Biodivers Conserv (2007) 16:2429–2444
DOI 10.1007/s10531-007-9196-0

ORIGINAL PAPER

The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia

Merijn M. Bos · Ingolf Steffan-Dewenter · Teja Tscharntke

Received: 31 March 2006 / Accepted: 13 August 2006 / Published online: 13 June 2007

Abstract The ongoing destruction of tropical rainforests has increased the interest in the potential value of tropical agroforests for the conservation of biodiversity. Traditional, shaded agroforests may support high levels of biodiversity, for some groups even approaching that of undisturbed tropical forests. However, it is unclear to what extent forest fauna is represented in this diversity and how management affects forest fauna in agroforests. We studied lower canopy ant and beetle fauna in cacao agroforests and forests in Central Sulawesi, Indonesia, a region dominated by cacao agroforestry. We compared ant and beetle species richness and composition in forests and cacao agroforests and studied the impact of two aspects of management intensification (the decrease in shade tree diversity and in shade canopy cover) on ant and beetle diversity. The agroforests had three types of shade that represented a decrease in tree diversity (high, intermediate and low diversity). Species richness of ants and beetles in the canopies of the cacao trees was similar to that found in lower canopy forest trees. However, the composition of ant and beetle communities differed greatly between the agroforest and forest sites. Forest beetles suffered profoundly from the conversion to agroforests: only 12.5% of the beetle species recorded in the forest sites were also found in the agroforests and those species made up only 5% of all beetles collected from cacao. In contrast, forest ants were well represented in agroforests, with 75% of all species encountered in the forest sites also occurring on cacao. The reduction of shade tree diversity had no negative effect on ants and beetles on cacao trees. Beetle abundances and non-forest ant species richness even increased with decreasing shade tree diversity. Thinning of the shade canopy was related to a decrease in richness of forest ant species on cacao trees but not of beetles. The contrasting responses of ants and beetles to shade tree management emphasize that conservation plans that focus on one taxonomic group may not work for others. Overall ant and beetle diversity can remain

M. M. Bos (✉) · I. Steffan-Dewenter · T. Tscharntke
Department of Crop Science, Agroecology, University of Göttingen,
Waldweg 26, Gottingen 37073, Germany
e-mail: boommarter@hotmail.com

Present Address:
M. M. Bos
State Museum of Natural History, Rosenstein 1, D-70191 Stuttgart, Germany

high in shaded agroforests but the conservation of forest ants and beetles in particular depends primarily on the protection of natural forests, which for forest ants can be complemented by the conservation of adjacent shaded cacao agroforests.

Keywords Arthropods · Biodiversity · Cultivated land · Deforestation · Habitat preference · Knockdown fogging · Lower canopy

Introduction

Landscapes throughout the tropics are increasingly dominated by agriculture (Achard et al. 2002). In such landscapes, agroforests often represent the only habitat with considerable tree cover (Schroth et al. 2004) and may be important refuges for tropical biodiversity (Rice and Greenberg 2000; Donald 2004; Schroth et al. 2004). Assessments of tropical biodiversity that have included agroforests have often found high levels of species richness within these systems, even resembling that of undisturbed tropical forests for certain groups (e.g., Perfecto et al. 1997; Lawton et al. 1998; Schulze et al. 2004; Pineda et al. 2005; Shahabuddin et al. 2005).

However, species-rich tropical agroforests are increasingly subject to modifications that involve reductions in shade tree diversity and thinning or even the complete removal of shade canopies. Such losses of agricultural heterogeneity are expected to increase the yields of the main crops (Johns 1999; Belsky and Siebert 2003; Zuidema et al. 2005), but decrease the diversity of most animal groups within the agroforests, including ants (Perfecto et al. 2003; Armbrecht et al. 2004; Philpott and Foster 2005), bees (Klein et al. 2002), beetles (Perfecto et al. 1997), butterflies (Perfecto et al. 2003) and birds (Perfecto et al. 2003).

There are two main reasons why the modifications of the shade canopy can result in biodiversity losses. First, reductions of shade tree diversity represent a form of habitat simplification that promotes a few ‘winner’ plant and animal species at the cost of many pristine ‘loser’ species (McKinney and Lockwood 1999). This increasing habitat homogeneity can drive biodiversity loss as the availability of nesting sites declines (Klein et al. 2002 for bees; Armbrecht et al. 2004 and Philpott and Foster 2005 for ants) and important food plants disappear (Perfecto et al. 2003 for fruit-feeding butterflies; Waltert et al. 2004 for birds). Second, the reduction or complete removal of the shade canopy is usually accompanied by changes in temperature and humidity that may indirectly lead to decreases in particularly ant diversity (Perfecto and Vandermeer 1996; Armbrecht et al. 2005) by favoring ecologically dominant ant species (Room 1971; Gibb and Hochuli 2003), which can even lead to cascades of further biodiversity losses (O’Dowd et al. 2003).

Studies on biodiversity conservation in agroforests that also included beta diversity, have found considerable differences in faunal composition between pristine forests and coffee or cacao dominated agroforests. These studies mostly focused on insects (e.g., Armbrecht et al. 2005; Pineda et al. 2005; Shahabuddin et al. 2005) but such a large turnover from natural to cultivated forests has also been found for birds (Waltert et al. 2004). Despite the wealth of studies on the role of agroforestry in biodiversity conservation, it remains largely unknown to what extent agroforests can support forest fauna, and how this faunal component responds to changing shade canopy management (but see Perfecto et al. 2003; Armbrecht et al. 2005).

In the tropics, ants and beetles are the major contributors to the richness of canopy dwelling insect fauna (e.g., Erwin 1982; Lawton et al. 1998). Moreover, ants are dominant elements of tropical ecosystems because of frequent interactions with other insect groups and include abundant predators, decomposers and herbivores (Room 1971; Majer 1972, 1976; Majer et al. 1994; O'Dowd et al. 2003). Nevertheless, the diversity of ants and beetles in cacao dominated agroforests still remains poorly studied, particularly in the context of biodiversity conservation (but see Room 1971; Majer 1972, 1976; Majer et al. 1994; Delabie et al. this issue for cacao ants).

