BEES, WASPS, AND THEIR PARASITOIDS IN TRADITIONAL COFFEE AGROFORESTS: COMMUNITY PATTERNS AND ECOSYSTEM SERVICES

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CHAPTER 1

BEES, WASPS, AND THEIR PARASITOIDS IN TRADITIONAL COFFEE AGROFORESTS: COMMUNITY PATTERNS AND ECOSYSTEM SERVICES

GENERAL INTRODUCTION

Introduction

The ongoing anthropogenic modification of landscapes, which is dramatically proceeding in the tropics, causes a substantial decline in global biodiversity (Vitousek et al. 1997). Species extinctions and population changes are assumed to considerably threaten ecosystem services, which provide important benefits for humanity (Daily 1997, Luck et al. 2003). In this context, traditional land-use practices receive increasing attention, because they can improve ecological and economic sustainability of land-use systems (Muschler & Bonnemann 1997). In the tropics, which constitute the main proportion of the world-wide biodiversity hotspots (Meyers et al. 2001), traditional agroforestry has recently gained increasing importance. For example, traditional coffee agroforests harbour a high diversity of plants and animals, and may constitute important refuges for former forest inhabitants, including many beneficial insects (Perfecto et al. 1996, Klein et al. 2003, Solis-Montero et al. 2005). Therefore they also may maintain many of the environmental functions of undisturbed forests. Consequently, coffee agroforests have a high potential to compensate for biodiversity loss caused by the disturbance of pristine forests. Bees, wasps, and their natural enemies are of crucial importance for human well-being, because they fulfil important ecosystem services, such as pollination, predation, and parasitism (Constanza et al. 1997, Kremen 2005). Within-habitat distributions of insect communities may largely vary in space and time and be influenced by habitat modification, which in turn may affect associated ecological functions. Resource availability is known to structure insect communities (Westrich 1996, Potts et al. 2004), and food resources such as flowers or prey, but also nesting resources and microclimatic conditions vary at different spatial and temporal scales (Wolda 1988, Schulze et al. 2001, Potts et al. 2004). Flower visitation by bees is an important ecological process that is related to floral resource availability (Potts et al. 2004). However, little is known about whether responses of bee communities to floral resource availability change at different spatial scales. Factors driving community patterns are known to be scale delimited or may operate differently at different spatial scales (Crawley & Harral 2001, Willis & Whittaker 2002).

Furthermore, economic evaluations of pollination services for crop production are still scarce; monetary assessments may underline the importance of ecosystem services for humanity. This is of special importance when crop production substantially contributes to the livelihood of people, as in the case of small-scale farmers in developing countries. Coffee is an important cash crop in the tropics and its production affects economic life of many people living in poverty (Perfecto & Armbrecht 2003, Oxfam 2005). Bee pollination is assumed to contribute significantly to coffee production (e.g. Roubik 2002, Klein et al. 2003a,b). However, so far only indirect evidence exists for a monetary value of bee pollination for coffee production (Ricketts et al. 2004), whereas an evaluation based on intrinsic yield data is still missing. Furthermore, shade in agroforests is said to affect coffee production, but due to the inconsistency in previous results its importance is still controversial (Perfecto et al. 2005).

Within forest-like habitats in tropical regions, vertical vegetation structure may influence community distributions. For example, vertical stratification has already been shown for butterflies and flies (de Vries 1997, Schulze 2001) and was related to vertical heterogeneity in resource availability and microclimatic conditions. However, little is known about the vertical distribution of bees and wasps in forest-like habitats. Furthermore, distinct seasonality in tropical regions may influence insect community patterns; but most evidence for seasonal differences exists for insect abundances; only recent results suggest seasonality in species richness of bees and wasps (Tylianakis et al. 2005). As vertical stratification of insects, also seasonality in insect communities can be caused by climatic changes and seasonal variation in resources (Wolda 1988, Jones 2001). Guild specific resources may vary in their vertical or seasonal heterogeneity, which in turn may cause varying vertical and seasonal community patterns of different guilds, such as bees and wasps. Additionally, habitat modification or complexity may either dampen or strengthen environmental heterogeneity, and thus influence vertical or seasonal patterns of insect communities (Su & Wood 2001, Tanabe 2002).

Within the debate about the contribution of diversity to ecosystem function and stability, multitrophic interactions have gained increasing attention (Hooper et al. 2005). Evidence from theoretical and experimental studies predicts a positive effect of diversity on function in multitrophic systems as for single trophic levels (Cardinale et al. 2003, Hillebrand & Cardinale 2004, Gamfeld et al. 2005, Thébault & Loreau 2005). However, little evidence exists for a diversity-functioning relationship in a natural food web (see Hooper et al. 2005, Silvastra & Vellend 2005), and it is not yet known whether recent results are also applicable to different ecological guilds at the prey level within a multitrophic system. Host-mediated variation in consumer communities such as parasitoids may influence the effects of diversity on an ecosystem function such as parasitism. Furthermore modification of agroforests may alter the diversity-function relationship by influencing biodiversity patterns of organisms and the associated ecological functions (Klein et al. 2003c).

The studies presented here were conducted in either 22 (first part) or 14 (second part) different coffee agroforests in Ecuador, which constituted a gradient in tree diversity and light intensity.

In the first part of the thesis the relation of flower-visiting bees to coffee flowering at three different spatial scales was investigated. Additionally, based previous reports of increased fruit set and fruit quality in coffee through bee pollination (e.g. Roubik 2002, Klein et al. 2003a,b), the relationship between the coffee-flower visiting bee community and farm-scale yield (and consequently, revenues from coffee production) was analyzed, and the effect of shade density on coffee yield was examined.

The second part of the thesis used a long-term study to investigate vertical and seasonal patterns of cavity-nesting solitary bees and wasps, and analyzed the relationship between diversity, ecosystem function and stability using the parasitism of those cavity-nesting bees and wasps by parasitoids.

Thereby the following main questions were addressed:

1) Do coffee flower-visiting bees respond similar to floral resource availability at different spatial scales? (Chapter 2)

2) Can previous indirect results on the economic value of bee pollination for coffee production be transferred to a farm-scale? (Chapter 3)

3) Is there vertical stratification and seasonal variation in the functionally important community of cavity-nesting bees and wasps, and are possible patterns guild specific? (Chapter 4)

4) Does diversity contribute equally to an ecosystem function such as parasitism and the stability of parasitism for different host groups such as bees and wasps in a multitrophic system? (Chapter 5)

Study region and system

The study was conducted in the province Manabi in coastal Ecuador (Fig. 1). This part of Ecuador constitutes the southern end of “El choco”, one of the global biodiversity hotspots (Meyers et al. 2001). The study sites themselves were located around the town of Jipijapa, in the cantons Jipijapa, Noboa and Pajan (Fig. 2). The area is situated at an altitude of 100-550 m (17 N546800 m, E 9849274 m) with an annual rainfall of 1500 to 1700 mm, and a mean annual temperature of 25°C. It is a semi-arid region with a distinctive seasonality; the dry season lasts approximately from June until the end of December, with hardly any rainfall, whereas in the rainy season daily heavy rainfalls are common. Agricultural land-use systems dominate the landscapes, only very few and rather small forest fragments are left within a mosaic of different land-use types. Land-use systems comprise annual monocultures of rice or maize, pasture, but also highly diverse traditional agroforests and abandoned agroforests.

Fig. 1: Map of Ecuador with the study region in the province Manabi.

Table 1: Monthly temperature (^{o}C) and rainfall (mm) in Pajan (17N 563969, E 9828342m alt. 142m) within the study region from December 2003 until November 2004. The rainy season begins in December and ends in May. (Climate data were provided by the "Instituto nacional de Meterologia e hidrologia" in Ecuador).

	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Temperature	25.8	25.7	25.8	26.	25.9	25.9	25.6	25.3	25.4	25.6	25.6	25.4
Humidity	73.3	197.1	276.1	307.1	293.6	143.2	35.8	18.4	7.3	6.7	4.5	28.8

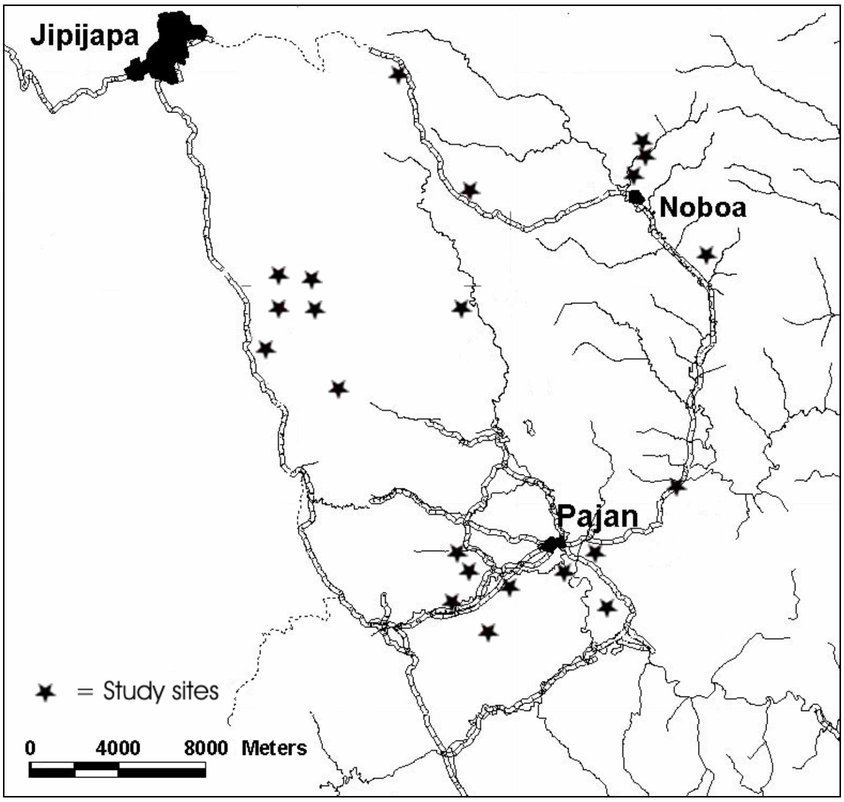

Fig. 2: Study region with study sites

The highland coffee (*Coffea arabica* L.) is cultivated in traditional agroforestry systems, which vary in the diversity of shade trees and light conditions (Fig. 3A,B). The shade tree canopy can was comprised of Leguminosae (*Inga* sp.), forest remnant trees or trees that provide products such as fruits, construction materials or timber for an additional income besides coffee production, but also for local subsistence. Certified organic and non-organic coffee agroforestry systems exist, but both generally lack agrochemical inputs. Weeds are cut once per year, just before the final ripening of coffee fruits in June/July, to facilitate harvest. Since these agroforests constitute the only forest-like habitat left (except the few small forest fragments), they are of high importance for the conservation of biodiversity in this highly anthropogenic disturbed region.

Fig. 3A: High shaded coffee agroforest with a diverse canopy of shade trees.

Fig. 3B: Low shaded coffee agroforest with predominantly banana (*Musa* sp.) as shade trees.

Study organisms

Coffee and coffee flower-visiting bees

Coffee is the second-most traded commodity in the world, next to petroleum (see FAOSTAT: http://faostat.fao.org/). The dramatic increase in coffee production through the increasing number of intensively managed monocultures, in countries such as Vietnam, has lead to global oversupply of coffee (Oxfam 2005), which in turn causes substantial declines of coffee prices on the world market. This considerable reduction in coffee prices particularly threatens the abundant small scale producers whose livelihood depends on the production and sale of coffee beans (Perfecto & Armbrecht 2003, Oxfam America 2005). In 2004, the highland coffee constituted about 60 percent of the globally produced coffee (Deutscher Kaffeeverband 2005). Although *Coffea arabica* is self-compatible, fruit set and fruit quality were found to considerably increase with bee pollination (e.g. Raw & Free 1977, Roubik 2002, Klein et al. 2003a,b, Ricketts et al. 2004).

Depending on the growing area, coffee can flower up to several times per year, triggered by single heavy rainfalls. In the study area, coffee shrubs only flower once per year in the dry season for only two days and almost all shrubs in one agroforest flower synchronously. The high number of flowers during these flowering periods, and the intensive odour of coffee flowers, attracts a high number of bees, which forage on nectar and pollen of coffee flowers. In the Neotropics the Africanized honeybee (*Apis mellifera scutellata* Lepelitier) is the dominant visitor of coffee flowers, but also species of stingless bees (Meliponinae) constitute a high proportion of the coffee flower-visiting bee community. Furthermore solitary bees feed on coffee flowers, but their number is rather low in contrast to the abundant social bees (Roubik 2002).

Cavity-nesting bees and wasps and their parasitoids

The community of above-ground cavity-nesting bees and wasps and their parasitoids enemies provides a set of important ecological functions. Solitary bees are important pollinators of wild and cultivated plant species (Corbet et al. 1991, Freitas & Paxton 1998, Vicens & Bosch 2000, Kremen et al. 2002, Klein et al. 2003b), thereby contributing to plant diversity but also to crop production (Kremen et al. 2002, Klein et al. 2003b). Solitary wasps may play an important role in biological control, by preying on pest caterpillars of wild and cultivated plants (Harris 1994, Tscharntke et al. 1998, Klein et al. 2002). Additionally, this group was found to be highly suitable as an indicator of biodiversity (Tscharntke et al. 1998). The community can easily be collected with the standardised method of exposing trap nests, which also affords the possibility of long-term observations. Traps constitute a plastic tube filled with internodes of reed. Adult solitary bees and wasps build their nests in these hollow reeds, lay in their eggs and provide larval food resources in form of other insect larvae (Eumenidae), spiders or insects (Pompilidae, Sphecidae) or nectar and pollen (Apidae). Natural enemies of those species feed on the larvae (parasitism) or their food provisions (cleptoparasitism).

An observation of cavity-nesting solitary bees and wasps and their parasitoids with standardised trap nests provides the possibility to examine community patterns, their relation to habitat modification and variation in space and time with respect to the capability of ecosystem services provided by bees and wasps. In addition it also affords the analysis of diversity/function relationships with parasitism and its temporal stability in real landscapes.

Results and conclusions

Community patterns of coffee flower-visiting bees and coffee yield and revenues

Flower-visiting bees showed contrasting responses to coffee flowering at different spatial scales. On a field scale, bee density decreased with increasing availability of floral resources, expressed by the percentage of flowering coffee shrubs, thereby showing a dilution effect. In contrast, on a shrub and on a branch scale, bee density increased with increasing availability of floral resources, expressed by the number of inflorescences per coffee shrub or per shrub part, thereby showing a concentration effect. Additionally, bee density was higher on coffee shrubs being only partly rather than totally surrounded by other flowering coffee shrubs, thus underlining the dilution effect found on a field scale. Bee diversity increased with increasing tree diversity on a field scale, but showed no relation to the percentage of flowering coffee shrubs, conversely on a shrub and a branch scale, bee diversity was related to a high number of inflorescences per shrub or shrub part, and additionally was higher on half-shaded and non-shaded than on totally shaded coffee shrubs. Our results show that patterns of flower-visiting bee communities of only one spatial scale can not be generalized, and emphasise the importance of considering different spatial scales, as the number of pollinators may be limited on higher scales (Chapter 2).

Coffee yield (kg/ha) and consequently net revenues ($/ha) from coffee production were positively related to the density of coffee flower-visiting bees. Shade density did not have an effect on coffee yield within a canopy cover of 80 to 100 percent, nor was it related to the density of bees. Coffee yield increased twofold and net revenues tenfold through a fivefold enhancement in bee density. These results, based for the first time on farm-scale yield data confirm and strengthen the economic value of bee pollination for coffee production (Chapter 3).

