Insect diversity responses to forest conversion and agroforestry management

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Summary

The ongoing loss of pristine tropical rainforests increases the potential importance of agroforestry systems for the conservation of tropical arthropod diversity. Shaded agroforestry systems can still support high levels of biodiversity, even resembling those supported by undisturbed forests, but intensively managed open agroforestry systems may cause severe losses in insect diversity. In this study we evaluate the conservation value of agroforestry systems for species richness and diversity (Simpson's index) of four insect groups at natural forest sites and three different types of cacao-dominated agroforestry systems in Central Sulawesi, Indonesia. The agroforestry systems were characterised by low, intermediate and high diversity of shade trees. Each habitat type was studied with 4 replicates, i.e. 16 study sites altogether. We compared responses of solitary bees and wasps, dung beetles and lower canopy dwelling beetles and ants. These taxa represent diverse and functionally important insect groups: solitary bees and wasps act as crop pollinators or pest predators, dung beetles as decomposers of mammalian excrements and canopy dwelling beetles and ants include abundant herbivores and predators. High percentages of forest species did not occur in agroforestry systems, but diversity and species richness in agroforests remained as high as or even higher than in the forest lower canopy. Diversity, species richness and abundance of the functionally important dung beetles and canopy ants showed strong resilience against both forest conversion and changes in agroforestry management. Diversity, species richness and abundance of solitary bees and wasps as well as

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canopy beetles even seemed to profit from the effects of opening the upper canopy that was related to forest conversion and changes in shade tree compositions. On the latter two groups the effects of opening the upper canopy were stronger than effects of reduced shade tree richness. Based on our results, we recommend the inclusion of agroforestry systems with a diversity of shade trees in tropical conservation plans in addition to pristine forest reserves. Furthermore, regional differences in local agroforestry management contributed to between 31% (for dung beetles) and 58% (for canopy beetles) of the total species richness, which stresses the importance of conservation policies aimed at a diversity of habitat types on a broader landscape scale.

Keywords: agroforestry, ants, beetles, biodiversity, lower canopy, conservation, habitat preference, knockdown fogging, management, pit-fall traps, solitary bees , solitary wasps, trap nests

1 Introduction

The global-scale conversion of natural ecosystems is a major cause of biodiversity loss and threatens ecosystem functioning, sustainable land use and economies (Hoekstra et al. 2005). Tropical rainforests are one of the most species-rich and functionally important terrestrial ecosystems (Myers et al. 2000). In the past 50 years an estimated 32% of these tropical rainforests have been converted to human-dominated systems and a further loss of 10-15% has been projected by 2050 (Millenium Ecosystem Assessment 2005). Hot spots of tropical rainforest conversion are Southeast Asia, with annual deforestation rates of 2.5 million hectares (0.91%) and Central America, with 2.5 million ha (0.38%) per year (Achard et al. 2002). With the continuing loss of tropical forests, cultivated areas are gaining interest for their potential value for conserving tropical biodiversity. Diversified agricultural systems such as agroforestry are suggested to serve as tools in nature conservation policies (Rice and Greenberg 2000; Putz et al. 2001; Donald 2004; McNeely 2004; Schroth et al. 2004).

1.1 The conservation potential of agroforestry systems

Agroforestry systems are generally characterized by a canopy cover of shade trees below which a wide range of crop plants can be grown (Schroth et al. 2004). In human-dominated, deforested landscapes, agroforestry systems provide the only remaining habitat type with a substantial tree cover (Schroth et al. 2004). Agroforestry supports some of the most important tropical cash crops including oil palm (*Elaeis* spp), rubber (*Ficus elastica*), cacao (*Theobroma cacao*) and coffee (*Coffea* spp.). Additionally, various kinds of timber, local fruit trees and annual crops are grown in agroforestry systems, thereby providing building material, firewood and food for local communities (e.g., Rice and Greenberg 2000, Siebert et al. 2002),

Agroforestry systems range widely in land-use intensity from extensively managed, patchy and densely shaded plantations owned by large numbers of smallholders to large scale, non-shaded and monotonous plantations owned by few farmers (e.g., Perfecto et al. 1997, Siebert 2001, Jones et al. 2003, McNeely 2004, Foley et al. 2005). Acknowledging the intrinsic and economic values of biodiversity (e.g., Meffe 1998, Altieri 1999, Sodhi 2004, Foley et al. 2005), studies increasingly focus on biodiversity as supported by various agroforestry types (e.g., Perfecto et al. 1997, Lawton et al. 1998, Siebert 2002, Jones et al. 2003, Klein et al. 2002, 2004, Schulze et al. 2004, Shahabuddin et al. 2005).

