Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia)

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Abstract. Little is known about how tropical land-use systems contribute to the conservation of functionally important insect groups, including dung beetles. In a study at the margin of Lore Lindu National Park (a biodiversity hotspot in Central Sulawesi, Indonesia) dung-beetle communities were sampled in natural forest, young secondary forest, agroforestry systems (cacao plantations with shade trees) and annual cultures (maize fields), each with four replicates ($n = 16$ sites). At each site we used 10 pitfall traps, baited with cattle dung, along a 100 m transect for six 3-day periods. The number of trapped specimens and species richness at the natural forest sites was higher than in all land-use systems, which did not significantly differ. Each land-use system contained, on average, 75% of the species richness of the natural forest, thereby indicating their importance for conservation. However, a two-dimensional scaling plot based on NESS indices ($m = 6$) indicated distinct dung beetle communities for both forest types, while agroforestry systems and annual cultures exhibited a pronounced overlap. Mean body size of dung beetles was not significantly influenced by land-use intensity. Five of the six most abundant dung beetle species were recorded in all habitats, whereas the abundance of five other species was significantly related to habitat type. Mean local abundance and number of occupied sites were closely correlated, further indicating little habitat specialisation. The low dung beetle diversity (total of 18 recorded species) may be due to the absence of larger mammals in Sulawesi during historical times, even though Sulawesi is the largest island of Wallacea. In conclusion, the dung beetle fauna of the lower montane forest zone in Central Sulawesi appears to be relatively robust to man-made habitat changes and the majority of species did not exhibit strong habitat preferences.

Introduction

Many studies document the loss of biodiversity caused by the ongoing modification or clearing of tropical forests (e.g., Watt et al. 1997; Holloway 1998; Lawton et al. 1998; Schulze 2000; Willott et al. 2000; Liow et al. 2001). In Indonesia, the area of remaining forest is decreasing rapidly and most provinces have already lost 80% or more of their lowland forest (Ministry of State for Population and Environment of Republic Indonesia 1992); Sulawesi lost 20% of its forest cover only between 1985 and 1997 (Holmes 2000). Despite this well-known development, the importance of forest conversion into land-use systems, such as agroforestry, for biodiversity losses is poorly understood (Perfecto et al. 1997).

The diversity of most taxonomic groups is negatively affected by forest modification and land-use activities, but taxa may show great differences in changes of diversity (Lawton et al. 1998). Diversity of some groups, such as solitary bees and wasps, may even increase with land-use intensity (Klein et al. 2002) and Bornean hawkmoths (Lepidoptera, Sphingidae) do not reflect the influence of habitat disturbance (e.g., Schulze and Fiedler in press). The diversity of carrion beetles may not be seriously affected by forest clearance and the establishment of plantations (Hanski 1989), although reduced abundance and diversity in clear cuts may occur (Vulinec 2002). Klein (1989) and Andresen (2002a) quantified the reduced diversity of decomposer organisms as a result of forest fragmentation (see also Didham et al. 1996).

Dung beetles (Coleoptera, Scarabaeidae) are of high ecological importance due to their role as decomposers of dung and other decaying organic material and their enhancement of ecological processes such as nutrient recycling and dispersal of seeds (e.g., Hanski and Cambefort 1991; Hanski and Krikken 1991; Andresen 2002a,b). Dung beetles are also used as an indicator group, because they reflect structural differences between habitats caused by forest type or human habitat modification (Klein 1989, Nummelin and Hanski 1989, Hill 1996, Davis and Sutton 1998, Davis et al. 2001). The potential of dung beetles as indicators for disturbance has been reviewed by Halffter and Favila (1993) and McGeoch et al. (2002). In addition, the body size of dung beetles may be an important factor interacting with habitat type and may be related to the presence of large mammals (Hanski and Cambefort 1991): smaller dung beetle species are more abundant and less habitat specific (Hanski 1982, Hanski and Cambefort 1991).

Novel aspects of this study on the effects of land use on dung beetles at the margin of a large closed forest (the Lore Lindu National Park in Central Sulawesi, Indonesia) include the following. First, the relative importance of well-defined land-use systems for conservation is generally little known. Second, this is the first study from the Oriental region quantifying changes of dung beetle communities from near-primary rainforests, secondary forests and agroforestry systems to open arable maize fields. We particularly address the following questions:

(1) How do land-use activities at the rainforest margin affect dung beetle diversity?
(2) Do species assemblages of land-use systems represent distinct components of the local fauna or are they only a fraction of forest inhabiting species? How habitat specific are dung beetle species?
(3) Is the distribution of the body size of dung beetles related to habitat type? Are smaller species less affected by habitat modification than larger ones?

Methods

The study area is located at the south-eastern margin of the Lore Lindu National Park in Central Sulawesi (Indonesia). This is a regional biodiversity hotspot covering an area of 229,000 ha and located southeast of Palu, the province capital of

Table 1. Descriptions of habitat types surveyed for dung beetles in Napu Valley.