We examined ants and beetles in the lower part of the canopy of natural forests and cacao dominated agroforests in order to investigate the following two questions concerning the role of shaded agroforests in the conservation of biodiversity: (i) Do agroforests resemble natural forests in terms of the ant and beetle assemblages in the lower canopy? and (ii) Does modification of the shade canopy of agroforests affect the diversity of forest and non-forest species within these two groups? The systems selected for our study were in the margin area of a large natural rainforest in Central Sulawesi, Indonesia, a major cacao producing region (Potter 2001) and a major biodiversity hotspot (Myers et al. 2000). By distinguishing between 'forest' and 'non-forest' species of two important insect groups in tropical canopies, we provide a quantification of the proportion of species richness that is possibly native to forest habitats that can also be supported by agroforests. Whereas biodiversity may overall remain high, forest species may be particularly sensitive to changing management practices.

Materials and methods

Study site

This study took place in and around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (1°30′24″ S, 120°2′11″ E, 800–900 masl). Toro is located at the western border of the unfragmented, 231,000 ha Lore Lindu National Park, about 100 km south of Palu, the capital city of Central Sulawesi. The region has an annual average (±SE) temperature of 24.0 (±0.16)°C and a mean monthly rainfall of 143.7 (±22.74) mm. There are no clear seasonal fluctuations. The natural vegetation of the National Park around the village is submontante rainforest.

The agricultural landscape in the region is highly heterogeneous, consisting of a patchy mosaic of pasture, hedges and cacao dominated agroforests, which is typical for the region. Cacao production in the region increased strongly in the 1990s when large areas of coffee agroforests were converted to cacao agroforests (Potter 2001). Cacao agroforests in the Toro village are owned and managed by small-scale farmers. Shade tree management in the region is dynamic and farmers generally planned to remove shade trees in the opinion that this would increase cacao production.

We defined a priori three types of agroforests, which represented a gradient of shade tree diversity but were comparable in terms of basal area and stem density (Table 1 and Gradstein et al. 2007):

(i) Cacao agroforests with diverse, natural shade trees that had been retained from previously undisturbed forest when it was thinned and underplanted with cacao trees (DNS). Cacao agroforestry was the first form of cultivation in these sites (since 8–15 years). These agroforests still had high numbers of native shade trees, and even some endemic species.
(ii) Cacao agroforests with shade tree stands dominated by various species of planted shade trees (DPS). These sites had a longer history of cultivation (longer than

Table 1 Characteristics of the tree flora of natural forest and three types of cacao agroforests at the study sites in Central Sulawesi, Indonesia, averaged per habitat type (means ± SE)

Site characteristic	NF (n = 4)	DNS (n = 4)	DPS (n = 4)	SPS (n = 4)
Tree species[1]	55.8 ± 2.75[a]	20.8 ± 3.90[b]	19.0 ± 3.75[b]	9.0 ± 2.25[b]
Tree families[1]	27.0 ± 1.70[a]	14.3 ± 1.80[b]	13.5 ± 2.25[b]	6.8 ± 1.65[b]
Native tree species[1]	55.8 ± 2.75[a]	18.5 ± 3.95[b]	10.3 ± 4.40[bc]	5.5 ± 1.85[c]
Endemic tree species[1]	8.0 ± 0.40[a]	2.3 ± 1.30[b]	0.8 ± 0.75[b]	0[b]
Planted tree species[1]	0[a]	2.3 ± 0.50[b]	8.8 ± 0.65[c]	3.5 ± 0.50[b]
Stems $\geq$ 10 cm dbh[1]	140.5 ± 8.65[a]	77.5 ± 10.55[b]	70.0 ± 11.05[b]	81.0 ± 27.75[b]
Basal area (m^2 ha^{-1})	56.7 ± 9.10[a]	20.5 ± 4.20[c]	14.9 ± 4.85[c]	11.9 ± 3.15[c]
Canopy cover (%)	95.8 ± 0.42[a]	72.5 ± 2.22[b]	61.4 ± 3.96[c]	58.1 ± 4.55[c]

All data except shade canopy cover are adapted from Gradstein et al. (2007)

[1] Values are per 0.25 ha

Different letters indicate significant differences at $P < 0.05$. NF = Natural forest, DNS = cacao plantation with diverse natural shade, DPS = cacao plantation with diverse planted shade, SPS = cacao plantation with simple planted shade, dbh = diameter at breast height

20 years e.g., as coffee agroforests) and trees from the previous forest cover were all replaced by various planted fruit and timber trees that provided the owners with non-market products. Among these trees were some native (including a few endemic) species.

(iii) Cacao agroforests with a low diversity of planted shade trees (SPS). These sites also had a longer history of cultivation (longer than 20 years e.g., as coffee plantations). Management of these agroforests was aimed at maximum cacao productivity. Shade was provided predominantly by the non-indigenous leguminous trees *Gliricidia sepium* and *Erythrina subumbrans* that are nitrogen fixing. Some native timber or fruit tree species were also grown, none of which were endemic.

We selected four replicates of each of the three types of cacao agroforests. Sites were selected based on the age of the cacao trees, which was on all sites between 7 years and 10 years. At the time of this study agroforestry was non-intensive in each site, with little use of fertilizers and pesticides. Farmers regularly pruned trees and weeded the plantations (2–3 times per year).

Additionally, four forest sites (NF) were selected close to the village, but well within the national park and representative for the submontane forest in the area. These forest sites were part of the continuous Lore Lindu National Park and at least 300 m away from forest sites where selective logging occurred. Selective logging was allowed in the national park's margins, only by local people and only for local timber use. In the selected sites minor rattan extraction occurred. The sites had more than 50 tree species per 0.25 ha and a basal area (m^2/ha) that was high compared to other primary forests in Southeast Asia. The forest sites had significantly higher basal areas and stem densities than the agroforests (Table 1, Gradstein et al. 2007).