1.2 Land-use management and the conservation of biodiversity

The entomofauna of agroforestry systems is very diverse (Kalshoven 1950, Room 1971, Entwistle 1972, Campbell 1984) but has mainly been studied in the context of pest management. Increasing intensity of agroforestry management means simplification of the habitat by reducing the diversity of canopy trees, partial or complete removal of shade tree layers, increasing chemical inputs and more frequent cleaning of dead wood and leaf litter (Perfecto and Snelling 1995, Perfecto et al. 1997, Klein et al 2002, Siebert 2002, Jones et al. 2003). Land-use intensification might fail to increase crop productivity because it is paralleled by the loss of functionally important species groups resulting in reduced pollination services or increased pest problems (Klein et al. 2003, Rice and Greenberg 2000, McNeely 2004, Perfecto et al. 2005). Many studies indicate that increasing land-use intensity leads to biodiversity loss. For example, Chung et al. (2000) found that species richness of canopy beetles remained in extensive timber plantations more similar to nearby forest sites than beetle richness in intensive oil palm plantations. Jones et al. (2003) showed a decrease of termite species richness in rubber plantations from extensively managed rubber plantations, preserving 62% of the level of forest richness, to intensively managed plantations which preserved 44%.

Agroforestry in tropical America recently underwent a significant intensification of coffee plantations (Perfecto and Snelling 1995, Perfecto et al. 1997, Perfecto et al. 2005, Philpott 2005). Rustic, shaded and small scale agroforestry was largely replaced by large, monotonous coffee plantations with little or no shade. In comparison to extensive, well shaded agroforests, beetle species richness decreased by 26% but increased in abundance by up to 17% in more intensively managed coffee agroforestry systems (Perfecto et al. 1997). Similarly, pruning and removal of shade trees changed community structure and caused losses in ant diversity (Perfecto and Snelling 1995, Philpott 2005). Rice and Greenberg (2000) and McNeely (2004) emphasise the importance of remaining well developed stands of shade trees for land-use sustainability, preserving soil fertility, reducing soil erosion and increasing resistance to disturbances by extreme climatic events. For example, farmers in Africa successfully increased amounts of available nitrogen in the soil by replanting leguminose shade trees, thus forming a basis for land rehabilitation (Sanchez 1999). Additionally, Ramirez et al. (2001) showed how intercropping of shade providing timber trees in cacao plantations can lead to lower sensitivity to fluctuating market-prices.

1.3 Landscape heterogeneity and the overall supported biodiversity

At a local scale the species richness of agroforestry systems can be expected to depend on their structure, including the diversity of crop plants and canopy trees and the management intensity (e.g., Chung 2000, Jones et al. 2003, Schulze et al. 2004). On a landscape scale the spatial turnover in the species composition of local communities can significantly contribute to regional biodiversity. Thus, landscape heterogeneity can have important effects on biodiversity. For example, regional landscape heterogeneity contributed 56% of regionally recorded plant species (Wagner et al. 2000), 39% of regional solitary bee and wasp species (Tylianakis et al. *in press.*) and about 25% of regional beetle and butterfly species (Gering et al. 2002, Summerville et al. 2003).

Generally, landscapes composed of a mosaic of different land use types, including extensively managed agroforestry systems, maintain highest overall species numbers. In addition, distance to undisturbed ‘source habitats’ such as undisturbed rainforest play a role for local species richness (Klein et al. *in press.*). With high biodiversity at a landscape scale, local disturbances are likely to be buffered by recolonisation from diverse neighbouring communities, resulting in less vulnerable faunal communities (Peterson et al. 1998).

2 Cacao management and the conservation of biodiversity in Indonesia

Here we present results from a study focussing on agroforestry systems in Central Sulawesi, Indonesia. The island underwent a ‘cacao boom’ throughout the 1990s (Potter 2001, Belsky and Siebert 2003) in which coffee-dominated agroforestry was largely replaced by cacao-dominated agroforestry systems, turning Indonesia into the world’s third most important contributor to the international cacao production.