Habitat type	Habitat description	Site codes
Natural forest	Lower montane forest; big emergent trees and numerous medium-sized trees form a multi-layered canopy; height of upper canopy layer 25–30 m with single big emergent trees up to 40 m; well-developed understorey layer of small trees/shrubs, ginger and rattan up to 4–8 m high; herb layer dominated by Rubiaceae sp. and ferns; some selective logging activities took place recently in the vicinity of all sites, however, effect on the plots was slight.	NF1-4
Young secondary forest	Ca. 5–6-years old young secondary forest fragments (1–1.5 ha); single emergent trees and palms up to 15 m; closed canopy layer 7–8 m high; herb layer 0.5–2 m high and dominated by ferns and Rubiaceae sp.	YSF1-4
Agroforestry system	Ca. 5-years-old cacao plantations (1–2 ha) with *Gliricidia sepium* (Leguminosae) as emergent trees; cacao trees up to 3–3.5 m high; *Gliricidia sepium* trees 9–10 m high; herb layer 10–30 cm high.	AF1-4
Annual culture	Maize fields (1 ha).	AC1-4

Central Sulawesi. All study sites were selected in Napu Valley, in the vicinity of the villages Kaduwaa, Wuasa, Watumaeta and Alitupu between 01°23.68′S–01°26.50′S and 120°17.74′E–120°20.92′E and are situated at an altitude between 1100 and 1200 m a.s.l. Dung beetle communities were studied in four habitat types (see Table 1) – natural forest (NF), young secondary forest fragments (YSF), agroforestry systems (cacao plantations with *Gliricidia* as shadow trees; AF) and annual cultures (maize fields, AC). For each habitat type four site replications were selected. The prerequisite that the proximity of sites to one another should not be less than 0.5 km could not be realised for all site combinations. In six cases, sites were more closely located to each other (AC4-AF4: 150 m; AC2-AF3 and YSF2-OSF4: 200 m; NF3-NF4, YSF1-AC2 and AF3-AC1: 300 m).

Dung beetles were sampled at each site by using pitfall traps. These were made from transparent plastic cups, with a diameter of 8.5 cm and a height of 12.5 cm. Each trap was baited with ca. 10 g of fresh cattle dung wrapped in a small square of textile and fixed with a string at the top of the trap. A metal plate protected the trap against rain. Traps were filled with a mixture of 20% saline solution and detergent.

At each site 10 traps were set up along a 100 m transect. Traps were baited and set synchronously six times during April and June 2002. We followed Davis et al. (2001) in setting the traps for three days before trapped dung beetles were removed. Collected specimens were preserved in bottles containing 70% alcohol. Samples were identified in the laboratory with available identification keys (e.g., Ochi et al. 1996). Additionally, the reference collection of the Zoological Museum of LIPI (Cibinong, Indonesia) was used. Taxa which could not be identified, were sorted to morphospecies. The total body length was used as measurement for the size of beetles.

In addition to the true species numbers, we estimated the total number of species, which can be expected per site by the first-order jackknife method (see Colwell 2000). This species richness predictor has been found to perform well in other studies (e.g., Boulinier et al. 1998, Hughes et al. 2002). As units for estimating the total species richness of individual sites, we used samples pooled for individual traps ($n = 10$ trap subsamples). The ranking of samples was randomised 50 times by not shuffling individuals among samples within species (for a closer description see Colwell and Coddington 1994).

The NESS index (Grassle and Smith 1976) was used to quantify between-habitat diversity. This similarity index avoids problems of other similarity measures related to size, diversity and incompleteness of samples (Wolda 1981). NESS values were calculated for a largest possible m ($=$ number of specimens randomly drawn from two samples). Additionally, the Sørensen index, which is based on presence–absence data, was used to measure beta diversity (e.g., Wolda 1981, 1983).

To quantify land-use intensity, we measured four habitat parameters at all sites. (1) The percentage of shade at ground level (on sunny days, 11:00–13:00) was estimated for ten $1 \, \text{m}^2$ squares along each transect. The squares, one every 10 m, were situated at a distance of ca. 5 m beside the transect line alternating between the sides of the transect. (2) The number of trees higher than 1.5 m was counted within four 5 $\text{m}^2 \times 5 \, \text{m}^2$ plots situated beside each transect, one plot every 20 m changing between sides of the transect. Tree density is the mean tree number per $25 \, \text{m}^2$ (mean of four plots). No measurement is available for NF2 because this site was clear-cut before the study could be finished. (3) Percent canopy cover was estimated by eye at each site for a corridor of ca. 30 m beside the transect line. (4) The maximum height of the uppermost closed vegetation layer was estimated by eye not taking into account single emergent trees.

The program Statistica 5.5 (StatSoft 1999) was used to perform all statistical analyses. Arithmetic means are given $\pm$ one standard deviation (SD). ANOVA and MANOVA were of a one-way type. Tukey's Honest Significant Difference-Test was used for multiple comparisons of means. First-order jackknife calculations were computed with the program 'EstimateS Version 6.0b1' (Colwell 2000), by randomising the ranking of the individual transect counts 50 times (see Colwell and Coddington 1994). The computer program 'biodiv' provided by Meßner (1996) was used to calculate NESS values for a largest possible m as well as Sørensen indices. Dissimilarity values ($=$ 1-NESS and 1-Sørensen indices, respectively) were used to conduct a two-dimensional ordination of all samples using multidimensional scaling (see Schulze and Fiedler 2003a), when raw stress was sufficient and visualisation in Shepard diagrams revealed a good fit of data (see Clarke 1993; StatSoft 1999). The two-dimensional scores of samples were used to perform a one-way MANOVA. Data were tested for normal distribution by Shapiro-Wilk's W-test. Spearman's rank correlation was used if the transformed or untransformed data were not normally distributed. Otherwise Pearson correlation was calculated to analyse relationships between two variables (Sachs 1992). Because most habitat parameters were inter-correlated, a factor analysis was used to combine them (Sokal and Rohlf 1995). The resulting factor values were used as index for land-use intensity. Because no mea-

surement for tree density was available for site NF2, only values for 15 sites were available for further analyses.

