transfer to the stigma. Small and very small bees landed directly on the petal, anther or pistil and then walked for a long time on anthers or pistil while feeding on pollen or nectar and thus distributing pollen. Due to their size, large and very large bees entered the flower directly without walking along the petals and remained between the petal and anther or pistil, while rubbing the pollen-carrying ventral part of the abdomen on the pistil of a female flower, or picking up pollen in case of a male flower. High pollen transfer was restricted to a part of the pistil, since large bees could not move around the pistil as did small and very small bees (Table 1).

Table 2: Mean ± standard error of flower visiting height, flower visiting time of day (local time ± minutes) and body size (size classes: VS–very small, S–small, M–medium, L–large and VL–very large) for each of the twelve most abundant species, resulting in a classification into eight functional guilds (from A to H). Significant differences ($p < 0.05$) are indicated by different letters (see Figure 2). Species in one guild do not differ in any of the three traits.

	Classification scheme			
Species	**Flower visiting height (cm)**	**Flower visiting time of day**	**Body size (mm) and size class**	**Guild**
Apis dorsata	0.8 ± 0.163^{ab} (n = 7)	9 : 04 ± 34^{abcd} (n = 7)	3.61 ± 0.04 (L) (n = 7)	A
Amegilla sp.	0.49 ± 0.049^{ab} (n = 56)	8:37 ± 6^{a} (n = 54)	4.19 ± 0.067 (L) (n = 7)	A
Nomia concinna	0.24 ± 0.085^{bd} (n = 8)	9: 14 ± 20^{abcd} (n = 8)	2.63 ± 0.037 (M) (n = 5)	B
Nomia fulvata	0.4 ± 0.129^{ab} (n = 7)	9:24 ± 9^{acd} (n = 7)	2.67 ± 0.057 (M) (n = 7)	B
Ceratina cognata	0.46 ± 0.079^{ab} (n = 22)	9:53 ± 5^{c} (n = 22)	1.88 ± 0.037 (S) (n = 5)	C
Lasioglossum halictoides	0.7 ± 0.032^{ad} (n = 156)	8:55 ± 3^{ad} (n = 156)	1.97 ± 0.049 (S) (n = 6)	D
Lasioglossum sp.	0.29 ± 0.027^{b} (n = 165)	9:08 ± 3^{d} (n = 165)	1.49 ± 0.028 (VS) (n = 9)	E
Trigona sp.	0.48 ± 0.062^{ab} (n = 45)	9:23 ± 8^{cd} (n = 40)	1.41 ± 0.021 (VS) (n = 8)	E
Xylocopa confusa	0.63 ± 0.055^{acd} (n = 39)	8:33 ± 9^{ab} (n = 39)	7.59 ± 0.104 (VL) (n = 8)	F
Xylocopa dejeani	0.4 ± 0.054^{bc} (n = 44)	8:26 ± 6^{ab} (n = 44)	6.52 ± 0.077 (VL) (n = 9)	F
Xylocopa nobilis	0.9 ± 0.105^{ac} (n = 8)	9:52 ± 14^{cd} (n = 8)	8.03 ± 0.084 (VL) (n = 8)	G
Apis cerana	0.38 ± 0.05^{bc} (n = 49)	8:09 ± 6^{b} (n = 49)	2.65 ± 0.042 (M) (n = 8)	H

We found significant preferences of bee species for certain heights, but there was no clear pattern between body size to pollinating height, even though very small species pollinated significantly lower flowers ($r^2 = 0.1$, $F_{4,582} = 18.128$, $p < 0.001$; 0.33 m ± 0.026, n = 209) than small (0.672 m ± 0.03, n = 178), large (0.523 ± 0.048, n = 62) or very large species (0.544 ± 0.04, n = 91). In contrast, small bees pollinated significantly higher flowers compared to medium-sized bees (0.368 ± 0.042, n = 64). We found that medium sized (8:25 ± 6 min, n = 64), large (8:40 ± 7 min, n = 60) and very large (8:37 ± 6 min, n = 90) bees occurred significantly earlier compared to small (9:02 ± 3 min, n = 178) and very small bees (9:11 ± 3 min, n = 203; $r^2 = 0.08$, $F_{4,574} = 14.99$, $p < 0.001$).

In a model where bee species richness was included first, after abundance was factored out, only bee species richness was significantly positively correlated with seed per fruit. However, when functional guild diversity was included ahead of richness in a Type I SS model, species richness became non-significant, because functional guild diversity explained much more variation in seed set (Table 3).

Table 3 Bee species richness and functional guild diversity in relation to seed set. Bold numbers indicate significant effects.

1. Model	r^2	$F_{1,11}$	p
Bee species richness	**0.32**	**6.68**	**0.025**
Functional guild diversity	0.15	3.15	0.103
2. Model	r^2	$F_{1,11}$	p
Functional guild diversity	**0.45**	**9.32**	**0.011**
Bee species richness	0.02	0.52	0.486

Discussion

Our results show how the ecosystem service of pollination can be promoted by functional pollinator diversity, based on species-specific traits driving complementary use of floral resources. Seed set increased strongly with bee richness, supporting previous studies that showed positive correlations between pollinator diversity and pollen deposition (Kremen *et al.* 2002) or fruit set (Klein *et al.* 2003 (b)). We quantified species-specific and complementary resource use in pollination and relate this to final crop yield. In our study, bee species strongly differed in their preferred flower height, time of flower visitation and within-flower behaviour, which was related to body size.