Indonesia is experiencing the world’s highest rates of deforestation, the majority of which is driven by agricultural expansion (Achard et al. 2004) and results in unprecedented biodiversity losses (Sohdi et al. 2004). In the light of the disappearing primary rainforest habitats, agroforestry systems are very likely to play a role in the conservation of tropical biodiversity, especially in intensively cultivated regions of Sulawesi, where 80% of Indonesia’s cacao is grown (Vingerhoets 2002).

Cacao is originally a shade dwelling tree species from the lowland forests of Central America (Urquhart 1955). In agroforestry, cacao is initially grown under shade which acts as buffer against major microclimatic changes, most important for younger cacao trees, but for adult trees highest productivity can be expected without shade (Urquhart 1955, Entwistle 1972). Shaded, cacao-dominated agroforestry systems can still support high levels of biodiversity, for some insect groups even resembling that of tropical rainforests (Schulze et al. 2004). Furthermore, in Central Sulawesi shade trees are increasingly removed (Belsky and Siebert 2003) posing a potential threat to the species rich flora and fauna supported by cacao dominated agroforestry (Siebert 2001), similar to the conversion of shade to sun coffee in tropical America. Unshaded agroforestry has not only negative effects on biodiversity but also results in higher dependence of cacao trees on watering and fertilizers (Urquhart 1955, Entwistle 1972).

The few studies that directly compared insect diversity between agroforestry systems and natural forest sites did not reach consensus on whether agroforestry systems support significantly lower insect diversity than forest sites or not (Lawton et al. 1998, Chung et al. 2000, Schulze et al. 2004). Effects of management intensification on biodiversity have shown to be much stronger than the initial conversion of forest to diversely shaded agroforestry systems (Perfecto et al. 1997, Chung et al. 2000, Jones et al. 2003). We tested the hypothesis that

1. *not forest conversion but increasing land use intensity results in reduced insect diversity*

On a larger spatial scale agroforestry systems differing in management regime, soil and water condition and landscape context comprise a heterogeneous landscape that can be the basis of a high, regionally supported biodiversity (as in Wagner et al. 2000, Gering et al. 2002, Summerville et al. 2003, see above). Therefore, we hypothesise that

1. *large spatial species turnover between different land-use systems contributes to regional species richness of insects.*

We tested the hypotheses using data on the insect fauna of 12 agroforestry systems and four natural forest sites. The agroforestry systems were classified according to three different compositions of shade trees: shade trees remaining from natural forest stands, a heterogeneous stand with a diversity of planted shade trees and a homogenous stand with one or two species of planted legume trees. The sequence from forest shade to homogenous shade represents a decline in structural diversity of the agroforestry systems as a habitat for insects. The study sites were situated around the Toro village about 100km south of Central Sulawesi's capital city Palu. The village is situated at the western border of the Lore Lindu National park. All study sites had a core area of 30 by 50 meters and were at least 300 meters away from each other. All forest sites were part of the national park.

The different insect groups we focus on here are solitary bees and wasps (Hymenoptera, Aculeata), dung-feeding scarabaid beetles (Coleoptera: Scarabaeidae, subfamilies Scarabaeinae, Coprinae and Aphodiinae, hereafter dung beetles), lower canopy ants (Hymenoptera: Formicidae) and lower canopy beetles (Coleoptera). Solitary bees are important pollinators of cultivated crops (Free 1993, Roubik 1995), solitary wasps can act as pest predators (O'Neill 2001) and dung beetles are important decomposers of mammal excrements (Klein 1989, Hanski and Cambefort 1991). Ants form a major component of tropical arthropod diversity and, as the most abundant group, play an important role in tropical ecosystems as predators (Hölldobler and Wilson, 1990). Lastly, the canopy dwelling beetles are the most species rich insect group found in tropical forested areas (e.g., Erwin 1982, Davies et al. 1997, Lawton et al. 1998) but also in tropical agroforestry systems (Perfecto et al. 1997, Chung et al. 2000).

The five selected insect groups have been poorly studied in the context of cacao agroforestry (e.g., Room 1971, Klein et al. 2002, Schulze et al. 2004, Shahabuddin 2005) and rarely in a comparison between differently managed cacao plantations and nearby located undisturbed forest sites.