The minimum distance between study sites was 300 m and the maximum distance was about 5 km. All sites were between 850 m and 1,100 m above sea level. The agroforests did not have sharp borders with other habitat types, but gradually changed into other forms of land-use. The agroforests formed a continuous band along the forest margin. Boundaries between agroforests were arbitrary based on ownership. Therefore, we marked core areas of 30 × 50 m in the middle of each site. Land-use and types of shade tree stands did not change within these areas. Sites of different habitat types were geographically interspersed so that none of the habitat types were spatially clustered.

The percent canopy cover above the cacao layer was estimated using a spherical densiometer. Canopy cover was estimated at two spots around each studied tree and the mean of these two estimates per tree was used in the analyses.

Collecting ants and beetles from small, lower canopy trees

Within the marked core areas, four trees were selected, which were of similar age and size. These were cacao trees in the agroforests ($n = 48$, height: 3.4 ± 0.56 m standard error) and small, shade-dwelling lower canopy trees ($n = 15$, height: 6.3 ± 1.90 m) in the natural forest sites with canopy sizes similar to those of the selected cacao trees. At one forest site, ants and beetles from only three trees could be sampled due to a technical problem.

In order to characterize the forest insect fauna as completely as possible, we sampled insects on a diverse set of trees in the forest understory. The 15 trees in the forest sites were identified by R. Pitopang (Herbarium Celebense, Palu, Indonesia) and belonged to 14 species of 10 families. Only on one occasion, two subject trees in one forest site were of the same family. None of the forest trees were recorded flowering or fruiting at the time the sampling took place. At the time of the survey, cacao in the region was between a main flowering and a harvesting period, although minor flowering and fruiting occurred throughout the year.

Lower canopy dwelling ant and beetle fauna was sampled using canopy knockdown fogging, which is an effective and widely used technique for collecting arthropods from tree crowns (Perfecto et al. 1997; Lawton et al. 1998). With a SwingFog TF35, a fog of 1% pyrethroid insecticide (Permethrin) was blown horizontally into the target canopy to avoid collecting insects from higher canopy layers. Killed arthropods were collected from a 4 square meter sheet of white canvas placed directly under each tree. We randomly selected one site per day and sampled all four trees between 8:00 and 9:00 at the time of day of lowest wind speed and rainfall probability from December 17 2003 to January 1 2004.

Identifications

To date, the extremely high species richness of tropical regions remains largely undescribed by taxonomists and the insect fauna in Indonesia is no exception (Basset 2001). Therefore, we chose to sort the collected insects into units based on external morphology (morphospecies). Ant sorting was carried out by Indonesian ant specialist Akhmad Rizali (IPB Bogor, Indonesia), based on literature (Bolton 1994) and reliable digital resources (e.g., http://www.antweb.org and http://www.antbase.de). Identifications of beetles were carried out by Boris Büche and Christoph Bayer (Berlin, Germany). Where necessary, beetle morphospecies were sorted based on genitalia preparations. All morphospecies were photographed and posted on the Internet (http://www.ant-diversity.com and http://www.beetle-diversity.com) through which specialists were contacted internationally for identifications based on the photographs (see acknowledgements) and for further taxonomic work.

In our quantifications of faunal turnover between the natural forest sites and the agroforests, we categorized species as 'forest species' when they occurred on any of the selected trees ($n = 15$) in the forest sites and as 'non-forest species' if they were only found on cacao trees. We acknowledge that the resulting summed amount of 'non-forest species' could be an overestimate that could decrease if more forest sites are sampled. Therefore, we only compare amounts of 'non-forest species' on the tree or site level.

Data analysis

From the observed species richness per site we calculated first order Jackknife estimators for species richness. Observed species richness in field studies is typically an underestimate of the actually occurring number of species (Colwell and Coddington 1994), which calls for the use of species richness estimators (see also Schulze et al. 2004). We calculated the Bray-Curtis similarity index for each pair-wise site comparison as a measure for between-site similarity of ant and beetle assemblages. This similarity index ranges between 0 (no shared species) and 1 (fully similar community composition) and takes abundances of species into account. Using the Bray-Curtis similarity indices we conducted a multidimensional scaling (MDS) to obtain a two-dimensional representation of the similarities between species composition at the study sites (Shahabuddin et al. 2005). MDS is a powerful method for ordinating similarity matrices as it is independent of the type of data distribution. The accompanied stress value of an ordination indicates the goodness of fit of the scaling to the similarity matrix. Stress values of 0.20 and lower indicate a good fit (StatSoft Inc. 1984–2004). The first order Jackknife estimator for total species richness and the Bray-Curtis index for faunal similarity served well in comparable studies (Schulze et al. 2004; Armbrecht et al. 2005).

The effects of habitat types (forest and three types of cacao agroforests) on observed and estimated species richness per site were tested in one-way ANOVA's. To test for effects of forest conversion to cacao agroforests on species richness and abundance per tree, we used general linear models (GLMs) with habitat type as a fixed factor and trees nested within sites. The effect of shade cover was only tested within the agroforests (12 sites and 48 trees, pooled across the three types of agroforests) in a GLM with habitat type as a fixed factor, trees nested within sites and canopy cover included as a covariate. Trees and sites were in all models entered as random factors. Post-hoc tests were conducted using Tukey's HSD (honestly significantly different) tests.

Data were square root transformed where necessary to achieve normal distribution of model residuals. Arithmetic means are given ± one standard error. The species richness estimator and similarity indices were calculated using EstimateS 7.0 (Colwell 2004). All other analyses were carried out using Statistica 7.0 (StatSoft Inc. 1984–2004).

Results

Upper canopy cover in the agroforests ranged from 82.3 ± 1.65% to 42.5 ± 7.46%. This was significantly less than in any of the natural forest sites ($F_{(3,\ 56)} = 32.0$, $P < 0.001$, Table 1). Further, canopy cover in agroforests with planted shade was significantly less than in the agroforests with natural shade.