Results

A total of 521 dung beetles belonging to 18 species were collected in the pitfall traps (see Table 2). The mean number of trapped dung beetles did not differ between the two land use systems (AF and AC) and young secondary forests, but was significantly higher at natural forest compared to all other sampled habitats (Figure 1(a)). The mean number of dung beetle specimens at natural forest sites (64.25 ± 9.12 specimens) was ca. two times higher than in young secondary forests (26.25 ± 9.22) and almost three times higher than in agroforestry systems (22.75 ± 6.65). The lowest abundance (17.00 ± 5.60) was in annual cultures.

Similarly, the mean number of species was highest at natural forest sites (Figure 1(b)). However, although the difference reached a significant level, it was less pronounced than abundance. While the mean number of trapped species was 10 ± 1.41 for natural forest, values for all other habitat types did not vary substantially (YSF: 7.00 ± 0.00 species, AF: 7.75 ± 9.57, AC: 7.25 ± 0.50). Each of these three land-use types supported 75% of the diversity of natural forest.

The first-order jackknife method was used to estimate how completely dung beetle communities were sampled at single sites. The ratio between the estimated number of species and the number of sampled species ranged between 1.12 and 1.63, but was not significantly related to habitat type (ANOVA: $F_{3,12} = 0.85$, $p = 0.492$). Estimates of species richness and the number of recorded species were significantly correlated (Spearman's $r = 0.73$, $p = 0.001$).

As already documented for the true number of recorded species, the estimated species totals were significantly related to habitat type (ANOVA: $F_{3,12} = 6.45$, $p < 0.01$). The mean number of species estimated for natural forest sites was significantly higher compared to the three other habitat types, while no differences could be found between young secondary forest fragments, agroforestry systems and annual cultures.

The index for land-use intensity calculated by factor analysis was significantly affected by habitat type (ANOVA: $F_{3,11} = 357.79$, $p < 0.001$) and was significantly related to all four habitat parameters (shade at ground: Spearman's $r = -0.97$, $p < 0.001$; tree density: $r = -0.80$, $p < 0.001$; vegetation height: $r = -0.72$; $p = 0.002$; canopy cover: $r = -0.90$, $p < 0.001$). High index values characterise high land-use intensity (as for annual cultures), while lowest values were reached for natural forest sites (see Figure 2). The index for land-use intensity was significantly related to the abundance of dung beetles (Spearman's $r = -0.65$, $p = 0.008$). Dung beetle abundance decreased with increasing land-use intensity (Figure 2(a)). No relationships were found between indices for land-use intensity and recorded species numbers (Spearman's $r = -0.31$, $p = 0.258$; Figure 2(b)) or first-order jackknife estimates (Spearman's $r = -0.029$, $p = 0.919$).

Table 2. The total number of specimens collected in each habitat and the mean body length of each species. For site codes see Table 1.

| Species	Size (mm)	Habitats			
		NF	YSF	AF	AC
Copris doriae	12.6	120	37	19	21
Copris sinicus	20.5	2	0	0	0
Gymnopleurus striatus	17.0	1	0	0	0
Onthophagus hanskins	7.0	0	0	0	1
Onthophagus pacificus	8.9	8	4	5	3
Onthophagus poenicocerus	14.0	41	11	13	9
Onthophagus sumatranus	10.0	13	0	5	2
Onthophagus sp. 04	9.4	4	2	1	1
Onthophagus sp. 06	6.2	6	21	26	17
Onthophagus sp. 08	11.0	0	0	0	1
Onthophagus sp. 09	6.7	1	0	2	0
Onthophagus sp. 12	7.2	6	3	0	3
Onthophagus sp. 13	13.6	44	15	6	3
Onthophagus sp. 14	6.3	5	2	3	2
Onthophagus sp. 15	5.2	0	5	1	0
Onthophagus sp. 16	15.0	1	0	0	1
Onthophagus sp. 17	8.8	0	0	6	4
Onthophagus sp. 18	4.4	5	5	4	0
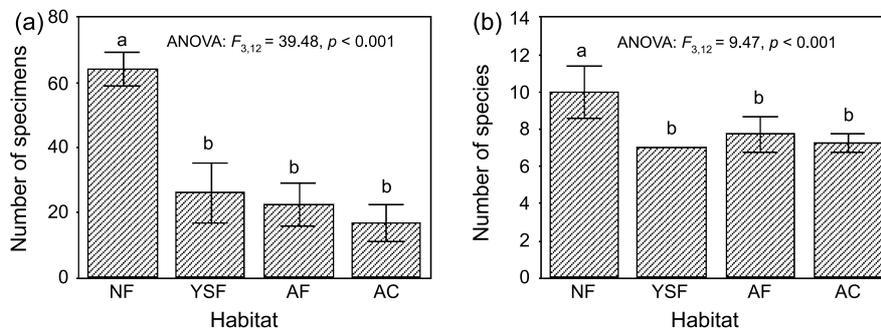
Figure 1. Mean number of dung beetles in relation to habitat type. (a) Number of individuals, and (b) number of species for the four sites of each habitat type (NF = natural forest, YSF = young secondary forest, AF = agroforestry system, AC = annual culture; see Table 1). Arithmetic means ± SD and the results of a one-way ANOVA are given. Different letters on top of the bars indicate significant differences between habitats.