Trap-nesting bees and wasps and their parasitoids

Species richness of cavity-nesting Hymenoptera showed distinct seasonality; species richness of both, bees and wasps was significantly higher in the rainy season. Likewise, bee abundance was significantly higher in the rainy season, but wasp abundance showed no seasonality. In contrast, vertical stratification (herb layer versus coffee shrub layer) was only pronounced for cavity-nesting bees. Both, species richness and abundance of bees were significantly higher at the herb layer, as solitary bees mainly forage on flowering herbs, whereas coffee flowers may not provide a continuous and suitable floral resource. Wasp species richness and abundance appeared to be distributed homogenously across the two heights. Abundance of both, bees and wasps, increased with the percentage of incident light, but for bees this was only found at lower traps. The results show that a distinct seasonality in tropical regions can influence diversity patterns, and that different guilds show similar seasonal variations. However, vertical stratification in Hymenoptera appeared to be guild dependent, and it is emphasised that even in relatively small vertical range diversity patterns can change significantly (Chapter 4).

Parasitism rates of both, wasps and bees, increased with increasing species richness of their parasitoids. Additionally, parasitism rates of wasps decreased with increasing species richness of wasp hosts, thereby increasing resistance against consumption. However, a relatively low species richness of bee hosts could not resist against parasitism. Temporal stability of parasitism rate increased with increasing species richness of parasitoids for both host groups (wasps and bees), but was not related to the respective host diversity. Temporal stability of parasitism rates also increased with temporal stability of parasitoid species richness, but this relation was restricted to wasp hosts. Temporal variation in host bee diversity was high and correlated with high variability in enemy diversity, which apparently could not stabilize parasitism anymore. The results provide evidence that the positive relation between diversity and ecosystem function in a multitrophic system is constant across different host guilds, but resistance effects of host diversity are guild dependent. Furthermore, stabilizing effects of a temporally stable parasitoid community appeared to depend on the respective host community patterns, which were likely mediated by temporal variation in host resource availability (Chapter 5).

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CHAPTER 2

CONTRASTING RESPONSES OF BEE COMMUNITIES TO COFFEE FLOWERING AT DIFFERENT SPATIAL SCALES

Abstract

While investigating biodiversity patterns on different spatial scales, ecological processes determining these patterns have been rarely analysed. Flower visitation by bees is an important ecological process that is related to floral resource availability. However, little is known about whether responses of bee communities to floral resource availability change at different spatial scales. We studied density and species richness of flower-visiting bees in relation to floral resource availability, provided by coffee, in traditional agroforestry systems on a field, shrub, and branch scale. On a field scale, mean bee density per shrub increased with decreasing proportion of flowering coffee shrubs per site, showing a dilution effect. Conversely, on shrub and branch scales bee density per shrub, or shrub part, increased with increasing number of inflorescences, showing a concentration effect. Additionally, bee density per shrub was higher on those that were only partly, rather than totally surrounded by other flowering coffee shrubs. Species richness of flower-visiting bees was positively affected by high resource availability on a shrub and a branch scale, expressed by a high number of inflorescences, but at the field scale the proportion of flowering shrubs per site did not have any effect on species richness. Our results show contrasting responses of the community of flower-visiting bees to floral resource availability, depending on the spatial scale considered. We conclude that patterns of flower-visiting bee communities of only one spatial scale can not be generalized, since the number of pollinators may be limited on a field scale, but not on smaller scales.

Key words: Apidae, concentration effect, dilution effect, ecosystem services, floral resources, flower visitors, foraging behaviour

Introduction

Biodiversity patterns vary across different spatial scales (Wagner et al. 2000, Gering & Christ 2002, Willis & Whittaker 2002, Summerville et al. 2003). Factors driving biodiversity are known to be scale-delimited such that variables accounting for species richness on a smaller scale may operate differently on broader scales (Crawley & Harral 2001, Steffan-Dewenter et al. 2001, Willis & Whittaker 2002, Tylianakis et al. 2006). Investigations of communities on different spatial scales have mainly paid attention to gradients from local fields to landscapes, regions or even larger geographical scales (latitudes, continents). Examples include studies on birds (e.g. Lennon et al. 2001**,** Rahbek & Graves 2001), bees (Steffan-Dewenter et al. 2001, Steffan-Dewenter et al. 2002), butterflies (Summerville et al. 2003) or herbivory and parasitism rates (Thies et al. 2003). Only few studies included community patterns on scales within single sites, like patches or quadrats for comparing plant diversity (Wagner et al. 2000, Crawley & Harral 2001) or even single plant individuals and seed heads for analyzing parasitoid density (Norowi et al. 2000). Moreover, the majority of studies on scale dependence of biodiversity failed to analyse the ecological processes determining these patterns (see Huston 1999, Wagner et al. 2000, Crawley & Harral 2001). Combining community structures and ecological processes on small scales below the local (field) scale may contribute to the assessment of large-scale biodiversity patterns, providing a better understanding of the ecological factors driving these patterns.

The distribution of bee communities is of particular interest. As pollen vectors, bees provide important ecosystem services (Daily et al. 1997) and thus not only contribute to the maintenance of plant diversity but also encourage crop production (Free 1993, Roubik 1995, Buchmann & Nabhan 1996, Daily et al. 1997, Allen-Wardell et al. 1998, Kremen et al. 2002, de Marco & Coelho 2004, Ricketts et al. 2004). A high species richness and abundance of pollinating bees can provide high pollination success, even in self-pollinated plants such as the highland coffee, *Coffea arabica* L. (Rubiaceae), a tropical cash crop (Raw & Free 1977, Roubik 2002, Klein et al. 2003, Ricketts et al. 2004). Even though some investigations have already produced insights into the scale dependence of bees and their foraging behaviour on a landscape scale (Steffan-Dewenter et al. 2002, Westphal et al. 2003), to our knowledge, a comparison of bee distributions at smaller scales, from habitat level down to single plant species or individuals, is still missing.

Foraging behaviour may change in response to the factors that operate at different scales (Crist & Wiens 1994). In particular, floral resource availability, the quantity of flowers but also floral reward structure (nectar and pollen) affects the foraging behaviour of flower visitors (Stone 1994, Steffan-Dewenter & Tscharntke 2000, Klein et al. 2004, Potts et al. 2004). Patterns of floral supply may differ between and within scales. On a field scale, synchronous flowering of a single plant species provides a high number of flowers, which is supposed to attract a large number of pollinators, thereby enhancing cross pollination (Sakai 2002, Forsyth 2003). On smaller scales, within a habitat, plant arrangement and the number of flowers on single plants respectively may influence foraging behaviour and flower or plant constancy of bees (Kunin & Iwasa 1996). On the smallest scale, the distribution of flowers on a plant may affect patterns of flower visitors on a single plant. In the case of coffee, inflorescences develop predominantly on the new shoots at the end of a branch or the upper part of the coffee shrub. Additionally, pollinators may prefer certain flower positions on a single plant (Hambäck 2001) and differences in pollen deposition at different heights have also been found (Lortie & Aarsen 1999). An investigation of bee communities over different spatial scales may provide new insights into bee foraging behaviour and thus bear implications for the management of crop cultivars with the aim of successful pollination.

We studied the responses of flower-visiting bees on coffee to floral resource availability at three different scales, a field, a shrub and a branch scale, considering the following questions on each scale respectively:

Field scale: How does synchronous flowering of coffee shrubs in a single coffee field influence the distribution of bee communities?

Shrub scale: Does the degree of floral resource availability on and around a single coffee shrub have an impact on foraging behaviour of bees?

Branch scale: Do flower visitors prefer certain spatially oriented flower patches on a coffee shrub?

Material and methods

Study area

The study was carried out from October to December 2003 in the cantons Jipijapa, Pajan, and Noboa in Manabi, coastal Ecuador. The study area is situated at an altitude of 100-550 m (17 N546800 m, E 9849274 m) with an annual rainfall of 1500 to 1700 mm, and a mean annual temperature of 25°C. Seasonality is very distinctive; the dry season lasts approximately from June until the end of December, with hardly any rainfall. Coffee (*Coffea arabica*) is cultivated in traditional agroforestry systems, planted under a canopy of various shade trees. The tree canopy is comprised of Leguminosae (*Inga* sp.), forest remnant trees, or trees that provide products for local or market subsistence, (e.g. fruits, construction materials or timber). Low-density or monospecific shade coffee or sun coffee scarcely occur in this region and thus were not included. Certified organic as well as non-organic coffee agroforestry systems exist, but the latter generally also lack agrochemical inputs. Weeds are cut once per year, just before the final ripening of coffee fruits in June/July, to facilitate harvest. In this region, coffee flowers only once per year in the dry season, with buds generally opening eight days after a single heavy rainfall. Coffee flowered at different times in different sites, due to temporal variation in rainfall between different parts of the study region.

For an investigation of coffee flower-visiting bees, we chose 22 agroforestry sites (Fig. 1). In most sites, more than 50 percent of coffee shrubs flowered synchronously within 1-2 days. In four sites we watered eight to ten randomly chosen shrubs, because buds had already started to dry out. Accordingly there was a gradient in the proportion of flowering coffee shrubs along sites.

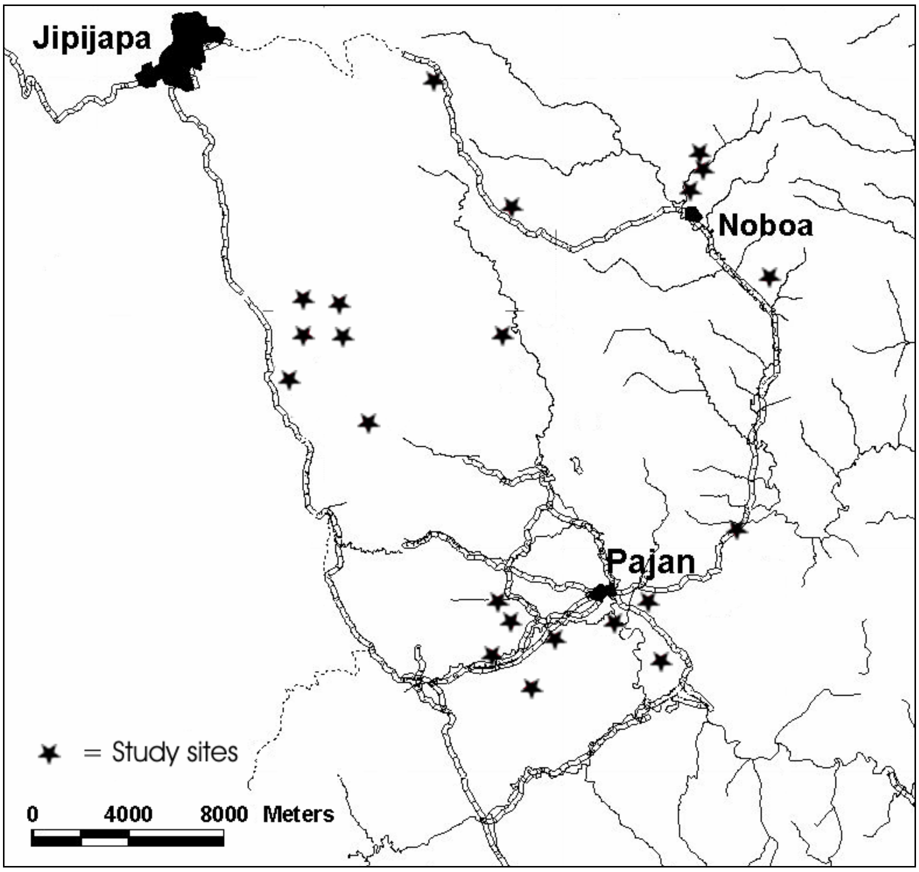

Fig. 1: Map of the study region with study sites.

Bee observations

For the observation of flower-visiting bees we chose four coffee shrubs per site. Shrubs were about the same height of 1.6 - 1.8 m, and approximately reached about the same age. Shrubs were situated in the middle of a field to avoid edge effects. Flower-visiting bees were observed 15 min on each of the four coffee shrubs (divided into five minute intervals) between 8:00 and 14:00 when bees were active. Each flower visitor was recorded and identified. After observations, bees were caught by sweep-netting for further identification. Short flowering times combined with a low number of individuals inhibited sampling of some of the observed morphospecies, so that only eight could be identified to genus or species level. Spatial distribution of the flower-visiting community foraging on coffee shrub was analysed on a total of 18 extra shrubs in three sites, chosen after the same criteria as the four shrubs per site. We defined the shrub parts as the half of the height of the shrub (excluding the branchless stem) for top/bottom (n = 9) and the half of each branch for outside/inside (n = 9). We observed bees on each shrub part for 15 min.

Floral resource availability and biotic and abiotic habitat parameters

Field scale

The flower availability per site was calculated as the proportion of all flowering coffee shrubs relative to all shrubs found in one site. Additionally the percent cover of all non-coffee flowering plants (of which all were herbs) was estimated.

Habitat characteristics of the 22 agroforestry sites were quantified to test for possible relations with species richness or density of bees. Percentage incident light was measured with a luxmeter (digital light-gauge with four scopes from 0-1999 W/m^2, Mavoloux, Gossen) and canopy cover was estimated using a densitometer (Spherical crown densitometer, Forestry Suppliers). Vegetation was sampled in nine quadrats per site. In 2.5 x 2.5 m quadrats for herbs and 10 x 10 m quadrats for shrubs and trees the number of morphospecies and the respective number of individuals were recorded. Height of trees was measured to calculate the coefficient of variation in tree height as an indicator of structural habitat diversity. Because some tree species were represented by only one or few individuals in a site, we calculated the Shannon-Wiener diversity index as a measurement for canopy tree diversity.

Shrub and branch scale

Floral resource availability per shrub was estimated by counting all flower inflorescences on the observed shrub. Here an inflorescence consisted of a collar in the leaf axils, comprising 10-20 flowers. Additionally we noted whether shrubs were totally surrounded by other flowering coffee shrubs, (all neighbouring shrubs flowered, 4-6 shrubs) or only partly surrounded by flowering shrubs (1-3 shrubs). During bee observations, we measured temperature and humidity on each observed shrub in five minutes intervals between observation periods to calculate mean values, and recorded the time by starting the observations. We classified shrubs into the three groups sunny, half-shaded, and shaded shrubs. On each of the 18 extra observed shrubs we counted inflorescences and estimated their proportion at branches at the top and at the bottom, and outside and inside of the respective shrubs.

Statistical analyses

All data were transformed to meet conditions of normality if necessary. Percentages were arcsin-square-root-transformed (Sokal & Rohlf 1995). Statistical analyses were performed using the software Statgraphic Plus 3.0 for Windows (Manugistics 1997) and Statistica 6.1 (StatSoft 2003).

For analyses at the field scale we calculated the mean value of the four observed shrubs for the number of individuals thereby yielding the mean bee density (number of individuals per shrub) per shrub but we used the total number of species found in a site. For analyses on the shrub scale we took the density per shrub and the actual species number per shrub. Similarly, we used the density and species richness per shrub part for branch scale analyses. To investigate relations with the biotic and abiotic habitat parameters on a field scale we conducted multiple regressions using backward selection until only significant variables were left. To show that sites were independent from each other we tested for spatial autocorrelation. We related the residuals from the results of the multiple regressions with either bee density or bee species richness to the geographic distances between sites with the Mantel statistics based on Spearman's rank correlations with 1000 permutations and Euclidian distances as similarity indices (Legendre & Legendre 1998). This method allows excluding the variation explained by the habitat parameters rather than arbitrarily pooling them. For the analyses we used the statistics program R (R development Core Team 2004). The results showed that there was no spatial autocorrelation in the data, neither for bee density nor for bee species richness (bee density: r = - 0.11, p = 0.94, bee species richness: r = - 0.08, p = 0.86). Because the four shrubs of one site were not independent of each other, we used a mixed effects model for analyzing the relation of floral resources or light conditions to bee density or species richness on a single shrub. With this model we were able to exclude within-site variation by using "site" as a random factor in the model (see Crawley 2002, p. 35), thereby accounting for spatial autocorrelation on a shrub scale. Differences between shrub parts were analysed with One-way ANOVAs. We estimated total species richness of bees using the Abundance-based Coverage Estimator ACE of the program EstimateS (Colwell & Coddington 2000), using 100 randomizations, and calculated saturation values of the recorded species numbers.