Effects of cacao agroforestry and shade management on ant and beetle communities

In total 3,247 ants were collected (55% of all arthropods) belonging to 6 subfamilies, 18 genera and 44 species (Appendix 1). The five most common species (Table 2) made up

Table 2 Total abundance of the five most common ant species (34% of all collected ant individuals) in natural forest and three types of cacao agroforests in central Sulawesi

	NF	DNS	DPS	SPS	Total
Dolichoderus sp. 1 (Dolichoderinae)	3	364	48	54	469
Paratrechina sp. 1 (Formicinae)	1	24	346	66	437
Polyrhachis (*Myrmhopla*) sp. nov. (Formicinae)	180	70	34	19	303
Crematogaster sp. 2 (Myrmicinae)	276	1	1	24	302
Anoplolepis gracilipes (Formicinae)	1	0	1	287	289

NF = Natural forest, DNS = Diverse natural shade, DPS = Diverse planted shade, SPS = Simple planted shade

34% of all ants collected and were encountered in both the forest sites and agroforests. The observed species richness per site did not differ between forest and agroforests ($F_{(3, 12)} = 1.64$, $P = 0.23$, Fig. 1a), and the same was true for the estimated species richness ($F_{(3, 12)} = 2.68$, $P = 0.09$, Fig. 1a).

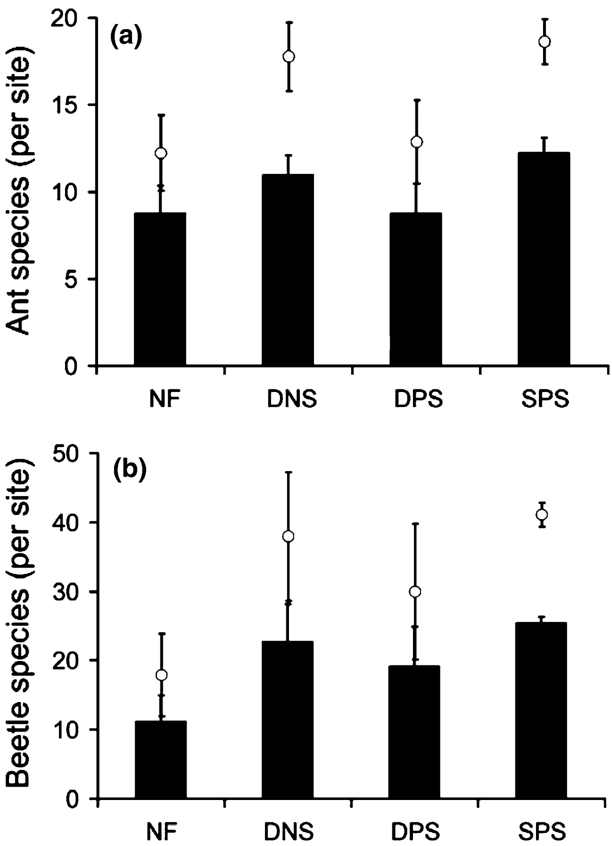

Fig. 1 Means and standard errors of species richness of ants (**a**) and beetles (**b**) in the lower canopy of four habitat types in Central Sulawesi, Indonesia: natural forest (NF), cacao agroforests with diverse natural shade trees (DNS), cacao agroforests with diverse planted shade trees (DPS) and cacao agroforests with simple shade tree stands dominated by one or two species (SPS). Bars are observed values and circles are first order Jackknife estimators

In total, 15 ant species (75% of all ant species recorded in the forest sites) were recorded in both the forest sites and in agroforests. However, the multidimensional scaling (MDS) of the Bray-Curtis similarity indices (Fig. 2a) showed that the ant fauna of cacao in