3 Results

3.1 Hypothesis 1: Not forest conversion but increasing land use intensity results in reduced insect diversity

The change from natural forest to agroforestry systems was accompanied by a significant increase in temperature and cover of the herb layer (Figure 1 a and d). Contrastingly, relative humidity and upper canopy cover dropped significantly (Figure 1 b and c). In a factor analysis we combined the environmental variables in a single factor because of strong auto-correlation (Spearman rank-correlations, p 0.05). The resulting factor explained 71.7% of all variance in the variables and was positively related to temperature and herb layer cover but negatively to relative humidity and canopy cover.

In a direct comparison of abundance, species richness and a diversity index (combining abundance and species richness) between forest and agroforestry sites we quantified faunal turnover and conservation potential of agroforestry systems for different insect groups. We show how different management of agroforestry systems may play a role in the conservation of insect diversity and forest specific insect fauna.

We used different methods to sample the involved insect groups: Bees and wasps were sampled with trap nests (n=8 per site, see Tscharntke et al. 1998 for methodology), dung beetles by baited pit fall traps (n=10 per site) and canopy beetles and ants by insecticide fogging (n=4 shade dwelling trees at forest sites and 4 cacao trees at the agroforests). We collected 2854 solitary bees and wasps belonging to 32 species, 761 dung beetles of 25 species, 3247

Table 1. The average and total abundances (N) and species richness (Spp.)collected per insect group and study site. Arithmetic means ± standard error per land-use type and ANOVA results are given. Means per land-use type are taken from the total values per site. Differences between means indicated with ^{a} and ^{b} are significant according to Tukey's HSD post-hoc test.

	Natural forest	Cacao under forest remnants	Cacao under diverse, planted shade	Cacao under homogeneous, planted shade	ANOVA results	Total
Abundance:						
Dung beetles	61.5 ± 10.76	39.8 ± 6.81	47.8 ± 19.41	41.3 ± 6.71	$F_{(3, 12)}=0.67$, $p=0.58$	761
Bees and wasps	12.5 ± 6.89^a	180.0 ± 46.47^b	216.0 ± 27.46^b	305.0 ± 28.20^b	$F_{(3, 12)}=15.96$, $p<0.001$	2854
Canopy ants	176.75 ± 51.48	187 ± 76.10	231.5 ± 90.58	216.5 ± 37.44	$F_{(3, 12)}=0.14$, $p=0.93$	3247
Canopy beetles	17.8 ± 6.38^a	34.5 ± 10.49^{ab}	42.5 ± 11.24^{ab}	63.5 ± 7.98^b	$F_{(3, 12)}=4.24$, $p<0.05$	633
Species richness:						
Dung beetles	11.5 ± 1.04	10.0 ± 1.08	7.5 ± 1.66	8.8 ± 0.25	$F_{(3, 12)}=2.32$, $p=0.13$	25
Bees and wasps	2.3 ± 0.63^a	8.3 ± 1.18^b	9.3 ± 1.55^b	9.8 ± 0.75^b	$F_{(3, 12)}=10.16$, $p<0.01$	32
Canopy ants	8.8 ± 1.60	11.0 ± 1.08	8.8 ± 1.70	12.3 ± 0.85	$F_{(3, 12)}=2.02$, $p=0.16$	44
Canopy beetles	11.3 ± 3.68	22.8 ± 5.42	19.3 ± 5.62	25.5 ± 0.87	$F_{(3, 12)}=1.64$, $p=0.23$	208