Results

We identified 29 morphospecies of flower-visiting bees on coffee in 22 sites including 19 morphospecies of social bees (2743 individuals) and ten solitary bee species (only 29 individuals). The bee community in a single site was dominated by one or two species, the Africanized honeybee *Apis mellifera scutellata* (Lepeletier) (10 to 67 %, mean: 41.83 ± 19) and/or the stingless bee *Partamona peckolti* (Friese) (2 to 66%, mean: 23.3 ± 18.4). Further significant visitors were the stingless bee species *Nannotrigona mellaria* (Smith), *Nannotrigona perilampoides* (Cresson), *Cephalotrigona capitata* (Smith), *Tetragonisca angustula* (Latreille), *Trigona almathea* (Vachal), and *Melipona mimetica* (Cockerell). The number of morphospecies observed was highly correlated with the estimated species number ($r = 0.91$, $n = 22$, $p < 0.0001$). The mean saturation value was 84.39 ± 14.5 % of the estimated species number. Because observed species richness revealed the pattern of estimated species richness we used the observed species number for further analyses.

Field scale

Density of flower-visiting bees did not correlate with species richness. Bee density (mean number of individuals per shrub) increased significantly with decreasing proportion of flowering shrubs per site (Fig. 2), but was not related to the percent cover of non-coffee flowering plants (average of 7.7 ± 12.13 %), nor to any of the habitat parameters. The number of bee species was not related to the percentage of flowering coffee shrubs per site or to the percent cover of non-coffee flowering plants, but it was positively correlated with the diversity of canopy trees (simple regression: $F_{1,20} = 9.21$, $r^2 = 0.18$, $p < 0.05$, $y = 3.96 + 4.5 * x$).

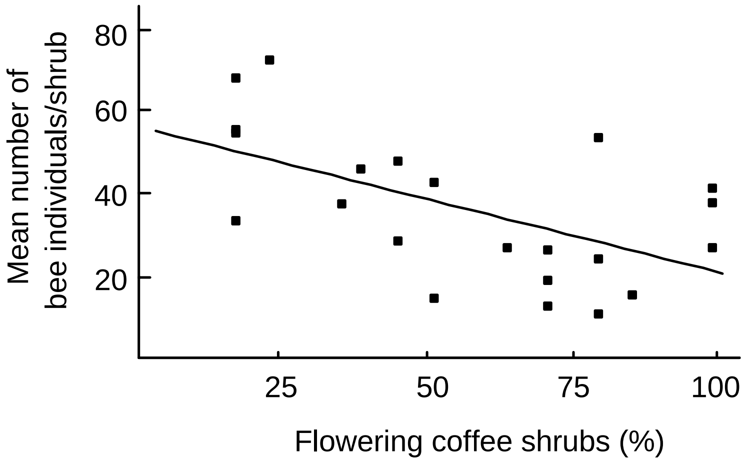

Fig. 2: Mean density of flower-visiting bees per shrub (observed within 15 min per shrub) in relation to the proportion of flowering coffee shrubs per agroforestry site. $F_{1,20} = 8.09$, $r^2 = - 0.28$, $p < 0.05$, $\log (y) = 2.32 - 0.32 * \arcsin (\mathrm{sqrt} (x / 100))$.

Shrub scale

Both density and species richness of bees on a shrub were significantly positively correlated with the number of inflorescences per shrub (Fig. 3A, B). Additionally, bee density was significantly higher on shrubs that were only partly rather than totally surrounded by other flowering coffee shrubs (Fig. 4).

More species were observed on sunny and half-shaded than on shaded shrubs ($F_{2,52} = 8.70$, $r^2 = 0.23$, $p < 0.001$). Species richness similarly increased with temperature, which was positively related with time and differed between the three shade categories of the shrubs (Correlation matrix, Tab. 1).

Table 1: Correlation[a] matrix of the abiotic shrub parameters and species number and density of flower-visiting bees per shrub[b].

	Temperature	Time of day	Species number	Bee density
Humidity	- 0.8169****	- 0.7327****	- 0.3700**	0.1606
Temperature		0.7160****	0.3848**	- 0.1215
Time of day			0.1659	- 0.2499
Species number				0.5136***

[a] Pearson correlation coefficient

[b] Significance, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$; n = 64 shrubs

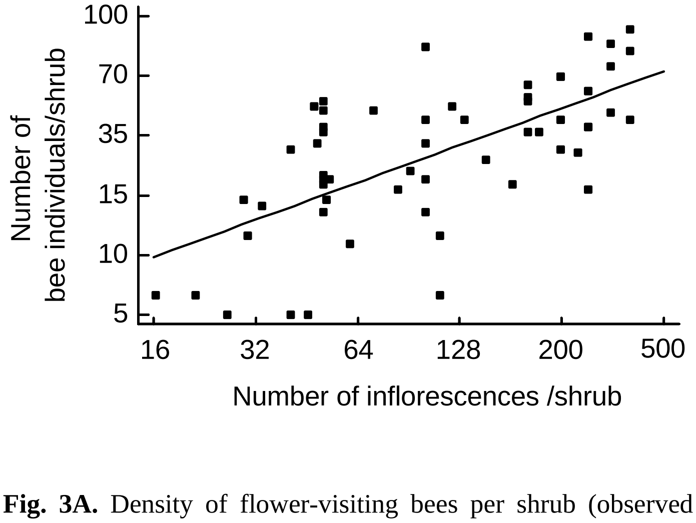

Fig. 3A. Density of flower-visiting bees per shrub (observed within 15 min per shrub) in relation to number of flower inflorescences per shrub. Mixed effects model: $F_{1,53} = 47.87$, $r^2 = 0.43$, $p < 0.0001$.

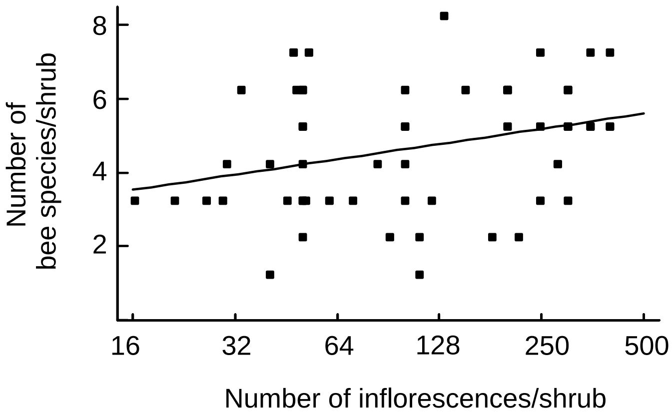

Fig. 3B. Species number of flower-visiting bees per shrub (observed within 15 min per shrub) in relation to number of flower inflorescences per shrub. Mixed effects model: $F_{1,53}$ = 7.45, r^2 = 0.09, $p < 0.01$.

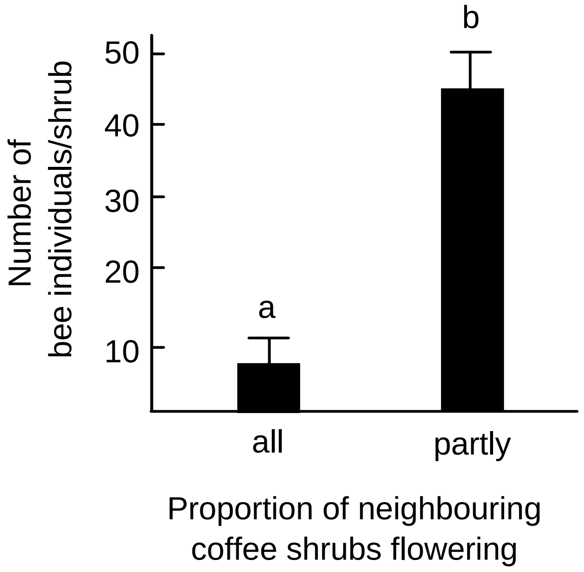

Fig. 4: Density of flower-visiting bees on shrubs being totally or only partly surrounded by other flowering coffee shrubs (observed within 15 min per shrub). Arithmetic mean and standard error are given. Mixed effects model: $F_{1,53}$ = 10.35, r^2 = 0.09, $p < 0.01$.

Branch scale

The proportion of inflorescences on a coffee shrub was significantly higher on branches at the top of a shrub than at the bottom (One-way ANOVA: $F_{1,17}$ = 46.49, $p < 0.0001$) and significantly higher at the outer than at the inner part of a shrub (One-way ANOVA: $F_{1,14}$ =

10.22, $p < 0.01$). The same pattern was revealed for both bee density (Fig. 5A, B) and bee species number (Fig. 6A, B), indicating that both corresponded to relative dense flower patches on a coffee shrub. When the proportion of inflorescences was included as a covariable in the analyses, differences in species number or density between the different parts of a shrub were no longer significant.

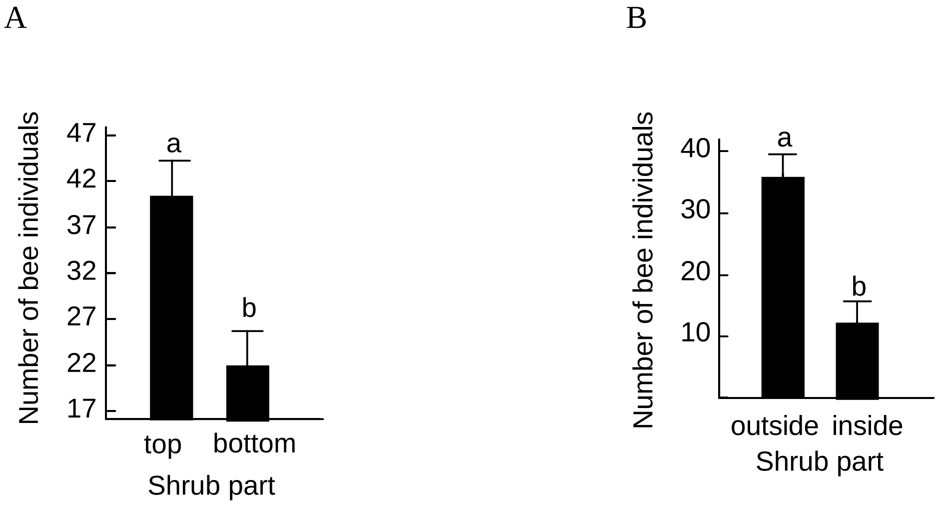

Fig. 5: Density of flower-visiting bees at (A) the top and at the bottom and (B) the outer and inner part of a coffee shrub (observed within 15 min per shrub part). Arithmetic mean and standard error are given. One-way ANOVA; (A): top/bottom: $F_{1,16} = 10.81$, $p < 0.01$, (B): outside/inside: $F_{1,16} = 20.39$, $p < 0.001$.

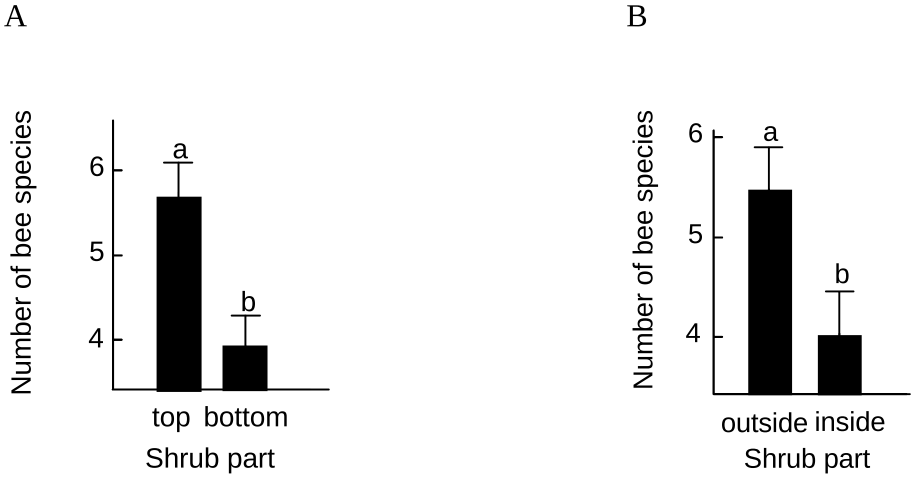

Fig. 6: Species number of flower-visiting bees at (A) the top and the bottom and (B) the outer and the inner part of a coffee shrub (observed within 15 min per shrub part). Arithmetic mean and standard error are given. One-way ANOVA: (A) top/bottom: $F_{1,16} = 11.08$, $p < 0.01$, (B): outside/inside $F_{1,16} = 5.16$, $p < 0.05$.

Discussion

Our results show that the density of flower-visiting bees on coffee responded contrastingly to the availability of floral resources at three different spatial scales. On the field scale, bee density increased with decreasing proportion of flowering shrubs per site, whereas on a shrub scale bee density increased with increasing number of inflorescences per shrub, but was higher on shrubs that were only partly, rather than totally surrounded by other flowering shrubs. On a branch scale, density of bees corresponded to dense flower patches at different parts of a coffee shrub. Bee species richness was positively affected by high resource availability on a branch and on a shrub scale, but not on a field scale.

Accordingly, on a branch and on a shrub scale, bee density was positively influenced by a high number of inflorescences, whereas at the field scale relative high floral resource availability due to a high proportion of shrubs flowering influenced bee density negatively. When all shrubs flowered synchronously, the number of bees per shrub was reduced, resulting in a dilution effect. Additionally, the reduced number of bees on shrubs that were completely surrounded by other flowering coffee shrubs also implies a dilution of bee density. However, when only few shrubs flowered in a site, the number of bee visitors per shrub increased, resulting in a concentration effect. The density of flower visitors seemed to increase proportionally with increasing resource availability only to a certain degree. That is in accordance with the suggestion that the pool of available pollinators might be saturated below the maximum flower density (Tøtland & Matthews 1998). However, these results do not support the assertion that synchronized flowering may increase activity of flower visitors through immigration and population growth (Sakai 2002). In contrast, on a smaller scale (i.e. shrub and branch scale), a high number of flowers enhanced the number of flower-visiting bees. This was in accordance with a previous study that found an increase in the density of flower visitors with increasing flower density on a shrub (Klein et al. 2002).

On the basis of these contrasting effects of high resource levels on different spatial scales, we conclude that the number of flower visitors seems to increase with a high number of flowers available but only as long as there still exists a pool of pollinators. This implies that the number of flower visitors in a site is constant but bee density per observation unit may decrease after saturation of floral resources is reached. In this study the relatively small number of non-coffee flowering plants did not have an impact on flower visitors observed on coffee plants. In the dry-season, flowering herbs are very sparse so the high number of coffee flowers may be the more attractive food source for bees. Furthermore, the heterogeneity of flower-visiting bee communities on a single plant was related to a similarly heterogeneous distribution of flower inflorescences. Flower visitors on a single plant seemed to be attracted by flower patches on a shrub with a relatively high number of flowers. Finally, floral reward structure, as the ultimate attractant of flower visitors (Bosch 1997), might have influenced foraging behaviour of bees on this smallest scale. Flower visitors are known to prefer high quality nectar (Stone 1994, Skyhoff & Bucheli 1995) and flowers at the top and outside of a shrub might have offered more favourable floral reward conditions. However flower visitors did not have apparent preferences concerning the spatial position of flowers per se. Hence, from this point of view we can not confirm the idea of a spatially heterogeneous bee community on single plants, suggested by Hambäck (2001).