Spatiotemporal niche partitioning of pollinator communities (e.g. Willmer & Corbet 1981, Tylianakis *et al.* 2005) include preferences of bee species to forage at certain heights, which may have been selected to minimize energy expenditure (Dafni & Potts 2004). Pumpkin exposes flowers at very different heights, thereby attracting pollinator species with different height preferences. Reduced species richness can therefore cause a lack of pollination at certain heights, thereby reducing average seed set within a plot.

Willmer (e.g. Willmer 1983) and Stone (1994) discussed the relationship between behavioural and physiological determinants of circadian species-specific activity patterns, such as temporally structured foraging activity of hymenopterans, showing that certain species have precise daily times of foraging activity (Stone *et al.* 1999).

Most studies hold morphological traits (such as body size and colouring) responsible for the circadian niche partitioning of bees (Peereboom & Biesmeijer 2003), but also pollen release from principal food sources in the case of specialized bee species (Stone *et al.* 1999). In fact, we found that the bees of the three larger pollinator size classes occurred significantly earlier (during cooler morning hours) compared with smaller-sized bees. Hence, bee body size might affect flower visitation, but other traits may also influence circadian bee activity. Gimenes *et al.* (1996) hold the species' response to the environmental light/dark cycle responsible for a coupling of circadian bee activity to the flower's anthesis and withering. We expect that temporal species turnover is beneficial for pollination success, as not just the amount of transferred pollen will increase through time, but also the distribution of pollen. Two very large bee species (*Xylocopa dejeani* and *X. confusa*), for example, occurred very early in the morning, transferring large amounts of pollen, whereas *Lasioglossum* sp., *Ceratina cognata* and *Trigona* sp. occurred significantly later providing the distribution of the pollen already transferred by other species on the stigma. The temporal change of pollinator species from pollen transferring to pollen-distributing species may improve seed set due to a combination of both traits. Our study showed temporal differences in the activity of bees during a day, but bee communities are also known to show spatiotemporal turnover at longer time scales (between months) (Tylianakis *et al.* 2005), and this may affect complementarity in pollen transfer throughout the season.

Our field observations revealed size dependent species-specific within- and between-flower behavioural traits supporting the inclusion of body size as a third classification criterion (Table 1). We assume that complementarity in pumpkin pollination has been provided by two main pollination traits: the amount of transferred pollen and the distribution of pollen on the stigma (Chagnon *et al.* 1993). Whereas smaller species seem to be more important for pollen distribution on the stigma, by spending more time inside the flower and walking on stigmas and anthers, larger species increase the total amount of transferred pollen. Furthermore, we observed body size-dependent competition between bees (Pinkus-Rendon *et al.* 2005) in plots with high pollinator densities, with smaller bees having been subordinate when they met larger species at the pumpkin flowers. However, due to low pollinator densities in almost all plots, competition was unlikely to have played an important role.

Published studies dealing with niche partitioning of pollinators focus on the relationship of complex flowers to the proboscis length and resource use by pollinators (Graham & Jones 1996, Fontaine *et al.* 2006). We showed species-specific differences in pollinator traits characterized by distinct spatiotemporal resource partitioning, and found that high species numbers led to maximum seed set, equal to that observed in hand-pollinated fruits (Figure 1). Diversity of functional pollinator guilds, based on significant differences in preferences for flower height, time of flower visitation and body size-related within-flower behaviour, explained variation in seed set better than did species richness. The models (Table 3) suggest that interspecific differences in these functional traits are major drivers of high complementarity resulting in enhanced fruit set.

In conclusion, we show how a native bee community may sustain pollination services without any managed honey bees. The species-rich bee community appeared to enhance pollination efficiency through complementarity in species-specific flower visitation traits, suggesting that a single or a few efficient species may not provide the same benefits as a rich community of functionally distinct species. Due to species-specific niche partitioning, a single functional group exploits only a portion of the overall resource. Our results provide a first step towards a mechanistic understanding of how pollinator diversity affects food production. Global changes greatly affect bee diversity (Biesmejer *et al.* 2006) and the associated loss of functional diversity threatens sustainable crop production (Klein *et al.* 2007). Conservation initiatives may profit from analyses proving economic benefits of maintaining high biodiversity in agricultural landscapes.

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Chapter 5

Spatiotemporal density patterns of a pest predator along a land-use gradient in tropical agroforestry

Rhynchium haemorrhoidale (F.) ♀ from a trap nest in Toro, Sulawesi. Photo by Susanne Schiele.

Patrick Höhn, Ingolf Steffan-Dewenter and Teja Tscharntke

(submitted)

Summary

Tropical species show year-round breeding activity due to favourable climatic conditions. However, most species display seasonal reproductive peaks, but little is known about underlying causes of temporal density patterns. We investigated seasonality of the pest predator *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera), in terms of changes in density in agroforestry systems of varying shade tree composition in Sulawesi (Indonesia) and the influence of climate, body size, parasitism and unknown mortality.

Nesting of *R. haemorrhoidale* showed clear seasonality with rising activity in the wet season and lowest activity in the dry season. However, this activity was not directly correlated with changes in temperature. Wasp density increased when canopy cover decreased, possibly because less shade improves microclimatic conditions within agroforestry systems. Pupal body size was higher in June than in November indicating better food supply at the beginning of the dry season. High wasp densities in November, appeared to increase intraspecific competition, which led to food resource limitation, whereas body size between habitat types was similar suggesting that season superimposes the potential influence of habitat in terms of food supply.