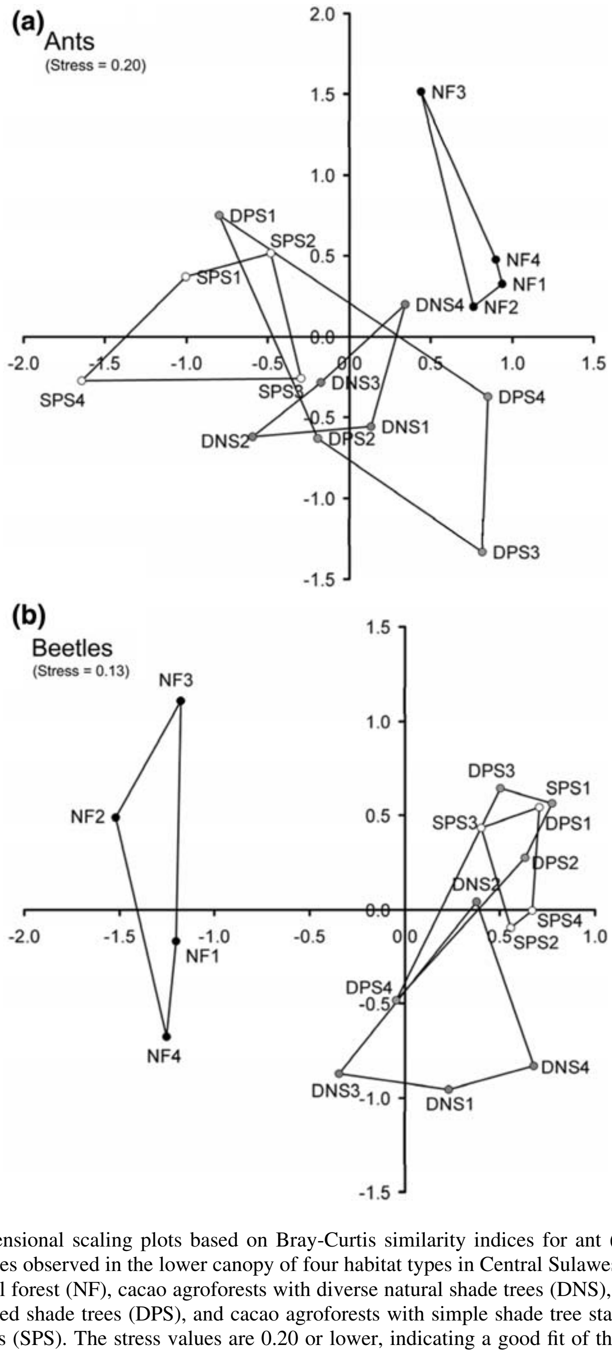

Fig. 2 Multidimensional scaling plots based on Bray-Curtis similarity indices for ant (**a**) and beetle (**b**) species assemblages observed in the lower canopy of four habitat types in Central Sulawesi, Indonesia (four sites each): natural forest (NF), cacao agroforests with diverse natural shade trees (DNS), cacao agroforests with diverse planted shade trees (DPS), and cacao agroforests with simple shade tree stands dominated by one or two species (SPS). The stress values are 0.20 or lower, indicating a good fit of the scaling with the similarity index

agroforests was distinct from that of forest lower canopy trees. Moreover, agroforests with natural shade had a distinct ant community from that of agroforests with shade tree stands dominated by one or two species of planted leguminous trees.

Ant species richness and abundance per tree did not differ between forest and cacao trees (overall averaged species richness: 3.8 ± 0.26, $F_{(3,\ 55.3)} = 1.57$, $P = 0.21$; overall averaged abundance: 51.4 ± 7.46, $F_{(3,\ 55)} = 0.27$, $P = 0.85$, Fig. 3a). Overall ant species richness on cacao trees was, however, negatively affected by decreasing shade cover ($R^2 = 0.09$, $P = 0.02$).

A total of 633 beetles were collected (10% of all arthropods) belonging to 37 families and 209 species (Appendix 2). The five most abundant beetle species (Table 3) made up 30% of all beetles and none of them was among the species collected from the lower canopy trees in the forests. Neither the observed species richness per site ($F_{(3,\ 12)} = 2.03$, $P = 0.16$, Fig. 1b) nor the estimated species richness ($F_{(3,\ 12)} = 1.92$, $P = 0.18$, Fig. 1b) differed between forest and agroforest sites.

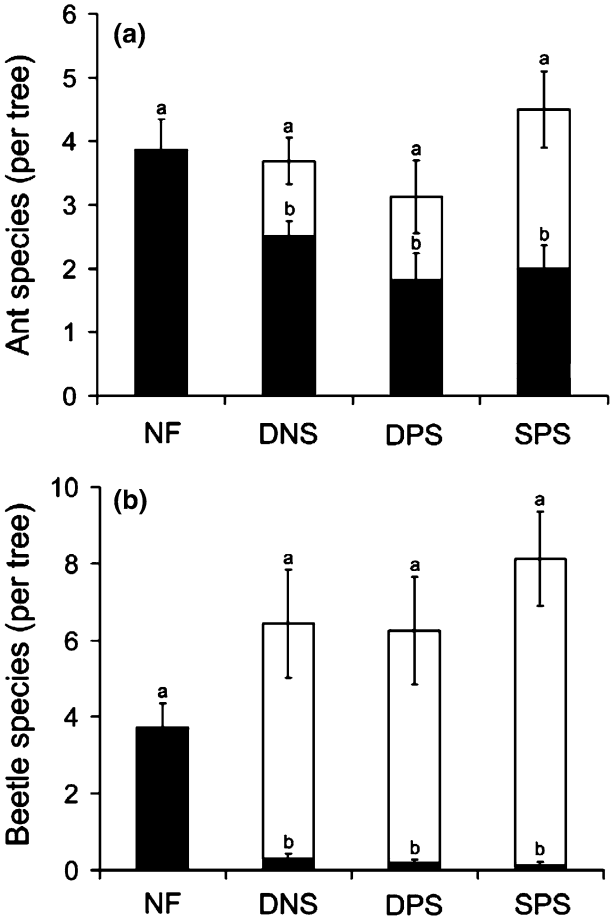

Fig. 3 Effect of forest conversion on the species richness of ants (**a**) and beetles (**b**) per tree in natural forest sites (NF) and cacao agroforests with diverse forest shade (DNS), diverse planted shade (DPS) and simple planted shade (SPS) in Central Sulawesi, Indonesia (means and standard errors). Black bars indicate forest species, white bars indicate other species. Different letters indicate significant differences at $P < 0.05$

Table 3 Total abundance of the five most common beetle species (30% of all collected beetle individuals) in natural forest and three types of cacao agroforests in central Sulawesi

	NF	DNS	DPS	SPS	Total
Monolepta jacobyi 40 (Chrysomelidae)	0	7	22	38	67
Anthelephila sp. 1 (Anthicidae)	0	0	15	25	40
Demotina sp. 6b (Chrysomelidae)	0	10	7	15	32
Apogonia varievestis 1 (Scarabaeidae)	0	2	14	11	27
Amarygmus discretus 5a (Tenebrionidae)	0	11	5	10	26

NF = Natural forest, DNS = Diverse natural shade, DPS = Diverse planted shade, SPS = Simple planted shade

Only five forest beetle species (12.5% of all species recorded in the forest sites) were recorded on cacao. The MDS of the Bray-Curtis similarity indices (Fig. 2b) showed a sharp distinction between the beetle fauna of cacao trees in agroforests and that of lower canopy trees in the forest sites. Moreover, agroforests with natural shade trees had a distinct faunal assemblage from that of the agroforests with shade tree stands dominated by one or two species of planted leguminous trees.

On a per tree basis, beetle species richness did not differ between forest and cacao trees (overall average: 6.2 ± 0.63, $F_{(3,\ 55)} = 2.30$, $P = 0.09$, Fig. 3b). Conversely, beetle abundance on cacao trees under simple planted shade (15.9 ± 3.26) was significantly higher than on lower canopy forest trees (4.7 ± 0.91; $F_{(3,\ 55)} = 3.37$, $P = 0.02$, Fig. 3b). Changes in canopy cover affected neither species richness nor abundance of beetles on cacao trees (species richness: $R^2 = 0.09$, $P = 0.21$; abundance: $R^2 = 0.04$, $P = 0.12$).