Species richness on a field scale showed no response to floral resource availability. On a shrub and branch scale it increased, similarly to bee density, with the number of inflorescences per shrub or shrub part. Dense flower patches seem to be the more attractive resource for many different bee species at smaller spatial scales. Furthermore, on a field scale, bee species richness increased with the diversity of shade trees, underlining the results found by Klein et al. (2002), who observed an increase in social bee species richness on coffee flowers with decreasing land-use intensity. Additionally, on a shrub scale, species richness of flower-visiting bees was higher at sunny and half-shaded coffee shrubs than at shaded ones, showing a preference for high light intensity in flower-visiting bees. Foraging behaviour of bees is known to be temperature dependent (Roubik 1989, Herrera 1995), and we also found a positive relationship between species number and temperature. At cold ambient temperatures, bees may prefer to visit sunny flowers to raise their body temperature (Roubik 1989). Consequently microclimate might have had also an effect on the distribution of foraging bees on the branch scale. Flowers at the top and outside of a shrub may be more exposed to sun light than those at the bottom and inside a shrub. Furthermore flowers in direct sunlight secrete nectar earlier and at a higher rate (Roubik 1989), increasing the availability of floral rewards and thereby attracting more visitors (Stone 1994, Skyhoff & Bucheli 1995).

Our results on smaller than landscape scales affirm the suggestion that factors which are responsible for either biodiversity or community patterns are scale-dependent (Clarke & Lidgard 2000, Crawley & Harral 2001) and reflect results of studies on broader scales, which show scale-specific dependences on different variables of communities. For example, Rahbek & Graves (2001) demonstrated that birds responded in a varied manner to a suite of environmental variables on different spatial scales in South America. Furthermore, de Vries et al. (1997) and de Vries & Walla (1999) found that butterfly communities are affected by scale-dependent factors such as forest strata and forest type.

Here we show that even on smaller scales below the local one, species richness can be related to different variables, depending on the respective scale considered. In addition, our results demonstrate that a single variable can even have reversed effects on the same community at different scales, as revealed by the contrasting responses of flower-visiting bee communities to resource availability from a field to a branch scale. Varying patterns of resource-density dependence at different scales are not unlikely. For example Norowi et al. (2000) found reverse parasitism rates for a single parasitoid-host relationship comparing the finest scale, represented by seed heads, with the intermediate scale, represented by plant individuals.

We conclude that community patterns such as the relation of flower-visiting bee communities to floral resource availability can not be generalized but have to be considered separately for each single scale, assuming that the number of bees may be limited in a site. From an applied perspective this may be taken into account in management schemes to reach optimal coffee productivity, by encouraging successively rather than synchronously flowering coffee shrubs, thereby enabling concentration rather than dilution effects on flower visitation by bees.

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CHAPTER 3

THE CONTRIBUTION OF WILD BEES TO COFFEE PRODUCTION:

NEW ECONOMIC INSIGHTS BASED ON FARM-SCALE YIELD DATA

Abstract

Fruit quantity and quality of the highland coffee *Coffea arabica* L. have been shown to increase through bee-mediated pollination, and recently the monetary value of pollination service for coffee has been indirectly estimated. We show for the first time on a farm scale, that yield (kg/ha) and consequently (net) revenues ($/ha) were positively and linearly related to a high density of wild coffee flower-visiting bees. Shade has also been suggested to affect yield, but canopy cover (80 % to 100 %) was neither related to yield nor to bee density.

Net revenues from coffee production increased tenfold by a fivefold increase in bee density. With our new results on a farm scale we were able to confirm and strengthen the economic value of bee pollination for coffee production.

Key words: agroforests, canopy cover, *Coffea arabica,* economic importance, pollination, shade density, farm scale, revenues, wild bees, yield

Introduction

The self-compatible highland coffee *Coffea arabica* L. is known to benefit from pollination by wild or managed bees. Initial and final fruit set increase due to bee pollination in comparison to passive self-pollination (e.g. Raw & Free 1977, Roubik 2002, Klein et al. 2003a,b, de Marco & Coelho 2004, Ricketts et al. 2004). Additionally fruit quality (fruit weight and fruit shape) increases through bee pollination (Roubik 2002, Ricketts et al. 2004). Based on these enhancements, Ricketts et al. (2004) recently calculated the monetary value of pollination service for coffee. However, extrapolating yield from fruit set data provides only indirect evidence of the economic importance of pollination. To prove if these results are also valid on a farm scale, a direct evidence of the economic importance of pollination service for coffee production based on yield data from a field level is still required.

Shade is also supposed to affect coffee yield by regulating pests and diseases (Perfecto et al. 1996, Staver et al. 2001, Soto-Pinto et al. 2002). But it also affects physiological traits of coffee plants, e.g. fruit quality (Cannel 1974, Muschler 2001, DaMatta 2004). However the importance of shade is still controversial and the inconsistency in results demands further analyses on smaller shade gradients to specify the importance of shade for coffee production (see Perfecto et al. 2005).

Materials and methods

In the study region, Manabi, Ecuador (100-550 m asl, 17 N546800m, E9849274m), the highland coffee (*Coffea arabica*, Caturra variety) is cultivated in traditional agroforestry systems with a rather dense canopy of various shade trees. Fertilizer or agrochemicals were not applied, and managed bee colonies did not exist in or around the studied sites. From October to December 2003 we observed wild coffee flower-visiting bees in 22 agroforests, each approximately one hectare, on four coffee shrubs per site. We observed 15 minutes per shrub, recorded morphospecies and number of individuals to get a mean value for bee density per coffee shrub. From July to August 2004 we quantified coffee yield for each site by weighing all harvested ripe fresh fruits to calculate yield (in kg) per hectare. We assessed coffee revenues per hectare based on yield per hectare and the long-term average price of \$0.2 (US) per kg (SICA 2003, Benítez et al. 2006). Net revenues were calculated by taking into account fixed costs for pruning and cleaning (independent of coffee quantity) of \$57 (US) per year and variable costs (dependent from coffee quantity) of \$0.07 (US) per kg for harvest and transport (Olschewski et al. 2006). The average price for coffee and fixed and variable costs are based on dried coffee fruits ("bola seca"). As two kilos of "frutos cereza" (fresh fruits) correspond to one kilo "bola seca", yields had to be divided by two to determine revenues and net revenues. We estimated canopy cover, as an estimator of shade density, at the four edges and in the middle of nine 10 X 10 m quadrats (9 x 5 points = 45 points per site) using a densiometer (Spherical crown densitometer, Forestry Suppliers). We calculated the density of coffee shrubs per hectare and used the mean height of nine coffee shrubs per site as an estimator of age of the coffee stand. Because all shrubs in a site offered similar quantity of flowers we calculated the mean number of inflorescences on four coffee shrubs as an estimator of flower quantity in a site. We transformed variables to meet the assumptions of a normal distribution when necessary. Proportions were arcsin-square-root-transformed (Sokal & Rohlf 2001). To analyze relationships between yield or (net) revenues per hectare and the respective variables we conducted multiple regressions with the software Statgraphic Plus 5.1 for Windows (Manugistics 1997) and used backward selection until only significant variables remained.

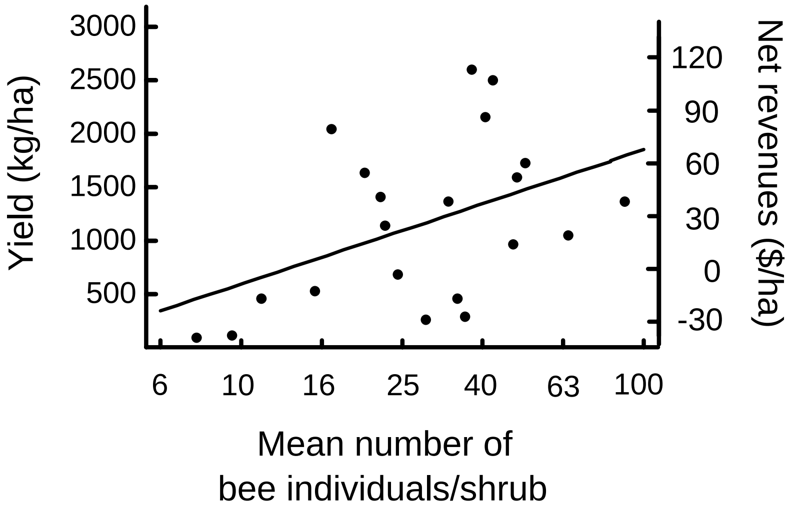

Fig. 1: Yield (fresh fruits) (kg/ha) and net revenues ($/ha) in relation to mean bee density per coffee shrub. (yield: $F_{1,19} = 4,7$, $r^2 = 0.20$, $p < 0.05$, $y = - 659 + 1252.42 * \log(x)$; net revenues: $F_{1,19} = 4,7$, $r^2 = 0.20$, $p < 0.05$, $y = -99.836 + 81.4075 * \log(x)$).

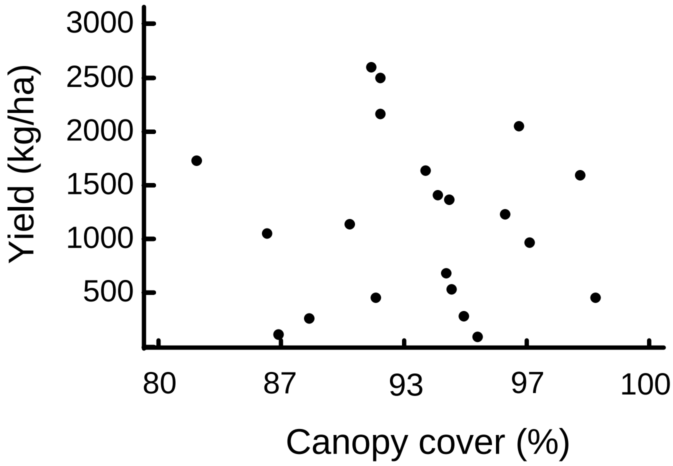

Fig. 2: Yield (fresh fruits) (kg/ha) in relation to canopy cover ($F_{1,19} = 0.07$, $r^2 = 0.0035$, $p = 0.8$, $y = 1873.51 – 546.7 * \arcsin(\mathrm{sqrt}(x/100))$).

Results and discussion

Coffee yield (kg/ha) increased with increasing mean bee density per coffee shrub (Fig.1) and accordingly did revenues and net revenues (revenues: $F_{1,19} = 4.7$, $r^2 = 0.19$, $p < 0.05$, $y = - 65.9 + 125.23 * \log(x)$; net revenues: Fig. 1). However, yield was neither related to canopy cover (Fig. 2), flower quantity, shrub density or age of coffee stand. Using the regression equations from the linear correlations we estimated that yield might be two times higher and net revenues even 10.5 times higher at 100 bees visiting a coffee shrub compared to 20 bees visiting a coffee shrub in a 15 min observation period (100 bees: 1845 kg/ha, \$63/ha, 20 bees: 969 kg/ha, \$6.1/ha). We could show for the first time on a farm scale, that real yield (kg/ha) is linearly correlated bee density. Thereby our finding supports and strengthens previous results on the contribution of bee pollination to coffee production (e.g. Raw & Free 1977, Roubik 2002, Klein et al. 2003a,b, de Marco & Coelho 2004). Based on this relationship we were also able to demonstrate for the first time on a farm scale the importance of bee pollination for coffee producers' income. Ricketts et al. (2004) already provided indirect evidence of the economic importance of bee pollination to coffee production, based on replicated fruit set data from one single coffee plantation. In contrast, we provide evidence for the monetary value of bee pollination based on actual yield data (weight/area) and including real replicates of 22 different coffee agroforests. There are probably two causes why weight of all fruits increased with an increasing number of bees foraging on a coffee shrub. First, fruit set (fruit to flower ratios) in coffee is known to increase by bee pollination. This enhancement is ascribed to high pollination efficiency by bees, comprising outcrossing effects (Klein et al. 2003a), a highly efficient deposition of pollen on the stigma (Kremen et al. 2002, Ricketts 2004) and a more effective distribution of pollen by bees than by wind. Yield was not related to the mean number of flowers per coffee shrub. Thus the positive relationship between yield and bee density indicates a higher number of fruits due to a high density of pollinating bees on a coffee shrub. Second, previous studies also showed that fruit weight is higher in bee pollinated than in self pollinated fruits (Manrique & Thiemann 2002, Roubik 2000b, Ricketts et al. 2004, Olschewski et al. 2006). A higher fruit mass can also be attributed to the effects of cross pollination (Free 1993, Roubik 2002, Ricketts et al. 2004). Consequently cross pollination in coffee increased both the number of fruits and the weight of each fruit (Olschewski et al. 2006). These complementary effects of bee pollination on coffee production appeared to cause the positive relation between bee density and yield/hectare. However, since there is a lot of unexplained variance in the relation between bee density and yield further factors such as microclimatic heterogeneity (e.g. the quality of light reaching leave surfaces) and factors causing fruit (or flower) abortion (e.g. drought, nutritional resource limitation etc. or heavy rainfall) may have additional effects on yield. In contrast to expectations shade density was not related to yield. Canopy cover varied between 80-100 percent, within this relatively small range variation in shade density appeared to be negligible for coffee production. A high degree of shading is supposed to be disadvantageous for coffee production (DaMatta 2004), but in low-elevated, high temperature regions, such as the study area, high shade densities with a canopy cover of 80 percent and more can be advantageous, by providing optimal microclimatic conditions for fruit ripening (Muschler 2001). The benefits of shade increase as the environment becomes less favourable for coffee cultivation (DaMatta 2004).

We conclude that bee density in coffee agroforests is related to yield in coffee production and may be responsible for a tenfold increase in net revenues. With our new results on a farm scale we were able to provide a further evidence of the economic value of bee pollination to coffee production.

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CHAPTER 4

VERTICAL STRATIFICATION AND SEASONAL VARIATION IN A TROPICAL COMMUNITY OF CAVITY-NESTING BEES AND WASPS

Abstract

Within-habitat distribution of insect communities may vary in space and time and affect associated ecological functions. Cavity-nesting solitary bees and wasps are important pollinators and predators, but little is known about their vertical and seasonal variation and interactions with habitat modification. In this context, the different ecological guilds bees and wasps might show deviating patterns. We studied vertical and seasonal variation of cavity-nesting bees and wasps in 14 traditional coffee agroforests in coastal Ecuador, constituting a gradient in light availability. We established traps as nesting resources, five at the height of coffee shrubs (1.5 m) and five at the height of the herb layer at (0.5 m) per site, and evaluated traps monthly for one year. Species richness of bees and wasps and bee abundance were significantly higher in the rainy than in the dry season, presumably due to a higher availability of food resources. Bee species richness and abundance were significantly higher at lower traps, as solitary bees mainly forage on flowering herbs. However, wasp species richness and abundance did not vary between trap heights. Bee and wasp abundance increased with light availability, but bee abundance only at lower traps at the herb layer which may profit more from reduced canopy cover than shrub layer. In conclusion, different ecological guilds using the same nesting site, showed congruent seasonal patterns. In contrast, vertical stratification was only pronounced for bees, thus diversity patterns can change even across a small vertical range. We emphasize the necessity to analyse diversity at different spatiotemporal scales and to differentiate between guilds to improve our understanding of diversity patterns for possible conservation management.