Two-dimensional scaling based on NESS indices ($m = 6$) for all possible pairwise combinations of dung beetle samples showed a clear separation between communities of the natural forest and all other habitat types. The secondary forests represented a second relatively distinct group of sites, while both agroforestry and
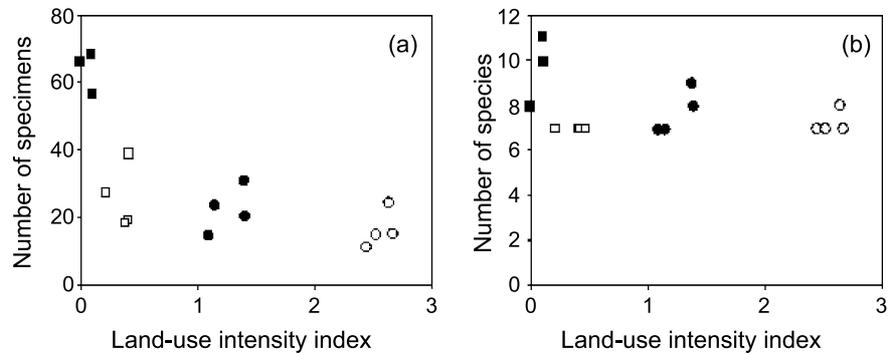
Figure 2. Land-use intensity in relation to the number of (a) collected specimens, and (b) recorded species. Land-use intensity is quantified by an index combining four habitat parameters (by factor analysis). Low values characterise low land-use intensity. Closed quadrats = NF, open quadrats = YSF, filled circles = AF, open circles = AC (for abbreviations see Table 1).
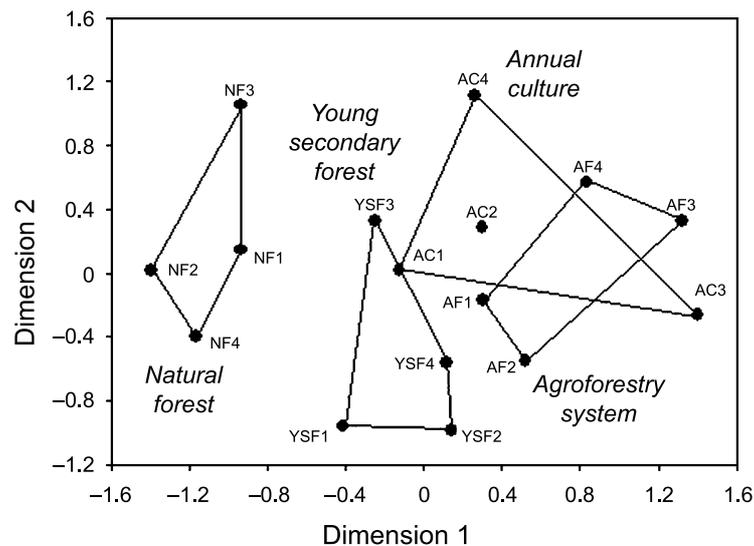

Figure 3. Two-dimensional scaling of faunal similarity based on NESS indices for $m = 6$ values for dung beetle communities in the four habitat types (stress = 0.166). Sites belonging to the same habitat type are connected by lines.

annual cultures showed a high degree of overlap (Figure 3). The two-dimensional scores of samples were used to compare habitats using a standard one-way MANOVA. The habitat type proved to have a significant explanatory power for the composition of dung beetle communities (Wilk's $\lambda = 0.21$, Rao's $R_{6;22} = 4.29$,

Table 3. Relationships between mean abundances of all dung beetles between the four sampled habitats. r = Spearman's rank correlation coefficient. For site codes see Table 1.

	YSF	AF	AC
NF	$r = 0.67$, $p = 0.002$	0.64, 0.004	0.61, 0.005
YSF	–	0.67, 0.002	0.54, 0.021
AF	–	–	0.71, < 0.001

$p = 0.005$). However, an identical analysis of data based on Sørensen indices failed to reach a significant level (Wilk's $\lambda = 0.74$, Rao's $R_{6;22} = 0.60$, $p = 0.726$). Both dimensions of the two-dimensional scaling-plot can be interpreted as measures for land-use intensity. The scores of both dimensions were significantly related to the index of land-use intensity (dimension 1: Spearmans's $r = -0.75$, $p = 0.001$; dimension 2: $r = -0.81$, $p < 0.001$). However, in both cases relationships between scores and single habitat parameters exhibited higher correlation coefficients. Scores of dimension 1 were most strongly correlated to shade at ground (Spearman's $r = -0.75$, $p < 0.001$), while dimension 2 exhibited the closest relationship to canopy cover (Spearman's $r = -0.64$, $p = 0.008$).

Dung beetle species did not appear to be restricted to only one habitat type, with a high overlap of the species composition between all sites (similar to the results from the community analysis using Sørensen indices). Only in natural forest and the annual cultures were two species collected that were not recorded from the other three land-use types, although these four species were very rare (total of 1–2 collected specimens per species) and, therefore, might also be detected in other habitats by additional sampling. Of the 10 most abundant species (total of > 10 collected specimens), only one could be reported from just two, while three species were recorded from three and six from all habitat types. Furthermore, all pairwise comparisons of mean abundances of the 18 individual dung beetle species between the four habitat types were significant (Table 3).