Responses of forest versus non-forest ant and beetle species to shade canopy composition and openness

The richness of non-forest ant species increased on cacao under shade tree stands that were dominated by planted leguminous trees ($F_{(2,\ 41)} = 3.66$, $P = 0.03$, Fig. 3a), whereas the species richness of forest ants on cacao trees was unaffected by shade tree composition ($F_{(2,\ 41)} = 1.07$, $P = 0.35$, Fig. 3a). However, the number of forest ant species on cacao trees declined significantly with increasing openness of the shade canopy ($R^2 = 0.22$, $P < 0.001$, Fig. 4), whereas the effects of shade thinning on the richness of non-forest species were not significant ($R^2 < 0.001$, $P = 0.96$).

Because the five beetle species that were shared between forest and agroforestry sites represented only 5% of all beetle individuals collected from cacao (Fig. 3b), we did not distinguish between forest and non-forest species in further analyses.

Discussion

The species richness of ants and beetles was similar on cacao trees in shaded, cacao dominated agroforests and on lower canopy trees in forest sites, thus underlining the potential of such agroforests for maintaining tropical insect species richness. However, there was a sharp distinction in the composition of ant and beetle communities across forest and agroforestry sites. Hence, without information on the identity of species, species richness comparisons may lead to erroneous conclusions concerning the actual conservation potential of agroforests.

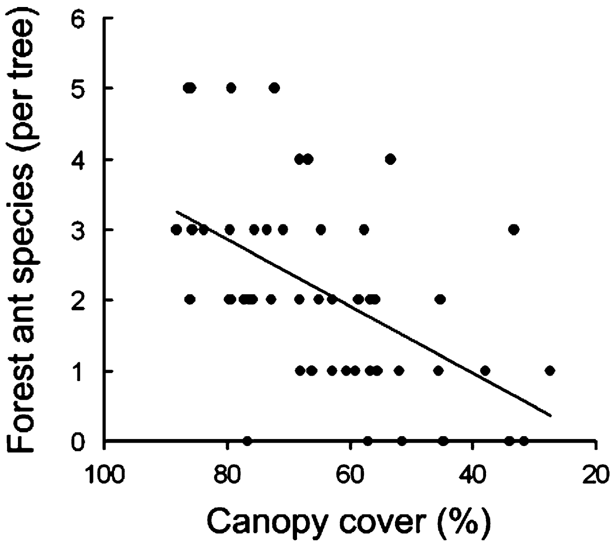

Fig. 4 Relationship between canopy cover (%) and the number of forest ant species observed per cacao tree in three types of cacao agroforests in Central Sulawesi, Indonesia. The relationship was not significantly different between the three types of agroforests

Ant species that occurred in the four forest sites were well represented in the 12 agroforests, with 75% of the species observed in the lower canopy of the forest being also observed on cacao trees. These results may be explained by the fact that ant species can profit from the nesting availabilities that are still offered by shaded agroforests (Armbrecht et al. 2004; Philpott and Foster 2005). In contrast, forest beetle communities changed drastically from forest lower canopy to cacao trees in agroforests. Only 12.5% of the beetle species recorded on the forest trees was also found on cacao trees, and these shared species made up only 5% of all collected beetle individuals. Thus, the replacement of forest by agroforests has pronounced effects on the ant and beetle communities. Conservation on the species level strongly depended on the taxon examined. Whereas forest beetles were almost completely replaced by non-forest species, forest ant species were comparably well preserved in the cacao agroforests.

The effect of agroforestry management on forest and non-forest beetles and ants depends on whether management changes the diversity of shade trees or the cover of shade canopy. Firstly, reduced habitat heterogeneity may drive species losses in that complex, heterogeneous habitats harbour higher species richness than simple, homogeneous habitats (McKinney and Lockwood 1999; Armbrecht et al. 2004). In our study, the reduction of shade tree diversity increased habitat homogeneity. Ant and beetle communities on cacao under homogeneous, planted shade were distinct from those on cacao shaded by trees from the original forest. The reduced shade tree diversity, however, did not affect total ant and beetle species richness per site and per tree, which suggests that none of the shaded agroforests were under such intense management that species richness per se was threatened. Such threats are known to occur in conversions to zero-shade cacao plantations or annual crops (Perfecto et al. 1997; Schulze et al. 2004; Armbrecht et al. 2005; Shahabuddin et al. 2005). Moreover, the richness of non-forest ant species even increased on cacao trees in agroforests shaded by just leguminous trees, compared to the other two types of agroforests. Similarly, the reduction of shade tree diversity led to an increase in beetle abundance (almost only non-forest species), but not species richness, which suggests that a few beetle species also profited from increasing shade tree homogeneity.

The species that profit from more intensive shade management are least interesting from a conservation point of view and are unlikely to be threatened by conversions of forests to agroforests. For example, the invasive Crazy Ant *Anoplolepis gracilipes* (Smith 1857; O'Dowd et al. 2003) was rarely found at forest sites, but was abundant under planted shade tree stands (Table 2). Additionally, the most wide-spread and abundant beetle species (10% of all beetles collected) on cacao in our study was a leaf beetle of the genus *Monolepta jacobyi* (Chrysomelidae: Galerucinae) that was only found on cacao trees (Table 3), although it did not feed on its leaves but was the most important herbivore on the planted shade tree species *Erythrina subumbrans* (Leguminosae) (M. M. Bos and B. Büche unpublished data).

Secondly, more intensive management of agroforests is often accompanied by the thinning of shade tree stands (e.g., Perfecto et al. 1997; Klein et al. 2002). In our study, planted trees created less shade than natural trees. Ant and beetle abundance and beetle species richness per tree were not affected by increasing canopy openness, whereas ant species richness declined when the canopy became more open, particularly because of the strong response of forest ant species. Responses of ants to microclimatic changes that are associated with shade thinning—higher temperatures and lower humidity—are known, and a reduction in shade levels has been found to increase dominance by a few ant species (Room 1971; Perfecto and Vandermeer 1996; Gibb and Hochuli 2003).