Key words: agroforests, diversity, Ecuador, resource availability, solitary hymenoptera

Introduction

Insect communities are known to show spatial and temporal variation in their distribution within habitats (de Vries 1997, Sperber et al. 2004, Tylianakis et al. 2005, Veddeler et al. 2006) and this variation may affect associated ecological functions (Luck et al. 2003). Understanding such variation is a prerequisite for potential habitat management with respect to the conservation of beneficial organisms in agroecosystems.

The vertical vegetation structure in forest-like habitats influences spatial distribution of insects (Southwood et al. 1979). However, despite the importance of vertical stratification in diversity measurements, comparative studies of insect diversity in managed forests have traditionally analysed single forest strata (Su & Wood 2001, but see De Vries 1997, Schulze et al. 2001). Vertical stratification can be caused by vertical resource heterogeneity and species-specific specialisations, both with respect to food, nesting sites, and microclimate (Schulze et al. 2001, Tanabe 2002, Veddeler et al. 2006). Additionally interspecific competition may result in a stratification of insect communities (Klein et al. 2003).

Also seasonality is supposed to influence diversity (DeVries 1997) and thus may be of special interest in tropical regions with a distinct seasonality (Wolda 1988). Seasonal variation in humidity, rainfall, and temperature can cause seasonal variation in tropical insect communities (Wolda 1988). Additionally seasonal differences in the availability of resources may result into seasonality in insect communities (Wolda 1978, Jones 2001). However, while there is evidence for seasonal patterns in tropical insect abundance (Wolda 1978, Kato et al. 1995, Novotny et al. 1998, Wagner 2001, Thiele 2005, Cuevas-Reyes 2006,) relatively few results are available for seasonal patterns in species richness of tropical insects (but see DeVries 1997, Hamer et al. 2005). Furthermore, habitat modification or complexity may influence seasonal or vertical patterns, by either dampening or strengthening environmental heterogeneity (Su & Wood 2001, Tanabe 2002).

The community of cavity-nesting solitary bees and wasps (Hymenoptera: Apidae, Sphecidae, Eumenidae, Pompilidae) fulfils major ecological functions: solitary bees are important pollinators of wild and cultivated plants (Corbet et al. 1991, Freitas & Paxton 1998, Vicens & Bosch 2000, Kremen et al. 2002, Klein et al. 2003), thereby contributing to plant diversity and crop production (Kremen et al. 2002, Klein et al. 2003). In contrast, solitary wasps may play an important role in biological control by preying pest caterpillars of wild and cultivated plants (Krombein 1967, Harris 1994, Tscharntke 1998, Klein et al. 2002). Furthermore bees and wasps are suitable indicators of biodiversity, ecosystem functioning and habitat quality (Westrich 1996, Tscharntke et al. 1998, Jenkins & Matthews 2004, Tylianakis et al. 2005). However, analyses of spatial variation in this community focused on scale gradients from plot to landscape level, whereas, little is known about vertical nest site preferences. Since bees and wasps belong to different ecological guilds (phytophagous vs. entomophagous) they might show discriminate vertical and seasonal distribution patterns (Kato et al. 1995, Wagner 2001, Sperber et al. 2004). Solitary bees provide floral products such as pollen or nectar as larval food in their nests, so a vertical and seasonal heterogeneity in floral resources can cause a similar heterogeneous distribution of bees (Veddeler et al. 2006). In contrast wasps, providing spiders, insects or larvae as larval food resource in their nests, may reflect possible patterns of their prey (Jones 2001, Wagner 2001).

An adequate habitat for analysing vertical and seasonal patterns in the community of cavity-nesting bees and wasps comprise traditional coffee agroforests. They harbour a high diversity of plants and insects (Perfecto et al. 1996), and by resembling natural forests with their vertical structured vegetation layers (Moguel & Toledo 1999), they offer an important refuge for former forest inhabitants (Solis-Montero et al. 2005). To expand our knowledge of species diversity patterns with regard to conservation management in tropical land-use systems we analyzed vertical stratification, seasonal changes and their interactions with habitat modification of cavity-nesting bees and wasps in traditional coffee agroforests in Ecuador, by exposing artificial nesting sites.

Materials and methods

Study area and sites

The study was carried out from June 2003 until May 2004 in the cantons Jipijapa, Pajan and Noboa in Manabi, coastal Ecuador. The study area is situated 100-550 m asl (17 N546800m, E9849274m). Annual rainfall lies between 1500 to 1700 mm, and the annual average temperature is 25°C. Seasonality is very distinctive, dry season lasts approximately from June until November, with hardly any rainfall (Table 1), and water shortage leads to a reduction in vegetational productivity and the loss of leaves (personal observation*)*. Within few weeks after the beginning of the rainy season new vegetational growth can be observed everywhere. Numerous traditional coffee agroforests are distributed randomly over the landscape, embedded in a mosaic of bushland, secondary forests, and agroecosystems such as arable crops (rice, maize) or pasture. The coffee agroforests consist of a community of various shade trees, comprising Leguminosae (*Inga* sp.), forest remnants, or trees which provide products for local or market subsistance, (e.g. fruits, construction materials or timber). Certified organic and non-organic coffee agroforests exist, both without any agrochemical input. For our investigation we chose 14 coffee agroforestry systems constituting a gradient in light availability.

Table 1: Monthly temperature (°C) and rainfall (mm) in Pajan (17N 563969, E 9828342m alt. 142m) within the study region from December 2003 until November 2004. The rainy season begins in December and ends in May.

	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Temperature	25.8	25.7	25.8	26.	25.9	25.9	25.6	25.3	25.4	25.6	25.6	25.4
Humidity	73.3	197.1	276.1	307.1	293.6	143.2	35.8	18.4	7.3	6.7	4.5	28.8

Trap nests

We provided nesting sites by establishing traps which consisted of plastic tubes filled with internodes of reed (*Arundo donax* L. Poaceae) of different diameters (see Tscharntke et al. 1998, Tylianakis et al. 2005). The exposure of trap nests comprises an unbiased standardised method for evaluating diversity and abundance, but also may indicate food and nesting resource availability (Klein et al. 2004), both factors being important to a successful reproduction of bees and wasps (Westrich 1996, Goodell 2003).

In each of the 14 systems we exposed ten traps, five at the approximate layer of coffee shrubs (1.5 m above ground) and the other five at the approximate height of the herb layer (0.5 m above ground). Traps were set up in branches of coffee shrubs, other shrubs or trees and stayed in the field continuously for one year, including a complete dry and rainy season. To prevent ants from entering the traps we put sticky glue on the traps suspension. Each month we evaluated traps by taking out the occupied reeds and replacing them with empty ones. We reared the occupied reeds in the laboratory until the insects emerged. We noted the morphospecies of each emerged individual, the number of brood cells for each morphospecies.

Habitat parameters

We estimated light availability of the 14 agroforestry systems to test for possible relations with the community of cavity-nesting bees and wasps. We measured light intensity with a luxmeter (digital light-gauge with four scopes from 0-1999 W/m^2, Mavoloux, Gossen) at the edges and in the middle of nine 10 x 10 m quadrates and outside the site under open sky to calculate the percentage of incident light (hereafter incident of light) in the systems.

Statistical analyses

To analyse vertical and seasonal community structure of cavity-nesting bees and wasps, we first divided the data into two groups dry season (June to November) and rainy season (December to May), and than for each trap height into the groups high and low traps. All analyses were performed using the statistical program Statgraphics Plus for Windows 5.1 (Manugistics 2001). We conducted General Linear Models (GLM) for each of the response variables number of bee species, number of wasp species, and the number of constructed brood cells as an estimator of the abundance for each group, with backward stepwise elimination. As predictor variables we included the categorical variables season (rainy and dry season) and height of traps (top and bottom) and the continuous variables incident of light. Model residuals were tested for normality and response variables transformed if necessary. Percentages were arcsin-square-root transformed. When trap height, or season or both had no effect, we respectively pooled the data for the analysis to avoid pseudoreplication.

Results

In total 23 species nested in the traps, of which nine were solitary bee species (Apideae) comprising 579 brood cells, and five eumenid wasp species with 1409 brood cells, seven sphecid wasp species with 335 brood cells and two pompilid wasp species with 824 brood cells. Altogether 1059 nests were built within one year.

Bees

Bee species number was positively related to the number of brood cells ($r = 0.6642$, $p < 0.0001$). Including number of bee brood cells into the analysis, significantly more bee species were found in the rainy than in the dry season and at lower than at higher traps (Fig. 1A,B), but species number of bees was not affected by habitat parameters. The number of brood cells constructed by bees was significantly higher in the rainy than in the dry season and at lower traps than at higher traps too (see legend Fig. 2A). Additionally there was a significant interaction between trap height and incident of light; at lower traps number of bee broodcells increased with incident of light, whereas at higher traps number of bee broodcells stayed constant (Fig. 2A).

Wasps

Species number of wasps was positively related to the number of wasp brood cells ($r = 0.5213$, $p < 0.01$). Including the number of wasp brood cells into the analysis, wasp species number was significantly higher in the rainy- than in the dry season (Fig. 1C), but did not differ between low and high traps (Fig. 1D), nor was related to habitat modification. The number of brood cells constructed by wasps increased with increasing percentage of incident light (Fig. 2 B) but did not differ between seasons or trap height.

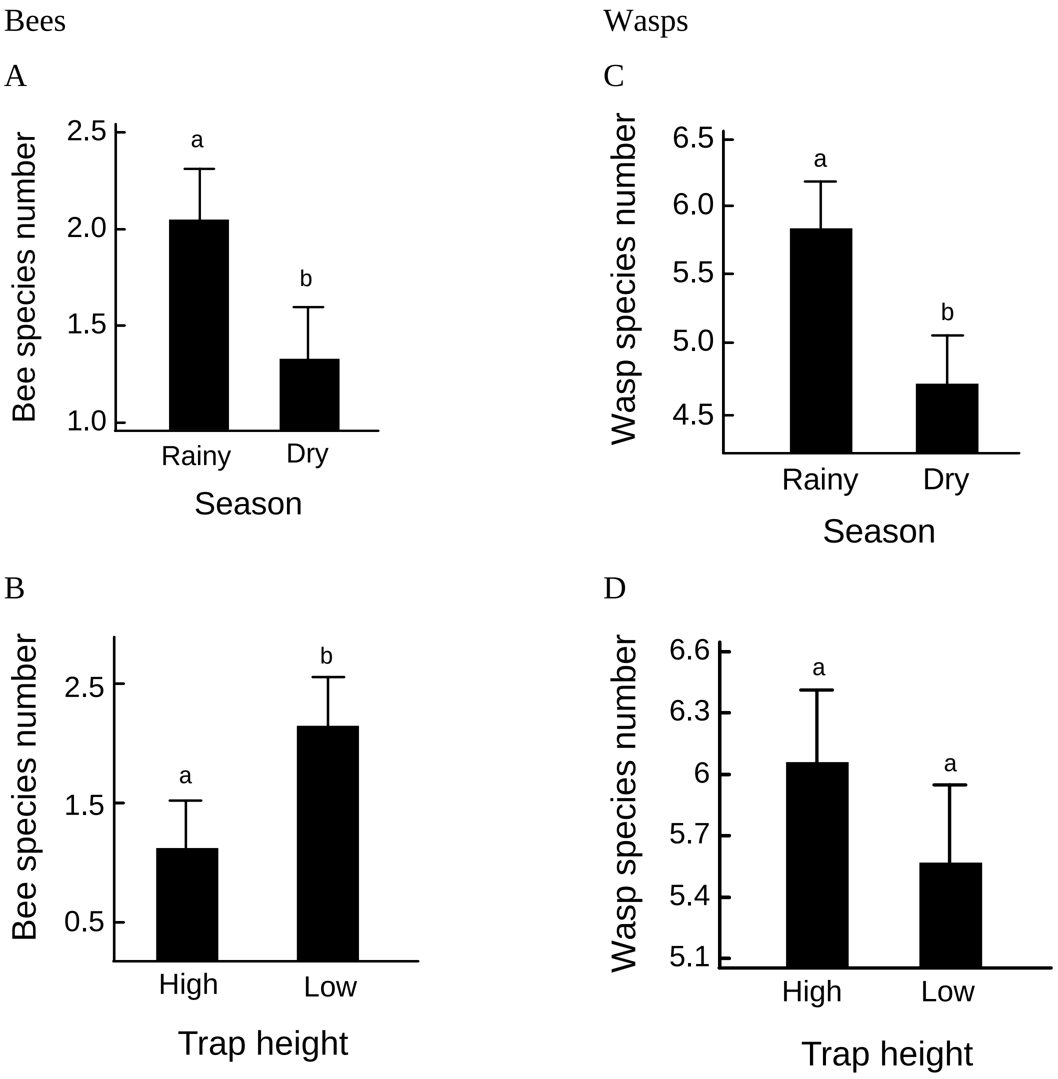

Fig. 1: Bee species number in relation to (**A**) season and (**B**) trap height, and wasp species number in relation to (**C**) season and (**D**) trap height. (**A**: $F_{1,52} = 5.51$, $p < 0.05$, **B**: $F_{1,52} = 6.97$, $p < 0.05$, not shown: bee brood cells: $F_{1,52} = 30.56$, $p < 0.0001$, overall model: $F_{3,52} = 14.35$, $r^2 = 0.45$, $p < 0.0001$, **C**: $F_{1,25} = 6.51$, $p < 0.05$, **D**: not significant, not shown: brood cells: $F_{1,25} = 8.95$, $p < 0.01$, overall model: $F_{2,25} = 7.73$, $r^2 = 0.38$, $p < 0.01$).