Seasonality in the tropics is less pronounced than in temperate zones. However, tropical organisms seemingly underlie strong seasonal fluctuations in population dynamics. The density of the investigated predator increased with land-use intensity, profiting from the opening of the canopy in agroforestry systems. Furthermore, the observed patterns appeared to be linked to seasonal climate, food supply and mortality by natural enemies.

***Keywords*:** Ecosystem functioning, host-parasitoid interactions, population dynamics, resource availability.

Introduction

Density and reproduction of tropical species show mostly distinct temporal peaks even though breeding seems to be possible over the entire period (Brown & Shine 2006). Hypothesized proximate causes for seasonality in tropical zones include abiotic factors, food limitation and parasitoid density (Harris & McDonald 2007, Richards & Coley 2007, Richards & Windsor 2007). For some taxa, such as shrews or butterflies, it has been shown that they synchronize breeding with optimal climatic conditions (Kemp 2001, Nicolas *et al.* 2005). Furthermore, habitat quality has been discussed to be a crucial factor influencing species density due to microclimatic conditions or food resource availability in tropical regions (Lambert *et al.* 2006, Richards & Windsor 2007). In this study we try to identify, whether primarily seasonal variation of habitat quality or top-down regulation by natural antagonists influence the density of an important pest predator in agroforestry systems of different land-use intensity throughout a year. We propose food supply, climate, parasitism rate and entomopathogenic infection to be responsible for fluctuations in species density between different seasons and month.

Due to changes in larval food supply between season and habitat adult fitness, sex ratio, body size or mortality, as some crucial aspects of a predator's population dynamic, might also vary (King 1996, Strohm & Linsenmair 1997, Cleary & van Ginkel 2004, Boggs & Freeman 2005). Predators are strongly affected by fluctuations in prey density (Forsman & Lindell 1997, Salamolard *et al.* 2000, Norrdahl & Korpimaki 2002). Even though generalist predators exploit a broader array of resources than specialists, which may enhance stability of population densities, they also face the problem of food limitation in space and time (Östman 2005). Intraspecific competition of an insect predator, caused by high population density, can be one reason for low prey densities (Bommarco 1999).

Beside larval food supply, climatic conditions are a second important factor, influencing the density of predacious wasp species. For some Hymenoptera, such as Vespidae, nesting activity is correlated with daily or seasonal changes in climate (Lima & Prezoto 2003, Elisei *et al.* 2005, Ribeiro *et al.* 2006). Temperature dependent activity of the nest-building adults influences generation times and population density due to different provisioning times (Strohm & Linsenmair 1998). In temperate zones ontogenesis of insects is strongly related to seasonality, including specific hibernation stages as egg, larva, pupa or imago. Minor climatic fluctuations occur in tropical areas but might nevertheless influence reproduction and fitness.

Third, parasitism rate is well known to increase with increasing host density (e. g. Tscharntke 1992, Teder & Tammaru 2003) and parasitoids have been shown to reduce host density in the field (Bischoff 2003). Therefore the occurrence and in particular the density of parasitoids should be considered as an essential factor influencing life history traits. As parasitoids vary in space and time, they might be a crucial factor for host densities in different seasons and habitats (Zhou *et al.* 2001, Liu *et al.* 2007).

As a fourth mechanism influencing species density, species mortality due to unknown reasons, such as fungal or nematode infections, can be considered (Furlong & Pell 2001, Morton & Del Pino 2007).

We investigated factors that may influence seasonality and spatial distribution of *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera) along a land-use gradient of agroforestry systems in Sulawesi, Indonesia. In the investigated agroforestry systems cacao plants are grown under different levels of shade tree diversity and densities as determinants of land-use intensity. Agroforestry systems become increasingly interesting for the conservation of global species richness (Dietsch *et al.* 2007, Steffan-Dewenter *et al.* 2007) and ecosystem services (MEA 2005). We are therefore interested in the question, whether agricultural habitats of different management intensities can maintain high densities of a functional group, exemplary the predatory wasp species *R. haemorrhoidale*. We also examined, whether climatic conditions and food resource availability are more relevant for spatiotemporal patterns in wasp densities, body size and sex ratios. Furthermore, we evaluate the influence of parasitism rate and unknown mortality agents on seasonality and habitat preferences of *R. haemorrhoidale*.

Method

EXPERIMENTAL SITE AND DESIGN

Sampling was conducted on the western margin of the Lore Lindu National Park in Central Sulawesi, Indonesia, in the agroforestry systems surrounding the village of Toro (E 120^{o}2’, S 1^{o}30’, 800-1100 m above sea level). Agricultural landscapes at the margin of the tropical rainforests are dominated by cacao agroforestry and paddy fields.

We selected plots ranging from natural forests to a gradient in land-use intensity of agroforestry systems. Each plot had a minimum core area of 30 x 50 m, where we placed the trap nests. The cacao agroforestry systems formed a gradient according to the composition of shade tree species and thereby shadow intensity, with low management intensity agroforestry having natural forest trees as shade trees (dense shade), medium intensity systems having a diverse shade tree community planted by farmers (medium shade) and high intensity plots with only a few planted shade tree species such as *Gliricidia sepium* (Jacq.) and *Erythrina subumbrans* (Hassk.) (light shade). The different habitat types were situated close together and alternated in the study area, without following a geographic gradient.