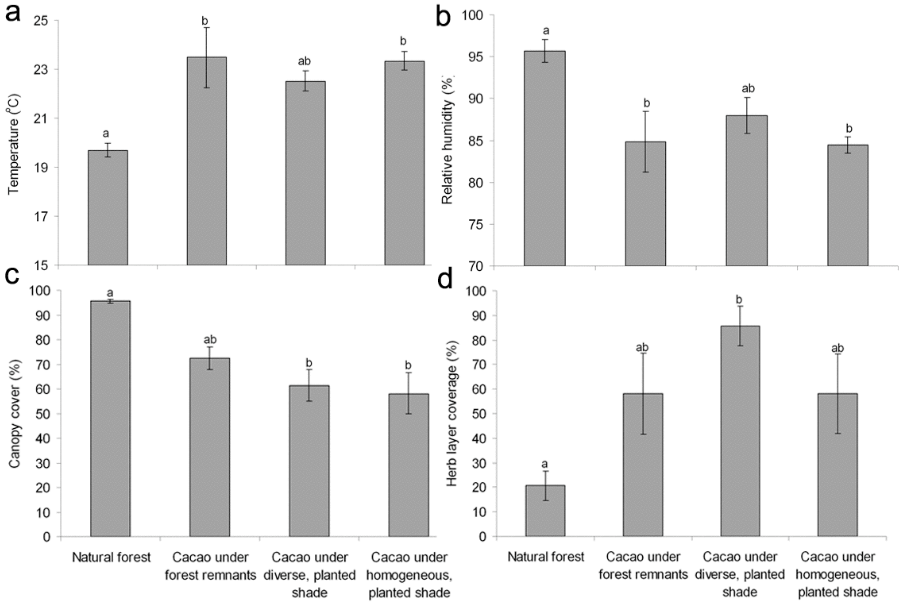

Fig. 1. The effects of forest conversion on a) Temperature (°C, ANOVA: $F_{(3,\ 12)}=6.52$, $p<0.01$) averages were taken from three morning measurements (by digital data-loggers), and averaged per site, b) Relative humidity (%RH, ANOVA: $F_{(3,\ 12)}=5.39$, $p<0.05$) was measured simultaneously with temperature, c) Canopy cover (ANOVA:$F_{(3,\ 12)}=5.39$, $p<0.05$), estimated with a spherical densiometer at 4 spots per site and averaged, and d) Herblayer coverage (%, ANOVA: $F_{(3,\ 12)}=4.43$, $p<0.05$) was estimated at four spots per site and averaged. All variables were averaged per land-use type, bars indicate standard errors between the four sites per land-use type, differences between values indicated with a and b are significant.

ants of 44 species and 633 canopy beetles belonging to 208 species. Identifications were made by specialists (see acknowledgements), on the basis of literature and on the basis of previously collected material from the same study region (by Klein et al. 2004, Shahabuddin et al. 2005). Unidentified species were sorted to morphospecies under supervision of specialists.

Per site abundances of solitary bees and wasps and of lower canopy beetles were higher in homogeneously shaded agroforests than in natural forests; however, abundances of dung beetles and canopy ants were not affected by land-use type (see Table 1). Species richness and abundance of solitary bees and wasps were positively related to the factor that was calculated from the environmental variables (species richness: $r=0.64$, $F_{(1,14)}=9.65$, $p=0.008$, abundance: $r=0.59$, $F_{(1,\ 14)}=7.58$, $p=0.02$). This means that solitary bee and wasp densities and species richness generally increased towards the least shaded agroforestry systems with dense herb layers, with a dryer and warmer microclimate than that of forest sites. Density and species richness of the other insect groups and diversity of all groups were not significantly affected by the factor ($p>0.05$).

For species richness, first order Jackknife estimations were calculated from observed values per site (EstimateS v7.00, Colwell 2004). The observed numbers of species covered between 63±0.9% (canopy beetles) and 67%±1.3% (canopy ants) of the estimates. Species richness saturation for solitary bees and wasps was significantly higher for the agroforestry systems than for the natural forest sites (ANOVA: $F_{(3, 12)}=4.47$, $p<0.05$). The observed number of species of all four insect groups were strongly correlated with estimated values for species richness ($r^2>0.90$, $p<0.00001$), so we used observed species richness for our statistical analyses, but acknowledge that actual species richness was presumably higher.

The species richness of solitary bees and wasps differed significantly between land-use types, with highest values in the three types of shaded agroforests (see table 1). Species richness of dung beetles,canopy beetles and ants showed no significant response to differences in land-use (see table 1).

Although species richness of canopy beetles increased towards the homogeneous agroforests, diversity (Simpson's reciprocal index for diversity insensitive to rare species) was significantly higher at agroforests shaded by forest remnants (27.1 ± 3.47) than at the forest sites (13.5±1.16) or the homogeneously shaded cacao agroforestry systems (13.0±2.40), see Figure 2d. The diversity of the other three insect groups also tended to be highest in cacao shaded by forest remnants, but differences remained insignificant (Figure 2a-c).

Accordingly, our results support the hypothesized negative effects of management intensification on diversity and that the effects are stronger than that of forest conversion to agroforestry systems.