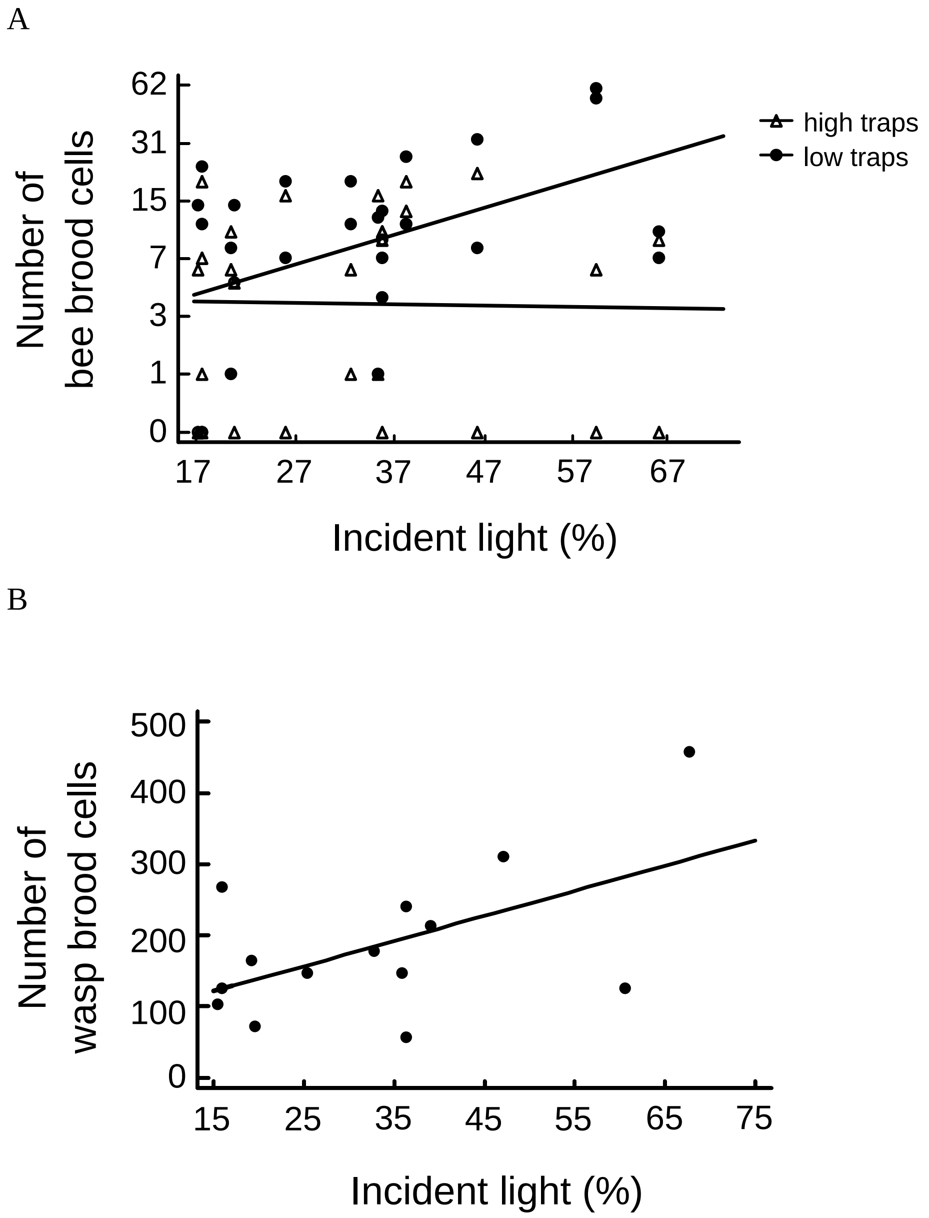

Fig. 2: Number of brood cells constructed by bees in relation to the percentage of incident light and trap height (**A**) and number of brood cells constructed by wasps in relation to the percentage of incident light (**B**). (**A**: $F_{1,52} = 6.12$, $p < 0.0167$, interaction: $F_{1,52} = 5.87$, $p < 0.05$, not shown: season: $F_{1,52} = 4.59$, $p < 0.0368$, overall model: $F_{3,52} = 5.53$, $r^2 = 0.24$, $p < 0.01$, **B**: $F_{1,12} = 5.14$, $r^2 = 0.3$, $p < 0.05$).

Discussion

Our results show that species richness of both, bees and wasps, as well as bee abundance were higher in the rainy than in the dry season. Species richness and abundance of cavity-nesting bees were also higher at lower traps at the herb layer. The abundance of bees and wasps increased with light availability, for bees this relationship appeared only for lower traps.

Vertical stratification across the studied vegetation strata was restricted to solitary bees, whereas wasps were distributed homogenously across the two trap heights. Both, bee species richness and abundance were significantly higher at lower traps. There are several, probably additive, explanations for this vertical stratification in cavity-nesting bee communities. Bees are known to often nest in aggregations, due to nest site or resource limitations (Wsiclo & Cane 1996). Heterogeneity in floral resources, in both, quality and quantity, can result in a similar heterogeneous distribution of bee communities (Potts et al. 2003, Veddeler et al. 2006). Blooming patterns varied between the two trap heights. Lower traps were located at the height of the herb layer. Pollen host specialization is especially pronounced in solitary bee communities (Wcislo & Cane 1996, Minckley et al. 1999) and solitary bees are known to feed on flowering herbs, which constitute important pollen and nectar resources for them (Klein et al. 2002, 2003, 2006). Solitary bees often choose nesting sites near to their host flowers (Wcislo & Cane 1996) and this might have resulted in a concentration of bee species and abundance at lower traps where a high quality and quantity of floral rewards was available. Furthermore, a higher nesting activity at lower traps might reflect an adoption to the availability of nesting cavities at this height. Nesting sites in form of dead wood or stems were concentrated on the ground (personal observation). The availability of potential nesting cavities is one of the main factors influencing bee community structures (Potts et al. 2005). Additionally traps closely above ground might have been better protected against wind, and other environmental perturbations. Another possible explanations for such vertical differences in bee species richness might be interspecific competition (Klein et al. 2002, Palmer et al. 2003), resulting in an escape of species to alternative strata. However we did not find any bee species being restricted to one trap height (except for very rare species), thus there is no evidence for interspecific competition. Higher traps were located at the layer of coffee shrubs, which constituted the only plant offering floral resources at this stratum. But coffee flowered only once per year for only two days (personal observation), thereby a continuous availability of floral resources at higher traps was not given. Besides, in another study investigating coffee flower-visiting bees (Veddeler et al. 2006) none of the trap-nesting bee species could be observed on coffee flowers, underlining that coffee is not a suitable food resource for solitary cavity-nesting bees.

But in contrast to bees, neither wasp species richness nor abundance showed any vertical stratification. This homogenous distribution of wasp diversity may be caused by a sufficient availability of food resources at both strata. At lower traps the herb layer offered a variety of arthropods for their offspring (Norris & Kogan 2005). At higher traps coffee shrubs provided a similar availability of insects and spiders (Pelley 1973, Veddeler et al. unpublished data). Seasonality was pronounced in species richness of both, wasps and bees and in bee abundance; all were significantly higher in the rainy than in the dry season. Arthropod densities are known to strongly decrease under the influence of seasonal dryness in tropical regions (Wagner et al. 2001), but we provide evidence, that also species richness of insects is affected by seasonal climatic changes in the tropics. Increasing seasonal diversity can be attributed to increasing variability and availability of resources (Sperber et al. 2004). In traditional agroforests herbal richness is supposed to be decisive for the diversity of many groups of arthropods (Moguel & Toldeo 1999). Herb growth is favoured in the rainy season (personal observation), and species richness of cavity-nesting bees and wasps can be related to high herb diversity (Gathmann et al. 1994, Klein et al. 2003, Tylianakis et al. 2005). Flower-feeding bee communities are organized by the seasonal quantitative and qualitative availability of pollen and nectar rewards (Jones 2001, Potts et al. 2005), and Thiele (2005) related an increased bee abundance to flowering peaks in Neotropical lowland rainforest. For wasps, an increased vegetational productivity in the rainy season of both herbs and coffee shrubs probably constituted more resource niches for foliage-dwelling arthropods, thereby increasing the availability of hosts. Foliage feeders, such as caterpillars, require new growth of leaves (Wolda 1978, Jones 2001), and thus are more abundant in the wet season (Wagner 2001).

The abundance of both bees and wasps increased with incident of light. Sunlight enhances temperature in agroforests (Perfecto & Snelling 1995), which offers many advantages for a successful reproduction in Hymenopteran nests (see Potts & Willmer 1997). In addition to an increased nesting activity of solitary bees and wasps in warm temperatures (Potts & Wilmer 1997, Wuellner 1999, Klein et al. 2002), herb growth is also favoured by high light intensities, thereby increasing the availability of floral rewards. For wasps, the availability of hosts may have increased with light intensity, especially for the caterpillar hunting Eumenidae (see Klein et al. 2006).

In conclusion, bees and wasps as two different ecological insect guilds using the same nesting sites showed congruent seasonal patterns, they were more diverse in the rainy season, presumably due to higher availability of food. In contrast, vertical stratification was only pronounced for the diversity and abundance of bees, but not wasps. We infer that cavity-nesting bees respond to a heterogeneous distribution of floral rewards, between the regularly flowering herb layer and the rarely flowering coffee shrub layer, whereas wasps do not appear to experience any vertical constraints in food resources. The differences in bee diversity even in small vertical gradients indicate that sampling in one vertical position might underestimate the diversity of a given habitat. We emphasize the necessity to investigate insect diversity at different spatiotemporal scales and to differentiate between different trophic levels to achieve an appropriate understanding of diversity patterns for possible conservation management

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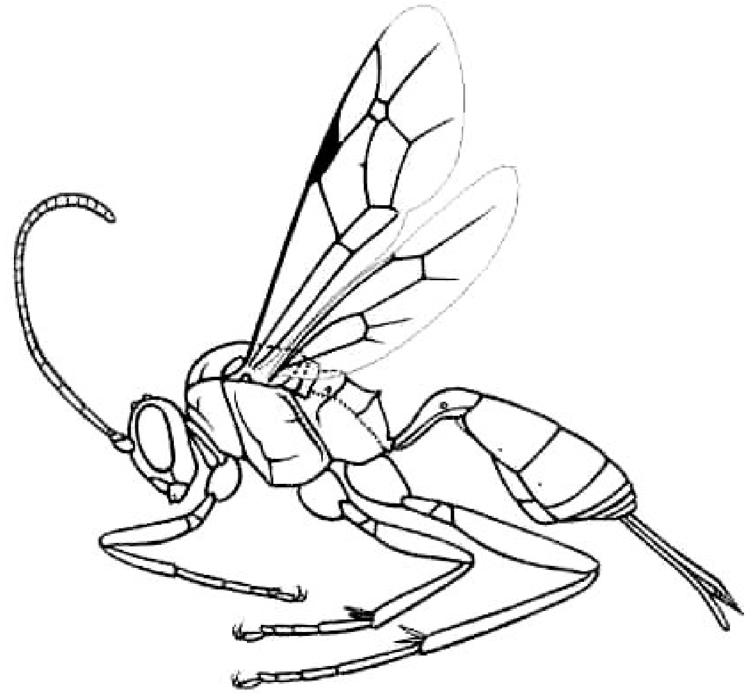
CHAPTER 5

DIVERSITY, FUNCTION AND STABILITY IN PARASITOID COMMUNITIES OF BEES AND WASPS



Abstract

Biodiversity may enhance and stabilize ecosystem functioning, but little evidence exists for a diversity-functioning relationship within natural food webs such as host-parasitoid interaction webs. Host-mediated variation in parasitoid communities may influence the effects of parasitoid diversity on parasitism rates. We analyzed the relation between diversity and parasitism rate and stability in parasitism, using communities of cavity-nesting bees and wasps, in 14 traditional coffee agroforests in coastal Ecuador. Diversity and abundance of host wasps were significantly higher than for host bees, whereas temporal variability in diversity and abundance were significantly higher for bees than for wasps, as floral resources for bees were presumably more variable than prey resources for wasps. Neither parasitoid diversity or its temporal variability nor parasitism rates or their temporal variability differed significantly between wasps and bees. We found parasitism rates of both wasps and bees to increase with the respective parasitoid diversity. Additionally, parasitism rates of wasps decreased with increasing host wasp diversity, but parasitism rates of bees were not related to bee diversity. Temporal variability of wasp and bee parasitism rate decreased with increasing diversity of parasitoids and increased with temporal variability of parasitoid diversity, the latter only for wasp hosts. Differences in habitat structure did not affect any of these relations.

Our results show that parasitoid diversity can increase parasitism rates and their stability, and that these relations applied for two different host guilds with their respective parasitoid communities. However, antagonistic effects of host diversity, and thus resistance against consumption, could only be found for wasp hosts and thereby changed with host guild. Stabilizing effects of a temporally stable enemy community on parasitism rates appeared to depend on the respective host community patterns, which were likely mediated by temporal variation in host resource availability. We conclude that a certain level of host diversity may be needed to resist consumption, and that resource-mediated heterogeneity in host diversity can obscure the stabilizing effect of temporally stable diversity on ecosystem functioning.

Key words: ecosystem properties, Ecuador, host guild, multitrophic system, parasitism resource heterogeneity, species richness, temporal variation, tropical ecology

Introduction

The world-wide loss of biodiversity due to continued anthropogenic modification of landscapes is feared to reduce ecosystem services, which are important for human welfare (Daily et al. 1998). Theoretical and empirical evidence suggests that diversity can influence ecosystem functioning through complementarity such as resource partitioning or facilitation, or sampling effects (see Kinzig et al. 2001, Loreau et al. 2001, 2002, Hooper et al. 2005). However, despite the importance of multitrophic interactions in ecosystems, mostly single trophic levels were considered (Petchey et al. 2004, Thébault & Loreau 2006). Only recently have multitrophic systems received attention in the diversity-functioning debate. Diversity at one trophic level can affect diversity and abundance at adjacent levels through trophic interactions (Hooper et al. 2005, Thébault and Loreau 2005). Additionally diversity changes at the higher trophic level can influence the ecological functions performed by the lower trophic level via trophic cascades (Bruno & O’Connor 2005, Duffy et al. 2005). Changes in diversity at both the prey and consumer level, might affect ecosystem functioning in a multitrophic system, either synergistically or antagonistically (Srivastra & Vellend 2005). However, studies examining multitrophic interactions have mostly investigated the effects of diversity changes at the consumer level, whereas the prey resource level remained unmanipulated in terms of diversity (e.g. Cardinale et al. 2003, Larsen et al. 2005, but see Montoya et al. 2003, Gamfeldt et al. 2005). In fact consumption rates may even be reduced through increasing prey diversity (Hillebrand & Cardinale 2005). Therefore diversity may contribute to resistance against consumption effects, which will be of particular importance if the prey guild itself performs an essential ecosystem service such as pollination by solitary bees or biocontrol by solitary wasps.

Multitrophic diversity-consumption patterns may differ for different ecological groups or guilds. Most studies to date have only considered consumer or prey diversity from one guild, or did not differentiate between them (e.g. Rodríguez & Hawkins 2000, Montoya et al. 2003, Hillebrand & Cardinale 2004, Gamfeldt et al. 2005, Tylianakis et al. submitted). The community structure of a prey guild depends on its specific resource requirements and their availability in space and time, which in turn could affect the interactions between prey and consumers (Wcislo & Cane 1996). Therefore, prey guilds with varying resource availability might cause varying diversity-function relationships in multitrophic systems.

Diversity is also predicted to stabilize ecosystem functioning (Srivastra & Vellend 2005), as different species respond differently to environmental changes, thereby insuring against environmental fluctuations (Lehmann & Tilman 2000). However, few empirical results are available on the stabilizing effect of diversity on ecosystem functioning (Hooper et al. 2005, Thébault & Loreau 2005, 2006), although trophic interactions can play an important part in community stability (Aoki & Mizushima 2001). Further the contribution of diversity to stability of consumer interactions may depend on the prey guild included in the system and the resources they require. Temporal variation in the availability of resources used by prey, for example seasonal variation in floral resources for bees, might cause temporal variation in prey, and consequently in consumer diversity, which can have destabilizing effects on ecosystem functioning (Tylianakis et al. submitted).

Habitat modification may further alter the diversity-function relationship. Fort example, traditional agroforests in the tropics contain a high diversity of flora and fauna (Perfecto et al. 1996), which is threatened by the conversion to modern monocultures (Moguel and Toledo 1999). Several studies show that intensification of these systems significantly reduces their biodiversity (Mas & Dietsch 2003, Perfecto et al. 2003, Armbrecht et al. 2005), which may also affect beneficial insects and their associated ecological functions (Klein et al. 2003). The effects of habitat modification can vary for different guilds, such as bees or wasps (Klein et al. in press), which in turn may influence the effects of diversity on ecosystem function.

We analyzed the effects of changing diversity at both consumer (parasitoids) and prey (cavity-nesting Hymenoptera) level on ecosystem functioning (parasitism rates). We considered two different host guilds, solitary bees (Apoidea) and solitary wasps (Pompilidae, Eumenidae and Sphecidae) in 14 sites that comprised an intensification gradient of traditional agroforests. In addition we tested for the importance of temporal changes in host and parasitoid diversity for the stability of parasitism rates. Solitary bees are known to be important pollinators of wild and cultivated plants (Corbet et al. 1991), whereas solitary wasps may play an important role in pest control (Harris 1994). We focus on the respective impact of different host guilds on the diversity-parasitism relationship and, with respect to the ecosystem service they provide, their ability to resist parasitism through enhanced diversity. Additionally we evaluate the importance of host guild type and possible resource-mediated variation in their community patterns for the stabilizing effects of diversity on rates of parasitism.