Canopy cover was measured with a spherical densiometer (Model-C, Robert E. Lemmon, Forest Densiometers, 5733 SE Cornell Dr., Bartlesville, OK 74006) by two people independently at twelve random positions within each plot above cacao tree canopy. Canopy cover varied between plots, with primary forest plots having the densest canopy (95.6 % ± 0.8 %), followed by low intensity plots (72.5 % ± 4.5 %), medium intensity plots (61.4 % ± 6.3 %) and high intensity plots (58.1 % ± 8.4 %). We therefore refer to the different agroforestry plots as dense, medium and light shaded plots. Four replicates were chosen for each habitat type.

We used trap nests to assess relative densities of above ground-nesting wasps. Trap nests consisted of PVC tubes (length 28 cm and a diameter 14 cm) with internodes of the grass *Saccharum spontaneum* (L.) (Poaceae) of varying diameter (3 – 25 mm) and a length of 20 cm inserted (Tscharntke *et al.* 1998). Sixteen trap nests per site were installed from October 2004 till September 2005 in different heights from understorey to canopy. The trap nests were checked every month and sticky glue was applied to the edge of the PVC tube to deter ants from colonizing the trap nests. We collected all internodes, which were occupied by Hymenopterans readily identifiable at the clayey walls closing the internode opening and incubated all larvae and pupae in glass tubes until they hatched, for later species determination. Due to simplification of terminology, we equated the term density with number of brood cells, as done in former studies (Gathmann *et al.* 1994, Steffan-Dewenter 2003). Voucher specimens are kept at the Bogor Agricultural University (IPB) in Indonesia.

Pupal body size is a widely used fitness-related trait for insects and can be used as a surrogate for food supply (e.g. Harvey *et al.* 2000, Östman 2005). We could not estimate prey density in the field, because the prey larvae fed in higher forest strata (e.g.: *Erythrina*). Instead we measured body size of wasp pupae with a vernier calliper in November 04 and June 05 for a seasonal comparison. Wasp larvae completely ate prey larvae in the brood cells and as we excluded the influence of internode diameter on wasp pupae size, we equated pupae size with food resource availability. Assessment of sex ratio and sex determination was also done in November 04 and June 05. We used the term month for comparisons between all months throughout the year and season if we compared November (wet season) with June (dry season). We recorded wasp individuals that were not parasitized, but died as egg, larva or pupa for unknown reasons, such as infections by entomopathogenic organisms (viral, bacterial, nematode or fungal infection), for every month. In order to exclude mortality due to breeding in the glass tubes, we maintained constant optimal conditions. The climatic conditions air temperature, humidity, solar radiation and precipitation were measured at a climate station in the centre of the research area to assess seasonal fluctuations.

STUDY ORGANISM

We used the tropical cavity nesting eumenid wasp species *R. haemorrhoidale* (F.) (Eumenidae, Hymenoptera) for this study (Figure 1). *R. haemorrhoidale* is a solitary, predatory wasp, building soil nests with several brood cells. It was the most abundant species out of 23 predacious wasps comprising a prey spectrum of only one morphospecies and showed high seasonality. *R. haemorrhoidale* must be considered as an effective pest predator, as we found that their prey species were the cacao and *Erythrina* spp. leaf-feeding larvae of *Agathodes caliginosalis* (Snellen) (Pyralidae, Lepidoptera) and each brood cell was provided with approximately seven larvae (Figure 2). The generation time from egg to adult never exceeded one month, which was the sampling frequency for the trap nests and therefore we can exclude that wasps developed, hatched and flew out unrecognized from trap nests. Parasitoids of *R. haemorrhoidale* comprise a spectrum from cleptoparasites (Chrysididae and Ripiphoridae), ectoparasites (Leucospidae) and endoparasites (Ichneumonidae) to hyperparasites (Trigonalyidae).

Figure 1 Nest-building female of *Rhynchium haemorrhoidale* within a trap nest.

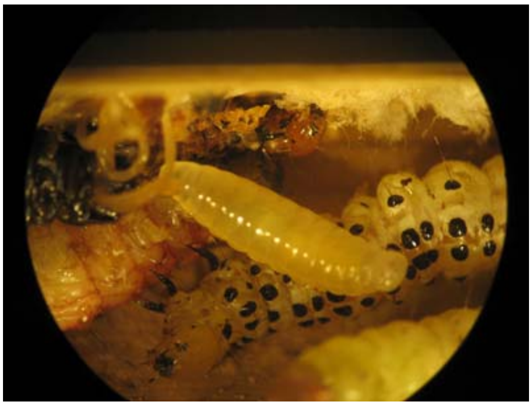

Figure 2 Larva of *Rhynchium haemorrhoidale* feeding on larvae of *Agathodes caliginosalis* within a trap nest internode.

STATISTICAL ANALYSIS

We used main effects ANOVA to test on differences in density and sex ratio per plot between months (density) and seasons (sex ratio), respectively, and habitat. Density was defined as number of brood cells occupied. Density and sex ratio were used as dependent variables and habitat type and month/season as categorical predictors. Sex ratio was calculated as number of male individuals per plot divided by number of female individuals. We show density values in primary forest plots only in Figure 4 and did not include the individuals from this habitat for further statistics, because *R. haemorrhoidale* proved to be a species depending on less dense forested habitats, such as agroforestry systems. Only 24 individuals of *R. haemorrhoidale* occurred in all four primary forest plots throughout the year.

We used Spearmans rank correlation to test whether wasp density per plot and month and canopy cover per plot were correlated.

We used a correlation matrix to test whether the climatic factors temperature, humidity, solar radiation and precipitation were correlated and used a principal component analysis (PCA) for correlated factors to reduce the number of variables. In another correlation matrix we tested, whether monthly density values of *R. haemorrhoidale* were correlated with climatic factors. As species density responses to climatic changes might be delayed we correlated density with climatic values not just from the same month, but also from the previous months.