Conclusion

Shaded agroforests that are dominated by cacao in the lower canopy appear to contribute to the conservation of ant and beetle species richness. However, biodiversity assessments should include direct comparisons with adjacent natural forests to avoid overestimates of actual conservation potential of agroforests for forest fauna. Our results support previous studies (e.g., Waltert et al. 2004; Armbrecht et al. 2005; Shahabuddin et al. 2005) that showed that forest species are often sensitive to the changes in habitat characteristics that accompany the conversion of natural forests into agroforests. Highly diverse taxonomic groups such as beetles may show drastic species turnover after conversion to agroforests. In contrast, shaded agroforests may be a suitable surrogate habitat for native ant communities, but management also matters in that forest ants suffer from reduced canopy cover, possibly because of altered interactions with ecologically dominant species that are promoted by the accompanied changes in the microclimate.

Ant and beetle assemblages in the cacao agroforests were dominated by species of low conservation priority that are unlikely to be threatened by the ongoing destruction of tropical rainforests. The different responses to the same agroforest modifications of the ecologically important ants and beetles emphasize the need to use multiple taxa as indicator organisms for habitat destruction and effects of conservation strategies. Shaded agroforests can support a high diversity of ants and beetles, but few forest species in the case of beetles, so conservation plans should primarily build upon the protection of natural forests, complemented by well-shaded agroforests.

Acknowledgments This study was funded by the German Research Foundation (DFG), grant SFB-552 ''STORMA''. We thank Christian H. Schulze and Simone G. Sporn for valuable suggestions during the fieldwork. Further, we thank Goetz Schroth, Celia Harvey, Jason M. Tylianakis, Tatyana Rand and 3 anonymous referees for their valuable suggestions that improved previous versions of this manuscript.

We are very grateful to Boris Büche, Christoph Bayer, Rudy Kohout and Akhmad Rizali for their detailed and careful identification and sorting of ant and beetle species. We thank Ramadanil Pitopang (Herbarium Celebense, Indonesia) for identifying forest trees, Damayanti Buchori (IPB Bogor, Indonesia), Pak Mann, Arifin, Daniel Stietenroth, Adam Malik, Wolfram Lorenz and Surya Tarigan for their help in this work, and the following coleopterists for their identifications after visiting www.beetle-diversity.com: Alberto Ballerio, Roland Gerstmeier, Denis Keith, Otto Merkl, Chris Reid, Wolfgang Schawaller, Dmitry Telnov and Jürgen Wiesner.

Appendix

Appendix 1 Number of ant individuals (A) and species (S) per genus collected in natural forest and three types of cacao agroforests in Central Sulawesi, Indonesia

Subfamily	Genus	NF		DNS		DPS		SPS		Total	
		A	S	A	S	A	S	A	S	A	S
Dolichoderinae	*Dolichoderus*	3	1	364	1	48	1	78	2	493	2
	Tapinoma	0	0	48	1	0	0	22	1	70	1
	Technomyrmex	0	0	3	1	0	0	0	0	3	1
Ectatomminae	*Gnamptogenys*	102	1	23	1	1	1	0	0	126	1
Formicinae	*Anoplolepis*	1	1	0	0	1	1	287	1	289	1
	Camponotus	2	2	38	3	75	2	9	2	124	3
	Echinopla	13	2	2	1	1	1	7	1	23	2
	Oecophylla	8	1	18	1	8	1	0	0	34	1
	Paratrechina	1	1	28	2	484	3	78	3	591	4
	Polyrhachis	289	8	164	8	97	6	297	11	856	15
Myrmicinae	*Cataulacus*	0	0	0	0	0	0	4	1	4	1
	Crematogaster	276	1	48	3	190	3	61	3	575	3
	Paratopula	0	0	6	2	4	1	1	1	11	2
	Pheidole	2	1	1	1	0	0	0	0	3	1
	Secostruma	1	1	0	0	0	0	0	0	1	1
	Tetramorium	0	0	0	0	10	1	15	2	25	3
Ponerinae	*Pachycondyla*	0	0	1	1	0	0	0	0	1	1
Pseudomyrmecinae	*Tetraponera*	0	0	4	1	7	1	7	1	18	1
Total		707	20	748	27	926	22	866	29	3247	44

NF = Natural forest, DNS = cacao under diverse natural shade, DPS = cacao under diverse planted shade, SPS = cacao under simple planted shade

Appendix 2 Number of beetle individuals (A) and species (S) per family collected in natural forest and three types of cacao agroforests in Central Sulawesi, Indonesia

Superfamily	Family	NF		DNS		DPS		SPS		Total	
		A	S	A	S	A	S	A	S	A	S
Buprestoidea	Buprestidae	1	1	1	1	0	0	1	1	3	3
Byrrhoidea	Dryopidae	2	1	0	0	0	0	0	0	2	1
	Limnichidae	0	0	3	3	0	0	3	1	6	3
	Ptilodactylidae	2	2	1	1	1	1	1	1	5	5