Although five of the six most abundant dung beetles species (total of 20 collected specimens) were recorded in all habitats, only one of these species (*Onthophagus pacificus*) did not significantly respond to habitat type (Figure 4(e)). The abundance of four species was highest in the natural forest (Figure 4a–c and f) although in one case the difference between natural forest and agroforestry system did not reach a significant level (Figure 4(b)). For one species (*Onthophagus* sp. 6) the opposite pattern was recorded. This species exhibited the lowest mean number of collected specimens in the natural forest and obviously profited from human land-use (Figure 4(d)). However, the abundance of individual dung beetle species (quantified as total number of specimens collected from all sites, which is like the mean local abundance) and the number of sites at which they were recorded by pitfall traps (the regional distribution) showed a strong relationship, which can be described by a logarithmic regression model (Figure 5).

The mean body size of recorded dung beetle species was not significantly affected by habitat type (ANOVA: $F_{3,12} = 2.49$, $p = 0.110$); nor was the mean body size of
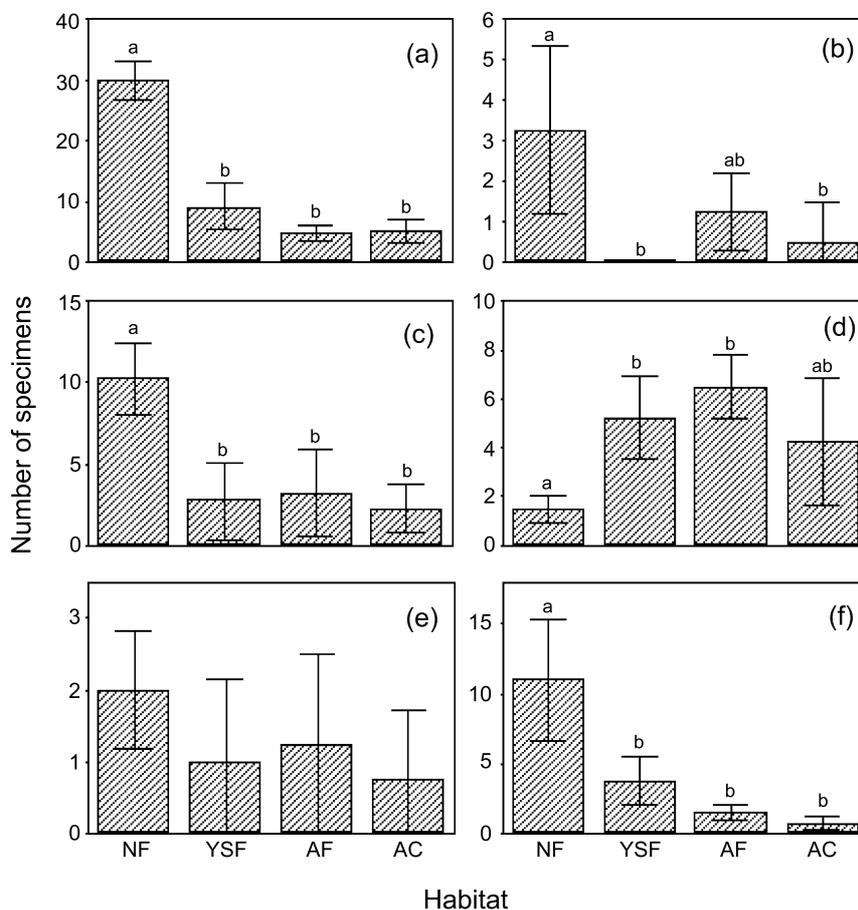
Figure 4. Mean number of dung beetles in each of the four habitat types, given for the six most abundant species. (a) *Copris doriae* (ANOVA: $F_{3,12} = 76.11$, $p < 0.001$), (b) *Onthophagus sumatranus* ($F_{3,12} = 5.30$, $p < 0.05$), (c) *Onthophagus poenicocerus* ($F_{3,12} = 11.57$, $p < 0.001$), (d) *Onthophagus* sp. 6 ($F_{3,12} = 6.11$, $p < 0.01$), (e) *Onthophagus pacificus* ($F_{3,12} = 1.04$, n.s.), (f) *Onthophagus* sp. 13 ($F_{3,12} = 15.33$, $p < 0.001$). Different letters on top of the bars indicate significant differences between habitats.

collected specimens ($F_{3,12} = 2.10$, $p = 0.153$). Additionally, no significant relationships were found between the mean size of species and their total number of collected specimens (Spearman's $r = -0.13$, $p = 0.617$) or the number of sites from which the species was recorded (Spearman's $r = -0.18$, $p = 0.464$).

Discussion

Our results show that the conversion of natural forest to secondary forests and land use systems had a negative effect on dung beetle diversity in Sulawesi. A decline of
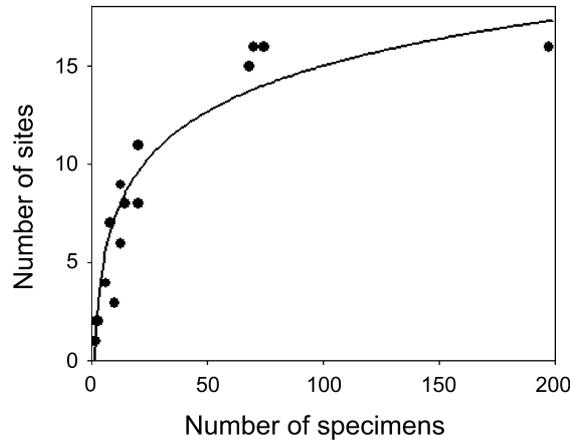
Figure 5. Relationship between abundance (= total number of collected specimens) and spatial distribution (= number of sites with record) of all recorded dung beetle species (n = 18) described by a logarithmic regression function [$y = -0.46 + 7.72 \log 10 (x)$].