Materials and methods

Study area and sites

The study was carried out in the cantons Jipijapa, Pajan and Noboa in Manabi, coastal Ecuador. The study area is situated 100-550 m asl (17 N546800m, E9849274m). Annual rainfall is between 1500 and 1700 mm, and the annual average temperature is 25°C. The dry season lasts approximately from June until November. Numerous traditional coffee agroforestry systems are distributed randomly over the landscape, embedded in a mosaic of bushland, secondary forests, pastures and other agricultural systems such as arable crops (rice, maize). The coffee agroforestry systems consist of coffee planted under a community of various shade trees, including Leguminosae (*Inga* sp.), forest remnants, or trees that provide products for local or market subsistance, (e.g. fruits, construction materials or timber). For our investigation we chose 14 of these traditional coffee agroforestry systems differing in tree diversity and light intensity,a s reduced tree diversity and a more open canopy are typically associated with increasing management intensity.

Trap nests

We provided nesting sites for cavity-nesting bees and wasps by establishing traps which consisted of plastic tubes filled with internodes of reed (*Arundo donax* L. Poaceae) of different diameters (see Tscharntke et al. 1998, Tylianakis et al. 2005). In each of the 14 systems we exposed ten traps, five at the approximate layer of coffee shrubs (1.5 m above ground) and the other five at the approximate height of the herb layer (0.5 m above ground). Traps were hung in branches of coffee shrubs, other shrubs or trees and remained in the field continuously from June 2003 until November 2004. To prevent ants from entering the traps we put sticky glue on the suspension point. Each month we removed occupied reeds and replaced them with empty ones of the same diameter. We reared the occupied reeds in the laboratory until the insects emerged. Insects were identified to subfamily level following Goulet & Huber (1993) for wasps and Michener (2000) for bees. Genera and species were partly identified by J. Gusenleitner and D.W. Roubik and partly by the authors using keys or reference collections from the Pontificia Universidad Católica del Ecuador. Unidentified species were classified as morphospecies. We noted the number and species of emerging individuals (hereafter named either “wasp” or “bee hosts”), the number of brood cells (abundance) for each wasp or bee morphospecies, the number of parasitized brood cells, and the number of parasitoids and cleptoparasites (hereafter generally named “parasitoids”) species and individuals.

Habitat parameters

As indicators of habitat modification, we assessed the two parameters tree diversity and incident light. We measured light intensity with a luxmeter (digital light-gauge with four scopes from 0-1999 W/m^2, Mavoloux, Gossen) at the edges and in the middle of nine 10 x 10 m quadrants and outside the site under open sky to calculate the percentage of incident light (hereafter incident light) in the systems. We sampled trees in nine 10 x 10 m quadrants, and recorded the number of morphospecies and individuals. Because some tree species were represented by only one or few individuals in a site, we calculated the Shannon-Wiener diversity index as a measurement for canopy tree diversity. Tree diversity and incident light were not intercorrelated ($r = -0.1731$, $p = 0.5541$).

Statistical analyses

All analyses were performed using the statistical program Statistica 6.1 (StatSoft 2003). We calculated the proportion of parasitized brood cells (hereafter named “parasitism rate”) for nesting wasps and bees. As there was strong variation in either host or parasitoid diversity and parasitism rates between months we calculated the mean of these variables per month ($n = 17$ months). To assess temporal variability in parasitism rate and host and parasitoid diversity we calculated the CV (coefficient of variation) across months for each of these variables. With general linear models (GLM) we tested the different dependent variables, bees and wasps separately for a relation to the following independent variables. Species number of hosts was tested for a relationship with host abundance and the two quantified habitat parameters. Species number of parasitoids was tested for a relationship with parasitoid abundance, species number and abundance of their hosts, and habitat parameters. Parasitism rate was tested for a relation to host and parasitoid diversity and abundance and to habitat parameters, and temporal variability was tested for a relation to host and enemy diversity and abundance and to temporal variability of host and enemy diversity. We used backward stepwise elimination until only significant variables were left. Because in a previous study we found trap height to affect number of nesting bee species (Veddeler et al. in prep.) we included trap height as a random factor to exclude its variance, but disregard it while presenting the results. We tested for a normal distribution of residuals and transformed variables if necessary.

For plotting single relations in models that included more than one predicator variable we used the residuals to control for the effect of the other variable in the model.

Results

In total 26 species nested in the traps, of which 11 were solitary bee species (Apideae) comprising 1187 brood cells, six were eumenid wasp species with 2122 brood cells, seven were sphecid wasp species with 505 brood cells and two were pompilid wasp species with 1177 brood cells. We found eight parasitoid species with 250 individuals feeding on wasp or bee larvae (parasitoids) or their food resources (cleptoparasites). Five percent of all host individuals died due to parasitism. Three parasitoid species were exclusively found feeding on bees, three exclusively on wasps, and two parasitoid species fed on both, bees and wasps (Table 1).

Table 1: Parasitoid species and their host species (B = bee, W = wasp).

Enemy family	**Enemy species**	**Host species**	**Host guild**
Bombyliidae	Bombyliidae Gen. sp.	*Centris* sp. Apidae Gen. sp.	B B
Megachilidae	*Coelioxys* sp. 1	*Megachile* sp. *Neofidelia* sp. *Tetrapedia* sp.	B B B
Megachilidae	*Coelioxys* sp. 2	*Megachile* sp.	B
Meloidea	Meloidae Gen. sp.	Eumeninae Gen. sp. 2	W
Ichneumonidae	Phygadeuontinae Gen. sp.	*Trypoxylon* sp. *Pseudodynerus* sp.	W W
Chrysididae	*Chrysis* sp.	Sphecidae Gen sp. 1 Pompilidae Gen sp. *Monobia angulosa* Pompilidae Gen. sp.1 *Pseudodynerus* sp.	W W W W W
Leucospidae	*Leucospis* sp.	*Megachile* sp. 1 *Neofidelia* sp. *Tetrapedia* sp. Eumeninae Gen. sp. 1 *Pseudodynerus* sp. *Centris* sp.	B B B W W W
Eulophidae	*Melittobia acasta*	*Neofidelia* sp. *Tetrapedia* sp. Eumeninae Gen. sp. 1 *Zeta* sp. Sphecid Gen. sp. 2 Pompilidae Gen. sp. 2 Sphecidae Gen. sp. 3 *Monobia angulosa* Pompilidae Gen. sp. 1 *Megachile* sp. *Pseudodynerus* sp. Eumeninae Gen. sp. 2	B B W W W W W W W W W W

Host diversity

We found diversity of nesting wasps and bees to be correlated with their respective abundance (wasps: $r = 0.77$, $p < 0.01$, bees: $r = 0.77$, $p < 0.01$), but not with the percentage of incident light or tree diversity. Mean species richness of host wasps was significantly higher than the number of host bees species ($F_{1,12} = 50.18$, $p < 0.0001$), but they were not correlated with each other ($r = 0.33$, $p = 0.25$). Similarly mean host wasp abundance was higher than mean host bee abundance ($F_{1,12} = 13.07$, $p < 0.01$).

Parasitoid diversity

Mean species richness of parasitoids attacking either wasps or bees was positively related to their respective abundance (wasp host: $r = 0.89$, $p < 0.0001$, bee hosts: $r = 0.93$, $p < 0.0001$) but not to species richness or abundance of their respective hosts or to habitat parameters. Mean parasitoid richness did not differ between those attacking either wasps or bees, although parasitoid abundance was marginally higher for those attacking wasps ($p = 0.07$, $F = 3.51$).

Parasitism rate

Mean parasitism rate did not differ between wasp and bee hosts. Mean parasitism rate of wasps increased with increasing species richness of natural enemies, and decreased with increasing species richness of host wasps (Fig. 1A,B) but was not related to habitat parameters. Mean parasitism rate of bees increased with increasing species richness of natural enemies attacking bees (Fig. 2A), but was not related to the diversity of bee hosts (Fig. 2B) or to habitat parameter.

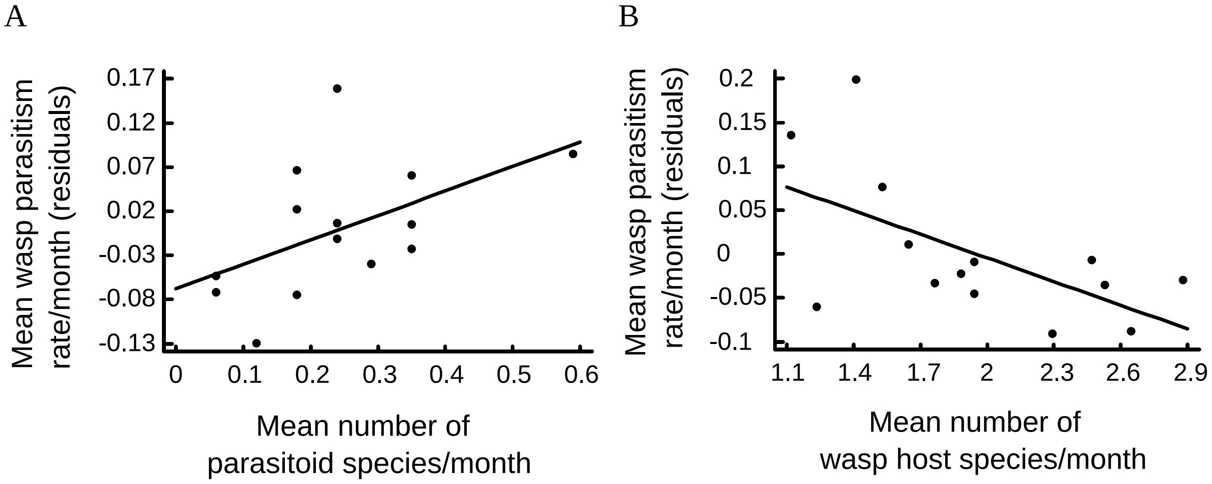


Fig. 1: Relation between mean parasitism rate of wasps per month and (A) mean species number of parasitoids per month and (B) mean species number of wasp hosts per month (A: $F_{1,11} = 5.79$, $p < 0.05$, B: $F_{1,11} = 9.41$, $p < 0.05$, overall model: $r^2 = 0.48$, $F_{2,11} = 5.24$, $p < 0.05$).

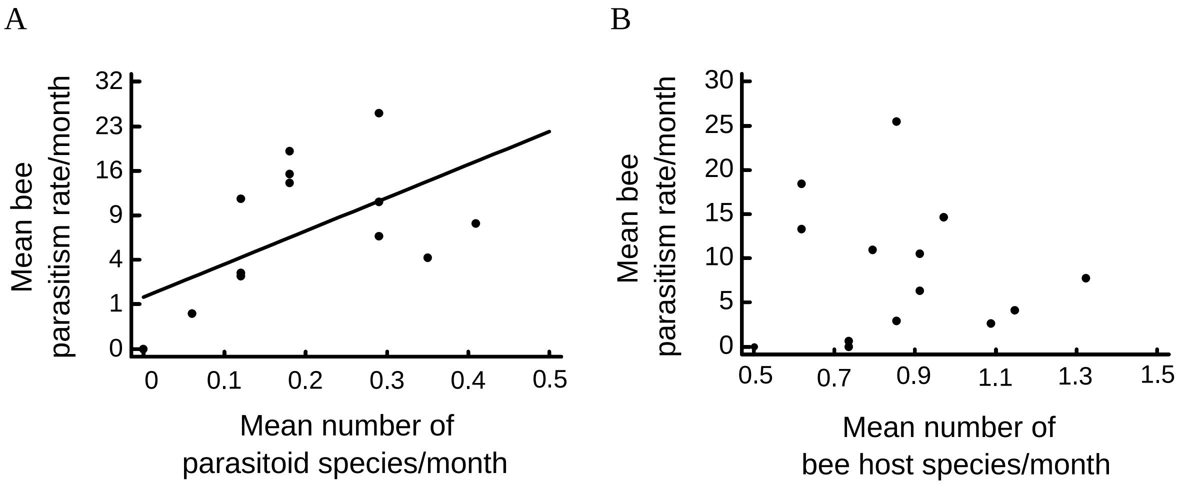


Fig. 2: Relation between mean parasitism rate of bees per month and (A) mean species number of parasitoids per month and (B) mean species number of bee hosts per month. (A: $r^2 = 0.34$, $F_{1,12} = 6.23$, $p < 0.05$, B: not significant).

Temporal variability

Temporal (between months) variability in host species richness and abundance was significantly higher for bees than for wasps (species richness: $p < 0.0001$, $F = 30.93$, abundance: $p < 0.05$, $F = 7.05$), but temporal variability in parasitoid richness and temporal variability in parasitism rate did not differ between wasps and bees.

Temporal variability in the diversity of parasitoids attacking wasps was not related to temporal variability of host wasp diversity ($r^2 = 0.07$, $F = 0.99$, $p = 0.34$,), but temporal variability in the diversity of enemies attacking bees was significantly positively related to temporal variability in diversity of bee hosts (bees: $r^2 = 0.51$, $F = 10.49$, $p < 0.01$).

Temporal variability in the parasitism rate of wasps decreased with increasing species richness of their parasitoids (Fig. 3A) and increased with variability in parasitoid species richness (Fig. 4A), but was not related to diversity of host wasps. Likewise, temporal variability in bee parasitism rate was significantly positively related to the diversity of parasitoids attacking bees (Fig. 3B), but not to host bee diversity. In contrast with wasps, temporal variability in the parasitism rate of bees was not related to temporal variability of parasitoid species richness (Fig. 4B).

A B

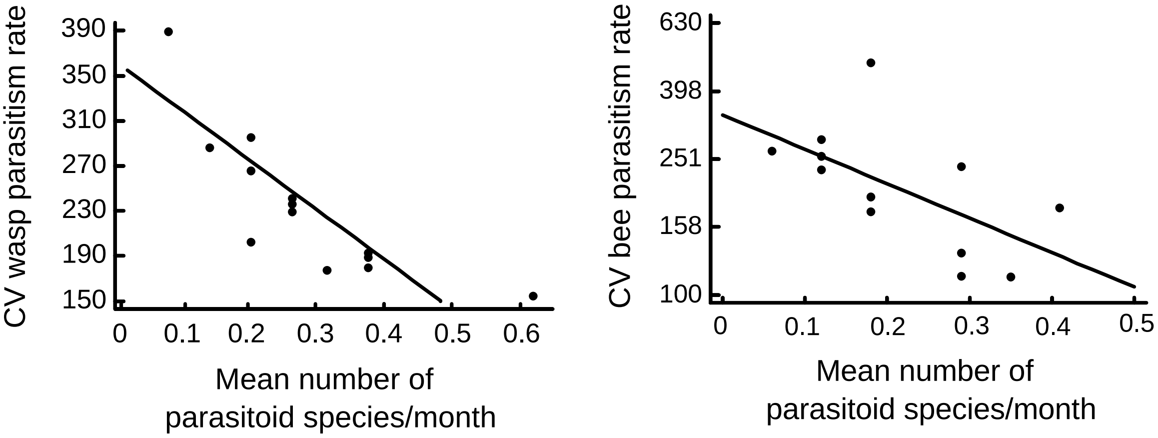


Fig. 3: Relation between (A) temporal (between months) variability of wasp parasitism rate (expressed by the CV= coefficient of variation) and (B) temporal (between months) variability of bee parasitism rate and the respective mean species number of parasitoids per month (A: $r^2 = 0.7$, $F_{1,12} = 29.33$, $p < 0.001$, B: $r^2 = 0.36$, $F_{1,12} = 5.6$, $p < 0.05$).