Appendix 2 continued

Superfamily	Family	NF		DNS		DPS		SPS		Total	
		A	S	A	S	A	S	A	S	A	S
Cantharoidea	Cantharidae	1	1	2	2	0	0	1	1	4	4
	Lycidae	2	2	7	5	2	2	0	0	11	7
Caraboidea	Carabidae	3	3	3	3	4	4	8	6	18	11
	Cicindelidae	1	1	0	0	0	0	0	0	1	1
Chrysomeloidea	Cerambycidae	2	2	4	3	2	1	13	5	21	10
	Chrysomelidae	7	4	42	17	43	9	96	13	188	33
Cleroidea	Cleridae	1	1	2	2	2	2	0	0	5	5
Cucujoidea	Coccinellidae	0	0	1	1	3	2	1	1	5	4
	Endomychidae	0	0	2	2	0	0	0	0	2	2
	Languriidae	1	1	0	0	10	1	4	1	15	2
	Phalacridae	1	1	0	0	0	0	0	0	1	1
	Rhizophagidae	0	0	1	1	0	0	0	0	1	1
Curculionoidea	Anthribidae	1	1	2	2	7	2	6	4	16	7
	Apionidae	0	0	0	0	0	0	1	1	1	1
	Attelabidae	1	1	0	0	0	0	0	0	1	1
	Brentidae	0	0	0	0	2	2	2	2	4	4
	Curculionidae	38	14	26	11	14	8	24	14	102	36
	Dryophtoridae	0	0	1	1	0	0	0	0	1	1
	Rhynchitidae	0	0	0	0	1	1	1	1	2	2
Elateroidea	Elateridae	3	1	8	6	6	3	3	2	20	11
	Eucnemidae	0	0	0	0	1	1	1	1	2	2
Histeroidea	Histeridae	0	0	1	1	0	0	1	1	2	1
Scarabaeoidea	Ceratocanthidae	2	1	0	0	0	0	0	0	2	1
	Scarabaeidae	0	0	4	3	25	5	28	5	57	8
Staphylinoidea	Staphylinidae	0	0	1	1	0	0	0	0	1	1
Tenebrionoidea	Aderidae	1	1	0	0	1	1	0	0	2	2
	Anthicidae	1	1	1	1	19	2	28	2	49	4
	Colydiidae	0	0	1	1	0	0	1	1	2	1
	Melandryidae	0	0	0	0	1	1	0	0	1	1
	Mordellidae	0	0	6	5	0	0	1	1	7	6
	Othniidae	0	0	0	0	1	1	0	0	1	1
	Salpingidae	0	0	1	1	0	0	0	0	1	1
	Tenebrionidae	0	0	17	6	25	10	29	16	71	24
Total		71	30	138	57	170	51	254	65	633	209

NF = Natural forest, DNS = cacao under diverse natural shade, DPS = cacao under diverse planted shade, SPS = cacao under simple planted shade

References

Achard F, Eva HD, Stibig H-J, Mayaux P, Callego J, Richards T, Malingreau J-P (2002) Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002

Armbrecht I, Perfecto I, Vandermeer J (2004) Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science 304:284–286

Armbrecht I, Rivera L, Perfecto I (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. Conserv Biol 19:897–907
Basset Y (2001) Invertebrates in the canopy of tropical rain forest. How much do we really know? Plant Ecol 153:87–107
Belsky JM, Siebert SF (2003) Cultivating cacao: implications of sun-grown cacao on local food security and environmental stability. Agric Human Values 20:270–285
Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts, USA
Colwell RK (2004) EstimateS: statistical estimation of species richness and shared species from samples. Version 7. User's Guide and application. http://purl.oclc.org/estimates
Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond B 345:101–118
Donald PF (2004) Biodiversity impacts of some agricultural commodity production systems. Conserv Biol 18:17–37
Erwin TL (1982) Tropical forests: their richness in Coleoptera and other arthropod species. Coleopt Bull 36:74–75
Gibb H, Hochuli DF (2003) Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. Oikos 103:469
Gradstein SR, Kessler M, Pitopang R (2007) Tree species diversity relative to human land uses in tropical rain forest margins in Central Sulawesi. In: Tscharntke T, Leuschner C, Guhardja E, Zeller M (eds) The stability of tropical rainforest margins: linking ecological, economic and social constraints of land use and conservation. Springer, Berlin, Heidelberg, New York, pp 321–334
Johns ND (1999) Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environ Manage 23:31–47
Klein A-M, Steffan-Dewenter I, Buchori D, Tscharntke T (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv Biol 16: 1003–1014
Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76
Majer JD (1972) The ant mosaic in Ghana cocoa farms. Bull Entomol Res 62:151–160
Majer JD (1976) The influence of ants and ant manipulation on the cocoa farm fauna. J Appl Ecol 13: 157–175
Majer JD, Delabie JHC, Smith MRB (1994) Arboreal ant community patterns in Brazilian cocoa farms. Biotropica 26:73–83
McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Tree 14:450–453
Myers N, Mittelmeier RA, Mittelmeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 493:853–858
O'Dowd DJ, Green PT, Lake PS (2003) Invasional 'meltdown' on an oceanic island. Ecol Lett 6:812–817
Perfecto I, Mas A, Dietsch T, Vandermeer J (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodivers Conserv 12:1239–1252
Perfecto I, Vandermeer J (1996) Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108:577–582
Perfecto I, Vandermeer J, Hanson P, Cartín V (1997) Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodivers Conserv 6:935–945
Philpott SM, Foster PF (2005) Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. Ecol Appl 15:1478–1485
Pineda E, Moreno C, Escobar F, Halffter G (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Vercruz, Mexico. Conserv Biol 19:400–410
Potter L (2001) Agricultural intensification in Indonesia: outside pressures and indigenous strategies. Asia Pac Viewp 42:305–324
Rice RA, Greenberg R (2000) Cacao cultivation and the conservation of biological diversity. Ambio 29:167–172
Room PM (1971) The relative distribution of ant species in Ghana's cocoa farms. J Anim Ecol 40:735–751
Schroth G, da Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac A-MN (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, DC
Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shahabuddin, Veddeler D, Muhlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. Ecol Appl 14:1321–1333

Shahabuddin, Schulze CH, Tscharntke T (2005) Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). Biodivers Conserv 14:863–877

StatSoft Inc. 1984–2004. STATISTICA for Windows [Software-System for Data-analyses] Version 7.0. Tulsa, USA

Waltert M, Mardiastuti A, Muehlenberg M (2004) Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv Biol 18:1339–1346

Zuidema PA, Leffelaar PA, Gerritsma W, Mommer L, Anten NPR (2005) A physiological production model for cocoa (*Theobroma cacao*): model presentation, validation and application. Agric Syst 84:195–225