insect diversity related to forest disturbance (e.g., Holloway et al. 1992; Hill et al. 1995; Lawton et al. 1998; Intachat et al. 1999; Schulze 2000; Brühl et al. 2001; Beck et al. 2002) and conversion of forests or forest plantations to agricultural habitats (Holloway 1987; Wolda 1987) has been also shown for other taxonomic groups. Remarkably, no differences in diversity and abundance of dung beetles could be found between young secondary forest fragments, agroforestry systems and annual cultures, although the structure of dung beetle communities changed between young secondary forests and the two land-use systems. Each of the four habitat types following destruction of natural forest supported 75% of the species diversity found in the natural forest, thereby indicating surprisingly little reduced diversity despite the great anthropogenic habitat transformation. Habitat area may have also affected the dung beetle communities of the only 1–2 ha large land-use systems compared to the sites within a continuous near-primary rainforest. This further emphasises the unexpectedly small decrease of dung beetle communities in response to land use. The trend that land-use intensity affected species richness more than abundance (for similar findings see Estrada and Coates-Estrada 2002) may mean that decomposition processes tend to be more affected than diversity.

This is the first study from the Oriental region quantifying changes of dung beetle diversity from near-primary rainforests and secondary forest towards agroforestry systems and open cultivated land. Davis et al. (2001) reported a significant decrease of dung beetle diversity across a gradient of forest disturbance ranging from primary to logged and plantation forest in Northern Borneo. Klein (1989) found a decline of dung beetle species richness as result of forest fragmentation (see Didham et al. 1996). Our multi-dimensional scaling analysis showed that the structure of dung beetle communities differed between forest habitats and land-use systems, and the distribution of the most abundant dung beetles showed species-specific habitat

preferences. However, the abundant species were recorded from a wide spectrum of habitats and mean abundances of dung beetles in all habitats (the local density) could be used to predict number of colonised sites (the regional distribution). This indicates that most species attracted by cattle dung in Central Sulawesi do not have strongly pronounced habitat requirements. Nevertheless, the density of five (out of six) most abundant species decreased with land-use intensity, whereas only one species showed a higher abundance in young secondary forest and agroforest compared to the natural forest. Similarly, in Amazonia most but not all dung beetles were negatively affected by habitat disturbance (Vulinec 2002). Furthermore, Roslin and Koivunen (2001) found that different species show very dissimilar responses to changes in landscape structure.

Because our traps where exposed over a period of 3 days, we caught diurnal (the majority of *Onthophagus* spp.) as well as nocturnal species (*Copris* spp.; Hanski and Cambefort 1991). The generic diversity of the local dung beetle community was low. Only three genera, *Copris*, *Gymnopleurus* and *Onthophagus* were recorded, while 83.3% of all recorded species during belonged to the genus *Onthophagus*. With ca. 2000 known species, this genus is one of the most diverse insect genera. The highest species richness of this genus occurs in southeast Asia (Hanski 1983, Hanski and Cambefort 1991), where *Onthophagus* species always represent a high portion of dung beetle species samples (see Hanski 1983, Davis et al. 2001). Only one species that belongs to the group of dung beetles with adults preparing and rolling dung balls (*Gymnopleurus striatus*) occurred in our samples. All other specimens belonged to species that can be classified as tunnelers (for definition of feeding types see Hanski and Cambefort 1991). The large majority of dung beetles are typically tunnellers in South-East Asian forests (Hanski and Cambefort 1991).

The total number of dung beetle species recorded by bait trapping at the margin of the Lore Lindu National Park was surprisingly low compared to other studies. For example, Andresen (2002a) found 61 dung beetle species in Central Amazonia, Davis (2000) collected 97 species in tropical rainforest at Danum Valley (Sabah, Malaysia), and Davis et al. (1991) recorded 86 species in a Bornean lowland rainforest. Due to the many sites sampled and our computed diversity estimates, this low species richness did not appear to be caused by a low trapping efficiency. Although it is known that other baits (such as human faeces compared to cattle dung) and larger baits may attract higher dung beetle numbers (Hanski 1983; Davis et al. 2001; Andresen 2002b), dung beetle species richness appears to be generally lower in Sulawesi compared to other islands. In North Sulawesi, Hanski and Niemela (1990) trapped dung beetles along an altitudinal gradient: from the lowland up to 800 m they recorded only an average of 18 species per site. At 1150 m they still recorded more than 10 species, but fewer species than we caught at our study site at Napu Valley situated at an identical altitude.

Many areas of southeast Asia exhibit only moderately seasonality in climate and in large areas there is no severe dry season at all (Whitmore 1975). The only study providing data on the seasonality of southeast Asian dung beetles was conducted by Paarmann and Stork (1987), who trapped beetles for 10 months in North Sulawesi. Numerically dominant dung beetles showed completely aseasonal activity, while

seasonal flight activity was found for the majority of scarcer species. Our study only covered a period of 3 months: further samples collected at different times are thus likely to result in some additions to the dung beetle fauna so far recorded from our study area.