To rule out the effect of internode diameter on pupal size, we tested whether the diameter influenced pupal size just in densely populated trap nests, where nest building adults might have to elude to nests with smaller diameters, as they would usually chose. We used a simple regression model with pupal length as dependent variable and diameter of the reed internodes as predictor variable. In a first model we included all individuals we measured, and in a second model we included only those individuals from trap nests with less than ten occupied reed internodes, as this assures for sufficient nesting possibilities and a free choice in nest diameter for the nest building adult. We measured nest diameter only for November, as the effect of nest size on pupal size due to restrictions in nesting possibilities can only be expected in a month with high densities. To test whether habitat or season influenced food resource availability, we used main effects ANOVA with body size of the pupae as dependent variable and habitat and season as categorical predictors. We did the analysis for both sexes separately, as females were significant larger than males.

We conducted a general linear model (GLM) to identify the factors that influence parasitism of *R. haemorrhoidale* and unknown mortality rate. The two models included parasitism and unknown mortality rate respectively as response variables, habitat and month as categorical predictors and host density as continuous variables. Parasitism rate was calculated as number of infested host individuals divided by number of parasitized individuals per plot. Unknown mortality rate was calculated as total number of individuals per plot divided by number of individuals that died for unknown reasons.

To test the effect of habitat and month on species richness of parasitoids of *R. haemorrhoidale* we conducted a main effects ANOVA with number of species as response variable and month and habitat as categorical predictors.

Statistical analyses were carried out in Statistica (StatSoft, Inc. 2004.), version 7. www.statsoft.com.). Square root transformation was done to assure for homogeneity of variance if necessary. The test for climatic variables and wasp density used a Bonferroni corrected α of 0.0125. We used type-I (sequential) sum of squares for each model. We give arithmetic mean ± standard error in the text.

Results

In total we reared 11,090 individuals from 50 species in the trap nests. 23 of these species were specialized predatory wasps with *R. haemorrhoidale* (7,403 individuals), a larvae hunting eumenid wasp, being the most abundant species, comprising 67 % of all individuals.

SEASON AND HABITAT QUALITY

Density of *R. haemorrhoidale* was strongly influenced by season with rising number of brood cells from October until February ($r^2 = 0.48$, $F_{11,107} = 11.8$, $p < 0.001$) (Figure 3) and increased number of brood cells with increased land-use intensity ($r^2 = 0.07$, $F_{2,107} = 8.8$, $p < 0.001$). Dense agroforestry plots had significantly less individuals per month and plot (36.7 ± 5.67, n = 48) compared to medium (53.3 ± 6.78) and light shaded agroforestry plots (64.8 ± 8.5) (Figure 4). There was no interaction between season and land-use intensity ($r^2 = 0.05$, $F_{22,107} = 0.63$, $p = 0.9$). Canopy cover and wasp density per plot and month were significantly negative correlated (N = 16, R = -0.54, p = 0.033). Neither habitat ($r^2 = 0.09$, $F_{2,19} = 1$, $p = 0.384$) nor season ($r^2 = 0.06$, $F_{1,19} = 1.31$, $p = 0.267$) influenced sex ratio of the wasp.

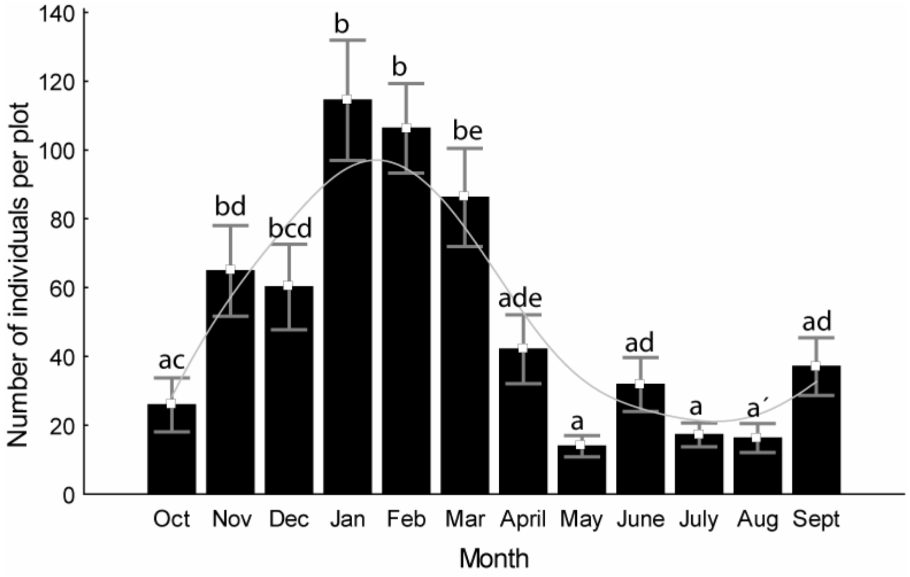

Figure 3 Mean ± standard error of numbers of individuals of *R. haemorrrhoidale* per month and plot from October 2004 until September 2005. Significant differences ($p < 0.05$) are indicated by different letters. Grey fitting line is according to distance weighted least squares.