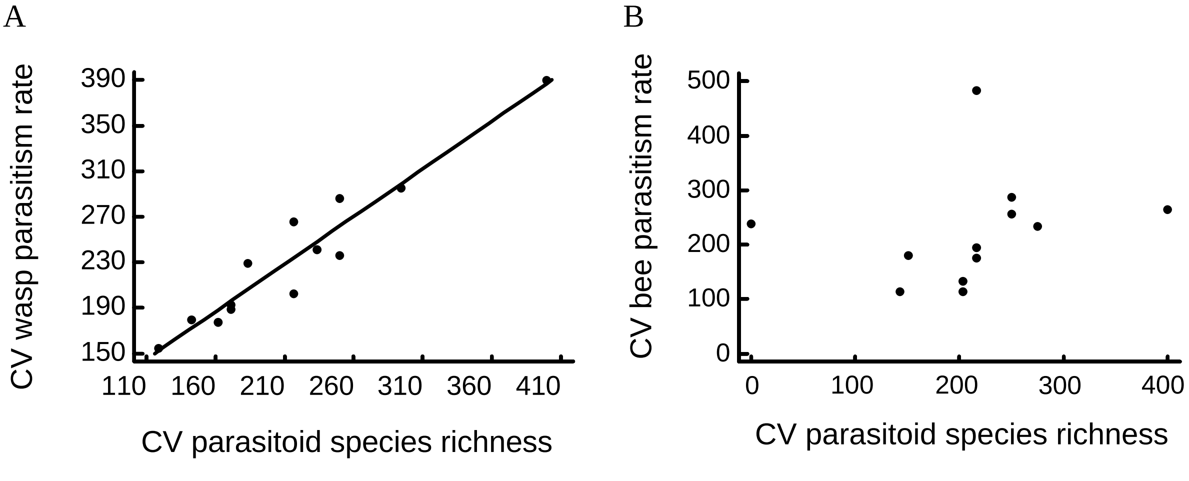


Fig. 4: Relation between (A) temporal (between months) variability (CV) of wasp parasitism rate and (B) temporal (between months) variability of bee parasitism rate and temporal variability (CV) of the respective parasitoid species number (A: $r^2 = 0.94$, $p < 0.0001$, $F_{1,12} = 197.66$, B: $r^2 = 0.04$, $F_{1,12} = 0.46$, $p = 0.5$).

Discussion

We found parasitism rates of cavity-nesting wasps and bees to be positively related to the diversity of their parasitoids. In addition, parasitism rates of wasps were significantly negatively related to the diversity of wasp hosts.

Our results of a positive relationship between parasitoid diversity and parasitism support theoretical and experimental evidence for a diversity-function relationship in multitrophic systems (e.g. Cardinale et al. 2003, Gamfeld et al. 2005, Ives et al. 2005). Here we showed that this positive effect of parasitoid diversity on parasitism rate was robust across the two different host guilds of bees and wasps, despite differences in resources (floral rewards vs. prey) used by the different guilds. An increase in parasitism rate may be attributed to complementary effects of diversity, by increasing host resource partitioning (Lehman & Tilman 2000). Most parasitoid species fed on no more than one to six wasp or bee host species. Therefore an increased number of parasitoid species should have resulted in an enhanced overall consumption (Tilman & Lehman 2000). The only exception was a gregarious parasitoid species (*Melittobia acasta*) feeding on 13 different (11 wasp species and two bee species) host species. Further, functional diversity of parasitoids, including differences between solitary and gregarious parasitoids and cleptoparasites may have increased consumption rates.

We also found antagonistic effects of host diversity, resulting in bottom-up control, thereby showing that the diversity-function relationship may be driven by different trophic levels (Hooper et al. 2005). A high diversity of host wasps decreased their rate of parasitism by natural enemies. Higher host diversity can imply an increased number of inedible species, thereby reducing overall consumption effects and increasing resistance against it (Hillebrand & Cardinale 2005). This result was only observed for wasps, whereas bee host diversity was not related to parasitoid consumption. As host bee diversity was significantly lower than host wasp diversity, diversity-mediated resistance against consumption may only become effective at a certain level in host species richness, and all of the relative few bee host species might have constituted edible resources for the consumers (Gamfeldt et al. 2005).

Furthermore, our results support the expectation that diversity can stabilize ecosystem functioning (Tilman & Lehman 2000) in multitrophic systems, as we found that temporal variability of both wasp and bee parasitism rate decreased with increasing species richness of parasitoids. These results contrast to those found by Rodríguez et al. (2000), who did not find such stabilizing effects of diversity in a, in contrast to our study, functionally extremely homogenous parasitoid community. Complementary effects of a diverse and functionally heterogeneous predator community may ensure a stable ecosystem function, such as predation over time, by compensating for species losses in temporarily less favourable environmental conditions (Tilman & Downing 1994).

We also found temporal variability in the diversity of parasitoids attacking wasps to be positively related to temporal variability of parasitism rate, supporting results of Tylianakis et al. (submitted). The lower the variation is within a functional group, the more likely it can provide a constant ecosystem service. However, a temporally stable enemy diversity did not increase temporal stability in bee parasitism rate. Temporal variability in diversity and abundance were significantly higher for bee hosts than for wasp hosts. Solitary bees feed on flowering herbs and the community structure of bees is organized by flower communities (Potts et al. 2003, 2004). The availability of floral resources is known to vary temporally in tropical regions (Jones 2001, Boulter 2006) and flower feeders adapt to this phenological variation (Jones 2001, Thiele 2005). In the studied agroforests, availability of floral resources was likely to be much more variable than the availability of prey resources for wasps. Variability in fundamental resources such as floral rewards that regulate productivity of a given community (Potts et al. 2003, 2004) can determine ecosystem processes in a multitrophic system (Huston 1997). The strong temporal variation in bees appeared to be the cause of the high temporal variation in parasitoid diversity and the latter might have been too variable to efficiently stabilize parasitism rate, thereby showing a bottom-up control of host variability on the stability of parasitism rates.

Differences in habitat characteristics such a tree diversity and incident of light did not affect host or enemy diversity. Consequently, we even found a diversity-function relationship with a comparatively low variation in parasitoid diversity. An increase of parasitism rate with parasitoid richness within such a small diversity gradient confirms and strengthens the idea that diversity can enhance ecosystem functioning in a variety of habitats.

We conclude that the contribution of high parasitoid diversity to high and stable parasitism can apply for host as different as pollinators and predators. In wasps, but not bees, increasing prey diversity could limit parasitism and such a resistance against consumption may have been caused by the higher level of species richness in wasps. Furthermore, we conclude that the stabilizing effect of a temporally stable parasitoid community on parasitism rates may be affected by resource-mediated temporal variation in host communities. If quality and quantity of available prey are temporally too variable, stabilizing effects of consumer diversity may be no longer effective.

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SUMMARY

The world-wide loss of biodiversity due to the anthropogenic modification of landscapes is known to greatly affect ecosystem services, such as pollination by bees or predation by wasps and parasitism, which are of substantial importance for human society. Traditional coffee agroforests are important refuges for biodiversity and may maintain many of the environmental functions of undisturbed forests. In this context, a well-founded understanding of community patterns in these systems, their relation to environmental conditions and the contribution of biodiversity to ecosystem functioning is urgently needed to achieve appropriate management guidelines. Furthermore an economic evaluation of ecosystem services such as bee pollination in coffee may underline the value of ecosystem services for human society.

The first part of the thesis describes the relation of coffee flower-visiting bees to floral resources at a field, shrub and branch scale and evaluates the economic value of bee pollination to coffee production based on farm-scale yield data. The results revealed that bee density showed contrasting responses to coffee flowering at different spatial scales. On a field scale, bee density decreased with increasing availability of coffee flowers, showing a dilution effect. In contrast, on a shrub and on a branch scale bee density increased with increasing availability of floral resources showing a concentration effect. Bee species richness was not related to quantity of flowers at the field scale, but increased with increasing quantity of flowers at the shrub and branch scale. Furthermore the relationship between yield in the self-compatible highland coffee (*Coffea arabica* L.) and community patterns of coffee flower visiting bees was analyzed. Yield (kg/ha) was positively related to the density of coffee flower-visiting bees. Consequently, revenues and net revenues increased with bee density. Based on these linear relationships it was estimated that yield can increase twofold and net revenues even tenfold with a fivefold increase in bee density. This implies that coffee production and income of coffee producers can considerably increase with increasing density of coffee-flower visiting bees.

In the second part of the thesis, seasonal and vertical diversity patterns in the community of cavity-nesting solitary bees and wasps were investigated and the effect of their natural enemy diversity on parasitism rate and its temporal stability were analysed. Both solitary bees and wasps showed a significantly higher species number in the rainy than in the dry season. Vertical stratification was only found in the community of solitary bees; species

richness was significantly higher at a height of 0.5 m than at 1.5 m. These results show that diversity measurements may be influenced by resource-mediated seasonal and vertical variability and emphasise the importance of analyzing different guilds separately. Parasitism rates of solitary bees and wasps increased with increasing parasitoid diversity; additionally, wasp parasitism rate decreased with increasing diversity of wasp hosts, thus diversity appeared to provide resistance against consumption. Temporal stability of parasitism rates in bees and wasps increased with increasing parasitoid diversity, and only for wasps, also increased with temporal stability of parasitoid diversity. The results provide evidence that diversity contributes to ecosystem functioning and stability, but show that the stabilizing effects of a temporally stable predator community may be host guild specific.

The main results of this thesis reveal that community patterns of bees and wasps vary at different spatial scales and between tropical seasons, and that these patterns are generated by variation in resource availability. Additionally, the monetary value of bee pollination for an important cash crop is emphasised. Evidence is also provided that a high and stable parasitoid diversity can enhance and stabilize parasitism rates. To encourage important ecosystem services such as pollination, predation and parasitism, which can be critical for human welfare, a high diversity and abundance of bees, wasps and natural enemies should be conserved. Conservation of nesting sites such as dead wood, large trees or adjacent forest fragments, and food resources, such as a high quantity and quality of flowers can help to maintain a diverse and abundant community of Hymenoptera.

ZUSAMMENFASSUNG

Der weltweite durch die anthropogene Veränderung von Landschaften verursachte Verlust der Biodiversität, beeinflusst Ökosystemleistungen wie Bestäubung durch Bienen, Predation durch Wespen oder Parasitierung, welche von substantieller Bedeutung für die menschliche Gesellschaft sind. Traditionelle Agroforstsysteme sind wichtige Refugien für Biodiversität und beinhalten viele der Umweltfunktionen von ungestörten Wäldern. In diesem Kontext ist eine fundierte Kenntnis über die Struktur von Lebensgemeinschaften in diesen Systemen, deren Beziehung zu Umweltbedingungen und des Beitrags der Biodiversität zu Ökosystemfunktionen dringend erforderlich um geeignete Managementrichtlinien zu erreichen. Des Weiteren kann eine ökonomische Evaluierung einer Ökosystemleistung wie Bienenbestäubung am Kaffee den Wert dieser Leistungen für die menschliche Gesellschaft unterstreichen.

Der erste Teil der Arbeit beschreibt die Beziehung von Kaffeeblüten besuchenden Bienen zu Blütenressourcen auf einer Feld-, Strauch- und Zweigskala und bestimmt, basierend auf Ertragsdaten auf Flächenebene, den ökonomischen Wert von Bienenbestäubung für die Kaffeeproduktion. Die Ergebnisse zeigen, dass die Bienendichte auf verschiedenen Skalen gegensätzlich auf die Kaffeeblüte reagiert. Auf einer Feldskala sinkt die Bienendichte mit einer steigenden Verfügbarkeit von Blütenressourcen, dabei zeigt sie einen Verdünnungseffekt. Im Gegensatz dazu, steigt auf der Strauch und der Zweigskala die Bienendichte mit der Verfügbarkeit an Blütenressourcen, dabei zeigt sie Konzentrierungseffekte. Der Bienenartenreichtum war auf der Feldskala nicht mit der Blütenquantität korreliert, er stieg aber mit der Blütenmenge auf der Strauch- und auf der Zweigskala.

Des Weiteren wurde die Beziehung zwischen dem Ertrag beim selbstkompatiblen Hochlandkaffe und den Mustern der Lebensgemeinschaft der Kaffeeblüten besuchenden Bienen untersucht. Der Kaffeeertrag (kg/ha) korrelierte positiv mit der Bienendichte. Folglich stiegen auch die (Netto) Einnahmen mit der Bienendichte. Basierend auf dieser linearen Beziehung wurde berechnet, dass der Ertrag zweifach und das Nettoeinkommen zehnfach steigen können bei einer fünffachen Erhöhung der Bienendichte. Dies bedeutet, dass die Kaffeeproduktion und das Einkommen der Kaffeefarmer erheblich durch eine erhöhte Bienendichte gesteigert werden können.

Im zweiten Teil der Arbeit wurden saisonale und vertikale Diversitätsmuster in der Lebensgemeinschaft der Höhlenistenden solitären Bienen und Wespen untersucht und der Einfluss der Diversität von natürlichen Gegenspielern auf die Parasitierung und deren Stabilität analysiert. Sowohl Bienen als auch Wespen zeigten einen signifikant höheren Artenreichtum in der Regenzeit als in der Trockenzeit auf. Eine vertikale Stratifizierung wurde dagegen nur in der Gemeinschaft der solitären Bienen gefunden, der Artenreichtum war signifikant höher auf einer Höhe von 0.5 m als bei 1,5 m. Die Ergebnisse zeigen, dass Diversitätsmessungen durch eine von Ressourcen hervorgerufene saisonale und vertikale Variabilität beeinflusst werden können und betonen die Bedeutung einer getrennten Analyse verschiedener Gilden.

Die Parasitierungsraten solitärer Bienen und Wespen stiegen mit der Diversität der natürlichen Gegenspieler; zusätzlich sank die Parasitierungsrate der Wespen mit steigender Diversität der Wespen, demnach kann Diversität auch eine Resistenz gegen Parasitierung bieten. Die zeitliche Stabilität der Parasitierungsraten von Bienen und Wespen stieg mit der Diversität der natürlichen Gegenspieler, zudem stieg sie bei den Wespen auch mit der zeitlichen Stabilität der natürlichen Gegenspieler. Die Ergebnisse geben Hinweise, dass Diversität zu Ökosystemfunktionalität und Stabilität beitragen kann, aber sie zeigen auch, dass stabilisierende Effekte einer zeitlich stabilen Gegenspielergemeinschaft wirtsgildenspezifisch sein können.

Die Hauptergebnisse dieser Arbeit machen deutlich, dass die Muster der Lebensgemeinschaften von Bienen und Wespen auf unterschiedlichen räumlichen Skalen und zwischen tropischen Jahreszeiten variieren, und dass diese Muster hervorgerufen werden durch Änderungen in der Ressourcenverfügbarkeit. Außerdem wird der monetäre Wert von Bienenbestäubung für die Kaffeeproduktion betont. Zudem werden Hinweise gegeben, dass eine hohe und stabile Parasitoidendiversität Parasitierungsraten erhöhen und stabilisieren kann. Um wichtige Ökosystemleistungen wie Bestäubung, Prädation und Parasitierung, welche entscheidend sind für das menschliche Wohlergehen, zu fördern, sollten eine hohe Diversität und Abundanz von Bienen, Wespen und natürlichen Gegenspielern erhalten werden. Die Erhaltung von potentiellen Nistplätzen wie Totholz, große Bäume oder angrenzende Waldfragmente, aber auch Nahrungsressourcen wie eine hohe Quantität und Qualität an Blüten, können helfen eine diverse und abundante Hymenopterengemeinschaft zu erhalten.

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