3.2 Hypothesis 2: Large spatial species turnover between different land-use systems contributes to regional species richness of insects

We distinguished between species richness at the α, β and γ level in an additive partitioning approach (Lande 1996, Veech et al. 2002). Between each of the spatial scales in our set-up we calculated the β-diversity (among-scale richness) as the difference between total species richness (γ) and mean species richness (α) within one spatial scale. The scales in our study were: sample unit (trap nest or tree), study-sites, land-use types and total study area. This way we explain total species richness by the differences in number of species between the spatial levels (see also Wagner et al. 2000, Gering et al. 2003, Summerville 2003). Species recorded only once were excluded from the calculations. The data on dung beetles was lumped per site and was not available per trap.

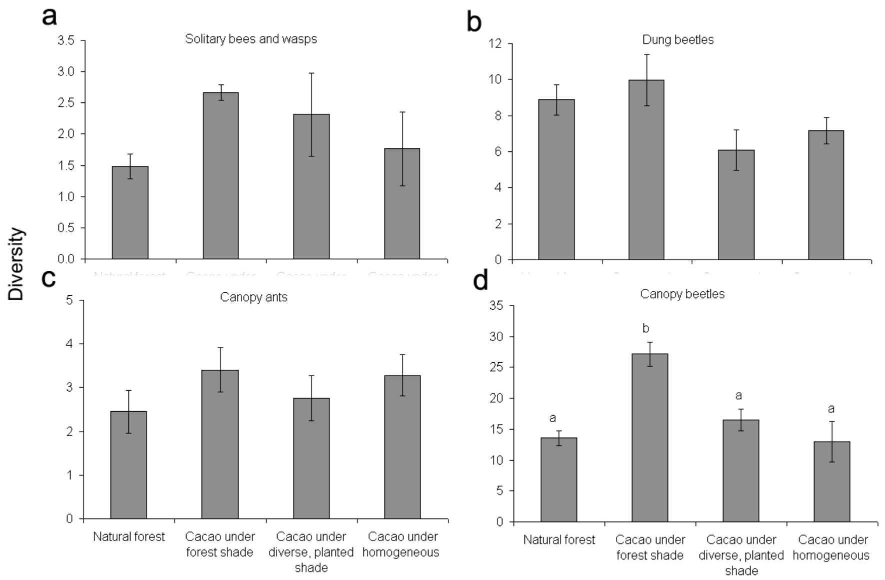

Fig. 2. Diversity (Simpson's reciprocal index) of a) Solitary bees and wasps (ANOVA: $F_{(3,\ 12)}$=1.73, p=0.21), b) Dung beetles (ANOVA: $F_{(3,\ 12)}$=2.67, p=0.09), c) Canopy ants (ANOVA: $F_{(3,\ 12)}$=0.87, p=0.48) and d) Canopy beetles(ANOVA: $F_{(3,\ 12)}$=5.7, p=0.01). Higher values stand for higher diversity. Bars indicate standard errors. Differences between letters a and b mentioned above the standard error are significant (based on Tukey's HSD post-hoc test). The index is calculated as 1 divided by the sum of the squared relative abundances of each species. The minimum values of 1 would stand for a community consisting of 1 species and the maximum possible value for a community cannot exceed the number of species.

Bees and wasps comprised a total of 32 species, of which seven occurred at forest sites. Three of those (42.9% of all forest species) were recorded only at the forest sites. The dominant eumenid wasp species *Rhynchium haemorrhoidale* (Hymenoptera: Eumenidae, 66% of all records) was the only species trapped at all land-use types but showed a pronounced preference for the monotonously shaded agroforestry systems. In the additive partitioning of species richness, the differences between study sites contributed 45% of the regional solitary bee and wasp species richness (Figure 3).

Fifteen of the 20 ant species (75.0%) found at the forest sites were also recorded at agroforestry sites. Remarkably, only three of these 20 species showed higher abundance at the forest than at the agroforest sites. Forty-four percent of regional species richness in the study area depended on the differences between the land-use types (Figure 3).