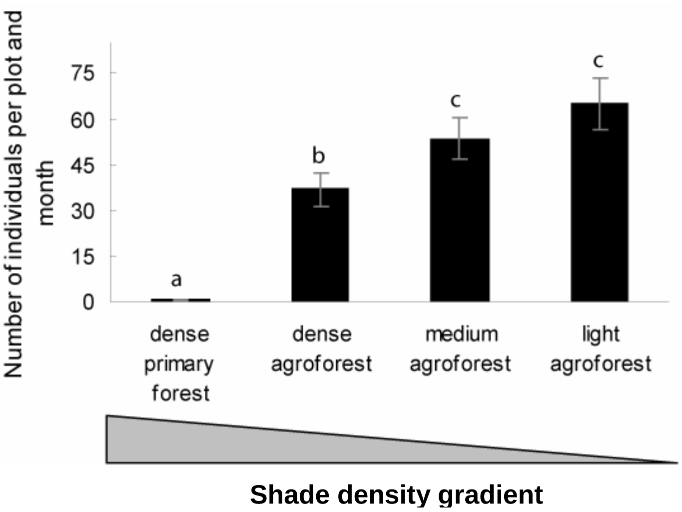

Figure 4 Mean ± standard error of numbers of individuals of *R. haemorrrhoidale* per month and replicate for one year and four habitat types with different shade regime. Different letters indicate significant differences between habitat types.

CLIMATIC VARIABLES

Climatic variables were not intercorrelated and no climatic variable was correlated with density of *R. haemorrhoidale* from the same month or the previous month. In a correlation matrix with climatic factors from the previous month, density was also not correlated with climate. Although solar radiation had a significance level below $p = 0.5$ ($N = 12$, $R = 0.6$, $p = 0.039$), it was above the Bonferroni corrected α of 0.0125.

FOOD RESOURCES

Trap internode diameter and wasp pupal size were positively correlated only when all individuals were included, even though internode diameter explained only minor variance of pupal size ($R^2 = 0.02$; $F_{1,454} = 10.06$; $p = 0.002$). In a model with individuals only from sparsely populated trap nests the significance did not persist ($R^2 = 0.01$; $F_{1,234} = 3.48$; $p = 0.06$). We therefore used individuals from trap nests with less than ten occupied internodes for further analyses to examine the effect of season and habitat on body size. Seasonal differences in pupal size were similar for both sexes. Females and males were larger in the dry season (June) compared to wet season (November) (females June: 1.88 ± 0.016 cm; November: 1.71 ± 0.019 cm; $r^2 = 0.17$, $F_{1,226} = 47.49$, $p < 0.0001$; males June: 1.53 ± 0.015 cm; November: 1.36 ± 0.017 cm; $r^2 = 0.19$; $F_{1,229} = 54.35$; $p < 0.001$) (Figure 5). Habitat did not influence pupal size in both sexes (females: $r^2 = 0.01$; $F_{2,279} = 1.84$; $p = 0.16$; males: $r^2 < 0.01$; $F_{2,293} = 0.06$; $p = 0.94$).

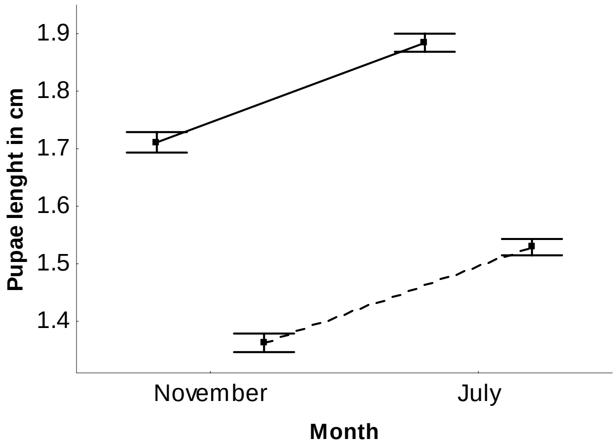

Figure 5 Mean ± standard error of wasp pupae lengths of *R. haemorrrhoidale* for two months, with solid line representing female individuals and dashed line representing male individuals.

PARASITISM AND MORTALITY

We found 579 individuals of antagonists from *R. haemorrhoidale* belonging to seven species (see Method: Study organism). These were 3 ± 0.38 parasitoids and 39 ± 3.5 host wasp individuals in average from each plot per month, resulting in a total parasitism rate of 7.7 %. For statistical analyses we pooled all parasite species, as all species caused mortality of *R. haemorrhoidale*. Parasitism rate of *R. haemorrhoidale* differed between months ($r^2 = 0.24$, $F_{11,109} = 3.146$, $p = 0.001$), with November having a higher parasitism rate compared to October, August and September (Figure 6), but did not show a difference between habitats ($r^2 = 0.01$, $F_{2,109} = 0.8$, $p = 0.449$) or host density throughout the year ($r^2 < 0{,}01$, $F_{1,109} = 0.57$, $p = 0.45$). Antagonists of *R. haemorhoidale* showed higher species richness in the rainy season ($r^2 = 0.62$, $F_{11,22} = 3.3$, $p = 0.008$) with significantly more species in February (3.66 ± 0.33) compared to October (1 ± 0), whereas habitat had no influence on species richness ($r^2 < 0.01$, $F_{2,22} = 0.04$, $p = 0.96$). The rate of unknown mortality was not influenced by any predictor variable (habitat: $r^2 = 0.05$, $F_{2,109} = 3.06$, $p = 0.051$; month: $r^2 = 0.13$, $F_{11,109} = 1.56$, $p = 0.122$; density: $r^2 = 0.05$, $F_{1,109} = 0.06$, $p = 0.8$).