The absence of large herbivorous mammals on Sulawesi during historical times may be the main factor that has acted against the evolution and establishment of species-rich dung beetle communities like those of the African savannah, for example (e.g., Hanski and Camsbefort 1991). In geographical regions where large herbivorous mammals are abundant, they are accompanied by large numbers of specialised dung beetles (Hanski and Cambefort 1991). Sulawesi is the largest island in the biogeographical region of 'Wallacea' (as defined by e.g., Coates et al. 1997). Whereas Borneo, Sumatra and Java were connected to mainland Asia several times during the last glacial periods, Sulawesi has always been isolated from the other islands of the Malay Archipelago. This long-term geographical isolation of Sulawesi caused not only the evolution of a unique flora and fauna characterised by a high proportion of endemic species (Whitten et al. 2002), but also seems to have prevented larger mammals from colonising this island. The two endemic pig species (*Sus celebensis*, *Babyrousa babyrussa*) and the two anoa species (the dwarf buffaloes *Bubalus depressicornis*, *B. quarlesi*) are the only larger mammals native to Sulawesi (Musser 1987). Large herbivorous mammals (such as elephant and rhinoceros), which are distributed on other large islands of the Malay Archipelago, are absent; the deer *Cervus timorensis* or domesticated water buffalo, Bali cattle, goats and domestic pigs have only been introduced in recent times (Musser 1987). Large mammals influence the community structure of dung beetles as well as their body size and weight (reviewed by Hanski and Cambefort 1991). However, we could not find any patterns related to the size of dung beetles in our study area: body size was neither related to species' abundance nor to land-use type.

In conclusion, dung beetle communities of the lower montane forest zone of Central Sulawesi appear to be relatively resistant to land-use activity. Only a 25% higher diversity was found at natural forest sites and the great habitat differences in secondary forests, agroforestry systems and annual crops did not translate into major diversity changes. The majority of dung beetle species was not restricted to certain habitat types, but appeared to cope with a wide range of habitats as different as a rainforest and annual culture. The likelihood of a single species occurring at a single site could be better predicted by its overall abundance than by land-use intensity. Further studies may focus on (1) whether food type is a major niche dimension, and (2) whether similar patterns are found for lowland forest areas in Sulawesi.

References

Andresen E. 2002a. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography 26: 87–97.

Andresen E. 2002b Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. Ecological Entomology 27: 257–270.

Beck J., Schulze C.H., Linsenmair K.E. and Fiedler K. 2002. From forest to farmland: diversity of geometer moths along two habitat gradients on Borneo. Journal of Tropical Ecology 18: 33–51.

Boulinier T., Nichols J.D., Sauer F.R., Hines J.E. and Pollock K.H. 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79: 1018–1028.

Brühl C.A. 2001. Leaf litter ant communities in tropical lowland rain forests in Sabah, Malaysia: effects of forest disturbance and fragmentation. Ph.D. Thesis, University of Würzburg, Würzburg, Germany.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.

Coates B.J., Bishop K.D. and Gardner D. 1997. A field guide to the birds of Wallacea. Dove Publications, Alderley, Australia.

Colwell R.K. 2000. EstimateS – Statistical estimation of species richness and shared species from samples. Version 6.0b1. http:/viceroy.eeb.uconn.edu/estimates.

Colwell R.K. and Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B 345: 101–118.

Cox T.F. and Cox M.A.A. 1994. Multidimensional Scaling. Monographs on Statistics and Applied Probability 59. Chapman & Hall, London.

Davis A.J. 2000. Species richness of dung-feeding beetles (Coleoptera: Aphodiidae, Scarabaeidae, Hybosoridae) in tropical rainforest at Danum Valley, Sabah, Malaysia. Coleopterist Bulletin 54: 221–231.

Davis A.J. and Sutton S.L. 1989. The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. Diversity and Distribution 4: 167–173.

Davis A.J., Holloway J.D., Huijbregts H., Krikken J., Kirk-Spriggs A.H. and Sutton S. 2001. Dung beetles as indicators of change in the forests of Northern Borneo. Journal of Applied Ecology 38: 593–616.

Didham R.K., Ghazoul J., Stork N.E. and Davis A. 1996. Insects in fragmented forests: a functional approach. Trends of Ecology and Evolution 11: 255–260.

Estrada A. and Coates-Estrada R. 2002. Dung beetles in continuous forest, forest fragments and in agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodiversity and Conservation 11: 1903–1918.

Grassle J.F. and Smith W. 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. Oecologia 25: 13–22.

Halffter G. and Favila M.E. 1993. The Scarabaeinae (Coleoptera): an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biology International 27: 15–21.

Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210–221.

Hanski I. 1989. Fungivory, fungi, insects, and ecology. In: Wilding N., Collins N.M., Hammond P.M. and Werber J.F. (eds) Insect-Fungus Interactions. Academic Press, New York, pp. 25–68.

Hanski I. and Cambefort Y. (eds) 1991. Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey.

Hanski I. and Krikken J. 1991. Dung beetles in tropical forests in South-East Asia. In: Hanski I. and Cambefort Y. (eds.) Dung Beetle Ecology. Princeton University Press, Princeton. New Jersey, pp. 179–197.

Hanski I. and Niemela J. 1990. Elevational distributions of dung and carrion beetles in Northern Sulawesi. In: Knight W.J. and Holloway J.D. (eds) Insects and the Rain Forests of South East Asia (Wallacea). Royal Entomological Society of London, London, pp. 142–152.

Hill C.J. 1996. Habitat specificity and food preferences of an assemblage of tropical Australian dung beetles. Journal of Tropical Ecology 12: 449–460.