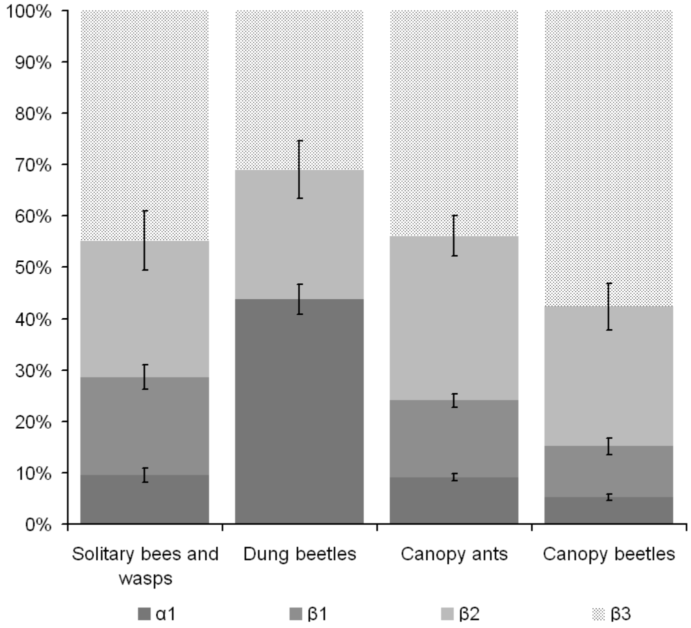

Fig. 3. The additive partitioning of species richness (species that were observed only once were excluded) showing the importance of each spatial scale for total species richness. Where values were averaged, bars indicate standard errors. α_1 = species richness per trap nest or tree (dung beetle data was lumped per study site, hence α_1 and β_1 could not be calculated); β_1 = the change in species richness from trap nest or tree to study site (α_2), β_2 = the change in species richness from study site to land-use type (α_3) and β_3 = the change in species richness from land-use type to the total species richness (α_4, or γ). Species richness at a spatial scale n equals $\alpha_{\text{n}} = \alpha_{\text{n-1}} + \beta_{\text{n-1}}$ in which the highest possible α_{n} equals total species richness γ.

Of all insect groups, dung beetles showed highest faunal overlap between forest and agroforestry sites. Of the 17 species recorded at the forest sites, 13 (76.5% of all forest species) were also found in agroforestry systems and all species were relatively common. The additive partitioning of the species richness showed that 31% of dung beetle species richness could be explained by differences between land-use types (Figure 3).

From the highly diverse canopy beetles, only five of the 40 species (12.5%) recorded at the forest sites were also found in the agroforestry systems, and, thus, they showed the smallest faunal overlap between the land-use types. Because of this high dissimilarity between agroforests and forest sites, 58% of the overall species richness was explained by the differences between land-use types (Figure 3).

Supporting the second hypothesis, the dissimilarity among the habitats (three agroforestry types and the forest) largely contributed to overall insect richness (31-58%). Further, we found high percentages of forest species that did not occur in agroforests.

4 Discussion

The cacao–dominated agroforestry systems still supported surprisingly high levels of insect diversity and species richness. Although forest conversion led to the loss of 24.5-87.5% of the species recorded at the forest sites, species richness and diversity in the managed agroforestry systems were similar to that found in the natural forest sites or even higher. Increasing management intensity of agroforestry systems with a reduction of shade-tree richness did have negative effects on the diversity (species richness and abundance combined in Simpson's index) of solitary bees and wasps, and canopy beetles, but not on the diversity of canopy ants and dung beetles. These results support the hypothesis that in addition to forest conversion land-use intensification is a major cause for decreases in insect diversity.

When we considered species richness and abundance separately, lower canopy beetles and solitary bees and wasps appeared to even profit from land-use intensification. Solitary bees and wasps had highest species richness and abundance in the homogeneous agroforests, and lower canopy beetle species richness and abundances were also highest in the homogeneously shaded agroforests. The differences in the patterns for species richness or abundance compared to the diversity index indicate that the insect communities of homogeneously shaded sites were dominated by relatively few abundant species whereas less intensively managed sites with a diverse shade canopy supported a more even species-abundance distribution.

We showed that responses of insects to forest conversion and agroforestry management depended strongly on the group studied and whether species richness or diversity was compared. Dung beetles showed no response to forest conversion and shade management. Most species at the forest sites were also able to survive in agroforestry systems. This is probably related to the high dispersal capability of dung beetles when they search for fresh feeding patches and indicates their adaptability to a broad amplitude of habitat conditions (Peck and Forsyth 1982, Hanski and Cambefort 1991). Lower canopy beetles and solitary bees and wasps showed stronger responses to both forest conversion and changes in agroforestry management but the overall diversity seemed to profit from intermediate human disturbance. We do not know how the studied insect groups would respond to further intensification and complete removal of shade trees. Perfecto et al. (1997) reports drastic declines in beetle and ant species richness from well-shaded coffee agroforestry systems to zero-shade coffee.