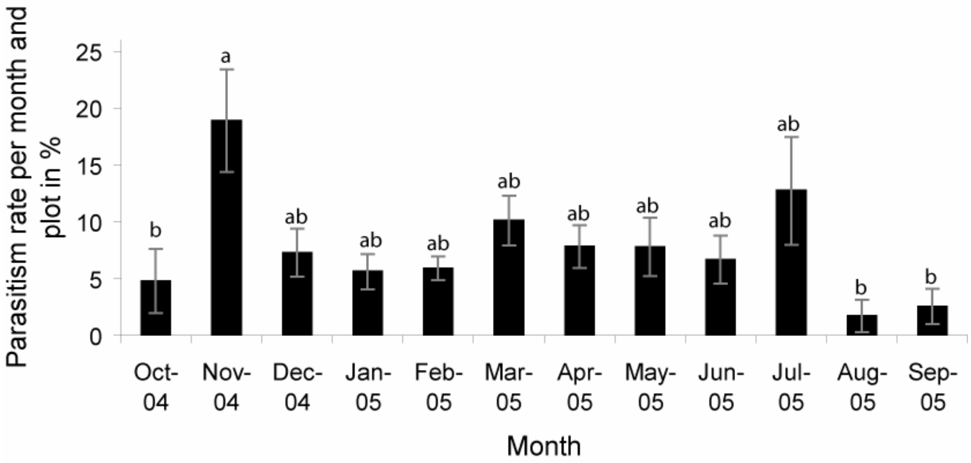

Figure 6 Mean ± standard error of parasitism rate of *R. haemorrrhoidale* by seven species of parasitoids per month and plot from October 2004 until September 2005. Significant differences ($p < 0.05$) are indicated by different letters.

Discussion

R. haemorrrhoidale was strongly influenced by month and land-use intensity, whereas a direct climatic influence appeared to exist only for habitat preference but not for seasonal climatic variation in densities. Although, we found a strong seasonality of *R. haemorrrhoidale* with higher monthly densities in the wet season wasp density was not correlated with climatic conditions in the same month. We could not find a significant direct synchronization between wasp density and climate, even though increased flight and foraging activity, which increases nest building and provision, have been shown to depend on temperature or solar irradiation (Strohm & Linsenmair 1998, Ribeiro *et al.* 2006). As climatic conditions influence prey density and generation time (Lysyk 2001) by accelerating physiological development (Smits *et al.* 2000) wasp density as a response on climate would be temporally protracted. However, density of *R. haemorrrhoidale* showed only a slight and nonsignificant correlation with solar radiation from the previous month. The observed cycles in nesting activity may result from species inherent physiological adaptations, as found for gekkonid lizards (Ota 1994).

Wasp density was influenced by land-use intensity, with dense shaded agroforest plots having fewer individuals compared to medium and light shaded agroforests and almost none in highly shaded primary forests. In less shaded plots solar radiation penetrates through the canopy and reaches the ground, thus increasing temperature and reducing humidity (Grimmond *et al.* 2000). Vespidae are known to profit from solar radiation and temperature (Ishay & Lior 1990, Elisei *et al.* 2005), in particular in terms of nest building and foraging activity. A relation between habitat type and wasp density was apparently due to the influence of canopy cover on climatic conditions in the plots, as wasp density and canopy cover were negatively correlated. Nesting site choice was therefore related to microclimatic conditions.

Body size of females and males of *R. haemorrrhoidale* was higher in June, indicating better larval food supply in the beginning of the dry season, rather than at the end of the dry season. Reduced food supply in November could be due to low prey densities according to unfavourable climatic conditions for the prey species or due to competition for food resources, as wasp density increased in November. In seasons with high wasp density, intraspecific competition could reduce individual food supply and result in smaller individuals, as abundant wasp species with a narrow prey spectrum, such as *R. haemorrrhoidale*, can effectively reduce prey densities in the field (Harris 1996, Schenk & Bacher 2002). Temporal variation in body size was synchronized among sites, showing the superposing effect of seasonal change on food supply independent of habitat type (Östman 2005). Klein *et al.* (2004) could show that *R. haemorrrhoidale* adjusted foraging trip duration to habitat quality and wasp density was not correlated with foraging time, indicating that food resource availability within the habitat is not necessarily decisive for body size and habitat choice of *R. haemorrrhoidale*.

Sex ratio was similar between seasons with high and low resource availability. Sex ratio has been discussed to depend on environmental factors, whereby unfavourable conditions produce a sex ratio towards males (Frank & Swingland 1988), as found for the European beewolf (*Philanthus triangulum* F., Sphecidae) (Strohm & Linsenmair 1997). Male individuals represent the ‘cheaper sex’ with higher relative fitness under poor conditions. For *R. haemorrrhoidale* relative fitness especially of the larger female individuals did not seem to be negatively influenced by food supply. This was also shown by the independence of unknown mortality in terms of season or habitat. Food supply did not seem to have an influence on fitness, as unknown mortality was not higher in the season with smaller individuals. Some authors discuss the relation between fitness and body size of insects (Harvey *et al.* 2000, Sokolovska *et al.* 2000, Östman 2005). However, we could not find a relation between different seasons with varying body size of the insects and unknown mortality as a fitness related trait.

Parasitism rate in November was considerably higher compared to August, September and October. This peak appeared to be a response to increasing host densities at the beginning of the wet season. Although parasitism rate throughout the year is not correlated with host density, increased host density in November appeared to act as a stimulus for increased activity of the parasitoids. Increased parasitoid density did not result in severe host reduction, because host density still increased until January. However, a slight and not significant host reduction in December might reveal a short term effect of parasitism rate on host density. Accordingly species richness of antagonists of *R. haemorrrhoidale* is higher in the middle of the rainy season compared to the end of the dry season. Indeed, the *Chrysis* sp. *smaragdula* group occurred only in the rainy season.