Hill J.K., Hamer K.C., Lace L.A. and Banham W.M.T. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. Journal of Applied Ecology 32: 754–760.

Holloway J.D. 1987. Macrolepidoptera diversity in the Indo-Australian tropics: geographic, biotopic and taxonomic variations. Biological Journal of the Linnean Society 30: 325–341.

Holloway J.D. 1998. The impact of traditional and modern cultivation practices, including forestry, on Lepidoptera diversity in Malaysia and Indonesia. In: Newbery D.M., Prins H.H.T. and Brown N.D. (eds.) Dynamics of Tropical Communities, 37th Symposium of the British Ecological Society. Blackwell Science, London, pp. 567–597.

Holloway J.D., Kirk-Spring A.H. and Chey V.K. 1992. The response of some rain forest insect groups to logging and conversion to plantation. Philosophical Transactions of the Royal Society Series B 335: 425–436.

Holmes D. 2000. Deforestation in Indonesia: A Review of the Situation in 1999. The World Bank, Jakarta.

Hughes J.B., Daily G.C. and Ehrlich P.R. 2002. Conservation of tropical forest birds in countryside habitats. Ecology Letters 5: 121–129.

Intachat J., Holloway J.D. and Speight M.R. 1999. The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. Journal of Tropical Forest Science 11: 61–76.

Klein B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology 70: 1715–1725.

Klein A.M., Steffan-Dewenter I., Buchori D. and Tscharntke T. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conservation Biology 16: 1003–1014.

Lawton J.H., Bignell D.E., Bolton B., Bloemers G.F., Eggleton P., Hammond P.M. et al. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical rain forest. Nature 391: 72–76.

Liow L.H., Sodhi N.S. and Elmqvist T. 2001. Bee diversity along a disturbance gradient in tropical lowland forest of South-East Asia. Journal of Applied Ecology 38: 180–192.

McGeoch M., van Rensburg B.J. and Botes A. 2002. The verification and application of bioindicators: a case study of dung beetles in a savannah ecosystem. Journal of Applied Ecology 39: 661–672.

Meßner S. 1996. Untersuchungen zur Biodiversität der Myrmecofauna (Formicidae) im Parc National de la Comoé (Elfenbeinküste). Diploma Thesis,University of Würzburg, Würzburg, Germany.

Ministry of State for Population and Environment of Republic Indonesia. 1992. Indonesia Country Study on Biological Diversity. Prepared for UNEP under the programme for environmental cooperation between The Republic of Indonesia and The Kingdom of Norway, Jakarta.

Musser G.G. 1987. The mammals of Sulawesi. In: Whitmore T.C.(ed.) Biogeographical Evolution of the Malay Archipelago. Oxford University Press, Oxford, UK, pp. 73–93.

Nummelin M. and Hanski I. 1989. Dung beetles of the Kibale Forest, Uganda: a comparison between virgin and managed forests. Journal of Tropical Ecology 5: 349–352.

Ochi T., Kon M. and Kikuta T. 1996. Studies on the family Scarabaeidae (Coleoptera) from Borneo. I. Identification keys to subfamilies, tribes and genera. Giornale Italia Entomologia. 8: 37–54.

Paarmann W. and Stork N.E. 1987. Seasonality of ground beetles (Coleoptera: carabidae) in the rain forests of N. Sulawesi. (Indonesia). Insect Science and Applications. 8: 483–487.

Perfecto I., Vandermer J., Hanson P. and Cartin V. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation 6: 935–945.

Roslin T. and Koivunen A. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia 127: 69–77.

Sachs L. 1992. Angewandte Statistik. 7th edn Springer, Berlin, Germany.

Schulze C.H. 2000. Effects of Anthropogenic Disturbance on the Diversity of Herbivores – An Analysis of Moth Species Assemblages Along Habitat Gradients in East Malaysia (in German). Ph.D. Thesis,University of Bayreuth, Germany.

Schulze C.H. and Fiedler K. 2003a. Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: Basset Y. et al. (eds) Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, UK.

Schulze C.H. and Fiedler K. Hawkmoth diversity in Northern Borneo does not reflect the influence of anthropogenic habitat disturbance. Ecotropicain-press.

Sokal R.R. and Rohlf F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. Freeman and Company, New York.

StatSoft 1999. Statistica for Windows, 5.5 StatSoft Inc., Tulsa, Oklahoma.

Vulinec K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34: 297–309.

Watt A.D., Stork N.E., Eggleton P., Srivastava D., Bolton B., Larsen T.B., Brendell M.J.D. and Bignell D.E. 1997. Impact of forest loss and regeneration on insect abundance and diversity. In: Watt S.D., Stork N.E. and Hunter M.D. (eds) Forests and Insects. Chapman & Hall, London.pp. 273–286.

Whitmore T.C. 1995. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, UK.

Whitten A.J., Mustafa M. and Henderson G.S. 2002. The Ecology of Sulawesi. Periplus, Hong Kong, Singapore.

Willott S.J., Lim D.C., Compton S.G. and Sutton S.L. 2000. Effects of selective logging on the butterflies of a Bornean rainforest. Conservation Biology 14: 1055–1065.

Wolda H. 1981. Similarity indices, sample size and diversity. Oecologia 50: 296–302.

Wolda H. 1983. Diversity, diversity indices and tropical cockroaches. Oecologia 58: 290–298.

Wolda H. 1987. Altitude, habitat and tropical insect diversity. Biological Journal of the Linnean Society 30: 313–323.