The conversion from tropical rainforest to agroforestry systems was accompanied by a significant decrease in the density of the upper canopy and an increase in herb-layer density and species richness of herbaceous plants (R. Pitopang, *pers. comm.*). Although we could not find significant relationships with environmental variables, the denser undergrowth vegetation of agroforestry systems presumably supported higher herbivore and pollinator densities (but not necessarily diversity) explaining the observed increase in solitary bees and lower canopy beetles. In our study, 52% of the collected lower canopy dwelling beetles represented herbivorous species and that guild showed an extreme increase towards the monotonous agroforestry systems (data not shown).

The increases in the herb layer and concomitant increases in herbivores could also have led to the higher densities of predaceous solitary wasps in the trap nests. Klein et al. (2004) observed the most common solitary wasp, *Rhynchium haemorrhoidale*, preying on cacao leaf consuming caterpillars. This wasp species accounted for 66% of all collected solitary wasps and increased sharply towards the homogenous agroforests.

As argued above, our results indicate that some insect groups from the lower canopy can profit from lower shade levels and the related increase in cover and diversity of the herb layer. However, insect communities from higher canopy layers are likely to respond oppositely to what we have found for bees, wasps and beetles in lower canopy. For example Lawton et al. (1998) and Chung et al. (2004) found a significant reduction in upper canopy beetle diversity from natural forest to agroforestry systems. Similarly, the diversity of butterflies and birds in agroforesty systems was lower than in natural forests (Schulze et al. 2004). Contrasting responses by insects in upper and lower canopy to habitat disturbance have been suggested before by Davis and Sutton (1998) and Fermon et al. (2005).

Whereas diversity remained high, species compositions changed drastically from natural forest sites to intensively managed agroforestry systems. Especially forest communities of solitary bees and wasps and lower canopy dwelling beetles were decimated after forest conversion. Canopy ants and dung beetles seemed to depend less on locally specific factors as species compositions remained more similar to those found at the forest sites.

The drastic changes of insect communities in response to forest conversion and changes in agroforestry management, led to large faunal turnover (i.e., β diversity). The differences between land-use types explained between 31% and 58% of the total recorded species richness. These results support the hypothesis that differences in local management can contribute significantly to the insect richness at the landscape level. The insect group that was most strongly affected by differences in management (lower canopy beetles) had the largest faunal turnover; more than half of their regional species richness could be explained by differences in land-use.

5 Conclusions and Outlook

Agricultural intensification and high disturbance levels due to intensified management practices have negative effects on faunal diversity in that a few 'winner' species make up a less diverse community at the cost of many 'loser' species (McKinney and Lockwood 1999). However, disturbance must extend beyond a threshold in order to cause a decline in biodiversity and before that threshold is reached, disturbance can lead to higher diversity (Connell 1978). In Europe, for example, extensive early 20th century agriculture has lead to an increase in rural biodiversity, whereas the agricultural intensification since the 1950s led to sharp declines (Tscharntke et al. 2005).

Although different insect groups respond in different ways, forest species generally declined after forest conversion. As reported here, however, overall species richness can remain high, even in agroforestry systems with homogeneous shade trees. Because species richness puts large emphasis on rare species, we combined species richness and abundance in a diversity index that was relatively insensitive to large numbers of rare species. This diversity index did not increase towards the homogeneous plantations and was for most insect groups highest at the intermediate agroforestry systems shaded by forest remnants. Hence, the most valuable type of agroforestry system from a diversity conservation point of view, are systems with a canopy of remaining forest trees where in other cases shade trees have been planted.

We did not detect effects of agroforestry intensification as strong as in tropical America where shade tree stands were completely removed in many landscapes. Under further intensification we predict similar negative effects on the still highly diverse insect fauna of the cacao-dominated agroforestry in Indonesia. Leaving shade tree stands contributes to the conservation of high insect species richness. Diversification of shade trees and the maintenance of natural forest remnants are recommended tools in the conservation of insect diversity in tropical agroforestry systems.

Faunal turnover as a result of land-use dependent differences in community structure greatly contributes to regional insect richness. The effect of different insect communities in different land-use types made up major parts of the regional insect in our study. To preserve the conservation value of cultivated areas with agroforestry, conservation policies should aim at heterogeneity at the landscape level and promote a variety of forested land-use systems.

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