In conclusion, food resource availability and climate may contribute to seasonal changes in life history traits in temperate zones as well as in the tropics (Kemp 2001, Nicolas *et al.* 2005, Polidori *et al.* 2007). However, the complexity of factors (Ota 1994) makes it difficult to determine the ultimate reasons for seasonality of tropical species. We showed that habitat choice for nesting appeared to depend on climatic conditions due to varying canopy cover between the habitat types, whereas phenotypic constraints may explain seasonality in wasp density.

We show that agroforestry systems in agricultural landscapes, can maintain high densities of a functionally important pest predator. The larvae-hunting *R. haemorrrhoidale* was almost absent in the primary forest and density increased with land-use intensity, potentially increasing biological pest control. However, we could not directly measure the effectiveness of this ecosystem service and other potential predators of pest insects might got lost during agroforestry intensification.

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Summary

The rate of deforestation of primary tropical forests due to agricultural expansion is higher in Southeast Asia compared to all other world's tropical regions. Deforestation in tropical forests is a major threat for global biodiversity, because estimated 50-90 % of the world's species are living in tropical forests. Therefore, human dominated landscapes and forested land-use systems such as agroforestry become increasingly important as a storage reservoir of global biodiversity. Biodiversity is related to ecosystem functioning, with complementarity in resource use as a major mechanism. Pollination is essential for plant-derived ecosystem services such as food production, and pollinators are one of the major functional groups for human well-being. Agroforestry systems often include coffee (*Coffea* sp. L.) and cacao (*Theobroma cacao* L.) as important cash crops, traditionally crown under a canopy of shade trees and with fruit set depending on pollination. Because of the variety of planted shade and fruit trees, agroforestry systems resemble primary forests more than any other agricultural habitat type and have great but little explored potential to offer substitute habitats for many tropical forest species.

My aim was to evaluate the importance of agricultural systems for conservation of trap-nesting Hymenoptera and the pollinator community. I analyzed a land-use gradient in a tropical forested landscape, from primary forests, agroforestry systems differing in diversity of the shade trees and openland such as grassland and fallow land. I assessed the relative importance of different strata for species richness with trap nests, which offer standardized nesting resources for different guilds of above-ground nesting Hymenoptera and their antagonists. Furthermore, I linked pollinator richness to habitat modification and final crop yield and analyzed species-specific differences in resource use. I also assessed the contribution of agroforestry system for the maintenance of high densities of a pest predating wasp species over the course of one year. This study took place in Central Sulawesi (Indonesia) in the surrounding of the village Toro at the margin of a primary tropical forest (Lore Lindu National Park).

The results show that total bee species richness in the herb layer increased with increasing land-use intensity and was highest in openland. However, species richness estimation and additive partitioning of biodiversity revealed higher overall bee species richness, presumably due to high management diversity, in agroforestry systems compared to primary forests and openland. Agroforestry systems offer higher floral diversity in the understorey, due to the richer herb layer and cash crops, than primary forests and provide more nesting sites for cavity-nesting bee species than openland.

The canopy in primary forests was far more important for trap-nesting bee and wasp richness than the understorey. This pattern reversed with intensification in agroforestry systems where highest richness was found in the understorey. Food resource availability and microclimatic conditions appeared to make the canopy in primary forests a more suitable habitat for most species and might cause underestimation of species richness when only lower strata are sampled. In addition, agroforestry habitats showed high beta diversity due to high land-use diversity and between-plot community dissimilarity, showing that agricultural management can be crucial for conservation plannings on a landscape scale.

I used standardized pumpkin plantations in different habitat types to test the effect of pollinator diversity on crop yield. Bee pollinators showed species specific differences in flower visiting traits, such as height, time and body size-related flower visiting behaviour. I provide the first empirical evidence of the relation between spatiotemporal and behavioural complementarity in resource use of a pollinator community causing increased crop yield. Furthermore, I show that the native bee community can sustain pollination services in absence of managed honey bees.

Using the highly abundant wasp species *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera), I show that agroforestry systems can maintain high insect densities of a pest predator, even under intense land-use management. Tropical regions experience lower climatic fluctuations between the seasons compared to temperate zones. However, *R. haemorrhoidale* undergoes seasonal changes in density and body size, due to a complex combination of potential reasons (e.g. climate, food supply, parasitism) independent of habitat type.

In conclusion, agroforestry systems can play a crucial role in the conservation of the understorey pollinator communities and densities of pest predators, whereas the importance of the canopy for species richness is increasing with decreasing land-use intensity and is highest in primary forests. Furthermore, I show that the ecosystem service of pollination and crop yield strongly depends on the bees' functional diversity. Low-intensity land-use and a complex shade-tree canopy appear to increase local and regional Hymenoptera richness and to sustain important ecosystem

services, showing the necessity to include such agricultural systems in landscape-wide conservation programs.

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Kessler, M., Abrahamczyk, S., Bos, M., Dwi Putra, D., Gradstein S.R., **Hoehn, P**., Orend, F., Pitopang, R., Saleh, S., Schulze, C.H., Sporn, S.G., Steffan Dewenter, I. & Tscharntke, T. (in prep.). Alpha and beta diversity of four plant and eight animal groups along a land use gradient in Indonesia.

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