

BIODIVERSITY INDICATOR GROUPS OF TROPICAL LAND-USE SYSTEMS: COMPARING PLANTS, BIRDS, AND INSECTS

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Abstract. Tropical landscapes are dominated by land-use systems, but their contribution to the conservation of biodiversity is largely unknown. Since changes in biodiversity in response to human impact are known to differ widely among taxonomic groups and guilds, there is a need for multidisciplinary collaboration of plant, vertebrate, and invertebrate experts. We used inventories of trees, understory plants, birds (subdivided into endemics, insectivores, frugivores/nectar feeders), butterflies (endemics, fruit feeders), and dung beetles in Sulawesi (Indonesia) to characterize a gradient from near-primary to secondary forests, agroforestry systems, and annual crops. As expected, overall species richness tended to decrease within this gradient of increasing habitat modification, but, in contrast to previous studies, we found the species richness between most taxonomic groups to be significantly correlated (36 out of 38 pairwise comparisons). However, on average only 48% of the variance could be explained (within the five main groups), and only a few taxonomic groups/guilds turned out to be good predictors for others: for example, trees for fruit- and nectar-feeding birds (88% explanation) and fruit-feeding butterflies (83%), endemic birds for endemic butterflies (72%), and frugivorous/nectar-feeding birds for fruit-feeding butterflies (67%). Although biodiversity of land-use systems showed taxonomic group- and guild-specific differences, most groups were affected in a similar way by habitat modification. Near-primary forest sites proved to be of principal importance for conservation; however, land-use systems such as secondary forests (for understory plants, birds, and butterflies) and agroforestry systems (for butterflies) supported relatively high numbers of species and might play a significant role for biodiversity conservation in tropical landscapes.

Key words: biodiversity assessment; biodiversity indicators; birds; butterflies; dung beetles; Indonesia, Central Sulawesi; land-use systems, tropical; rainforest; species richness, predicting; species richness, correlation among taxonomic groups; trees; understory plants.

INTRODUCTION

Due to the dramatic loss of one of the most diverse ecosystems on earth, tropical rainforests (e.g., Groombridge 1992, Wilson 1992), an increasing number of studies have focused on the effect of modification and clearance of this habitat on biodiversity. In general, forest modification and clearance have negative impacts on biodiversity (e.g., Bawa and Seidler 1998). However, most studies just quantified the human impact on diversity of single taxonomic groups (e.g., Holloway et al. 1992, Johns 1992, Lambert 1992, Pinheiro and Ortiz 1992, Belshaw and Bolton 1993, Chung and Mohamed 1996, Dahaban et al. 1996, Chey et al. 1997, Eggleton et al. 1997, Hamer et al. 1997, Intachat et al. 1997, 1999a, b, Watt et al. 1997, Holloway 1998, Costa 1999, Parthasarathy 1999, Willott 1999, Willott et al.

2000, Liow et al. 2001, Costa and Magnusson 2002, Thompson et al. 2002) or guilds (e.g., Canaday 1996, Beck and Schulze 2000, Fermon et al. 2000, Fermon 2002, Waltert et al. 2004, Schulze et al. 2004, Shahabuddin et al. 2004). Therefore, it is still difficult to conduct meaningful comparisons between different taxonomic groups and guilds concerning their response to habitat alteration caused by human land-use activities. So far the only study reporting the impact of tropical-forest modification on a taxonomically diverse inventory was conducted in south-central Cameroon by Lawton et al. (1998). We here present data from a second area located at the eastern margin of the Lore Lindu National Park in Central Sulawesi (Indonesia), covering a gradient of land-use intensity ranging from near-primary forest to secondary forests, agroforestry systems, and annual cultures. To analyze whether different taxonomic groups or guilds respond in a similar way to land use at the margin of the Park, we surveyed trees, understory plants, birds, butterflies, fruit-feeding

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PLATE 1. The butterfly *Faunis menado* Hewitson (Nymphalidae: Morphinae) is restricted to the Sulawesi region and strongly depends on the understorey of natural and old secondary forests. Photo credit: C. H. Schulze.

butterflies, and dung beetles. As an extension to the study by Lawton et al. (1998), we also included two groups of plants to document changes in vegetational species richness. Butterflies and birds were surveyed because they frequently serve as flagship taxa and can be rapidly monitored in the field, and all or at least most of the specimens can be assigned to known species (e.g., Lawton et al. 1998) (see Plate 1). Dung beetles were chosen because they proved to respond very sensitively to habitat modification (Davis and Sutton 1998, Davis et al. 2001) and, therefore, the number of diversity studies focusing on this taxon has been increasing recently (e.g., Klein 1989, Nummelin and Hanski 1989, Hanski and Krikken 1991, Halfpeter and Favila 1993, Hill 1996, Davis 2000, McGeoch et al. 2002).

When different plant and animal groups respond in a similar way to anthropogenic forest modification and land use, this does not necessarily mean that one group can serve as an effective tool to predict changes in species richness of other taxonomic groups or guilds. A group that can act as suitable indicator for the species richness of other groups has to fulfil a number of requirements (see, for example, Beccaloni and Gaston

1994, Tscharnkte et al. 1998, Schulze and Fiedler 1999). We evaluate the potential of all surveyed groups to determine if the species richness of other groups can be predicted.

STUDY AREA

The study area is located in Central Sulawesi (Indonesia) ~75 km southeast of the province capital Palu at the eastern margin of the Lore Lindu National Park. The area is characterized by a mean annual rainfall of ~2500 mm per year (range: 1700–3000 mm between 1983 to 1997, Andreas Ibrom and Gode Gravenhorst, *personal communication*). More detailed information on the climatic conditions as well as the soil composition of this part of Central Sulawesi is not available (Whitten et al. 2002).

As in our study area, the margin of the National Park is characterized in many parts by a mosaic of secondary forests, young fallows, and several land-use systems with cacao, coffee, maize, and paddy (rice) as the dominating crops.

Our study sites were located between 01°23.68'–01°26.50' S and 120°17.74'–120°20.92' E in the northern part of Napu Valley in the vicinity of the villages

TABLE 1. Sampling framework for all surveyed animal and plant groups in the Central Sulawesi (Indonesia) study area, given as number of sampled sites per habitat type.

Surveyed plant and animal groups	Number of sampled sites				
	Near-primary forest	Old secondary forest	Young secondary forest	Agro-forestry system	Annual culture
Trees	2	0	4	4	4
Understory plants	4	4	4	4	4
Birds	4	0	3	4	4
Butterflies	4	4	4	4	4
Fruit-feeding butterflies	4	4	4	4	0
Dung beetles	4	0	4	4	4

Notes: Four replicate sites were selected for all five habitat types studied. For reasons of time, not all surveyed groups could be sampled or observed on all selected plots.

Kaduwaa, Wuasa, Watumaeta, and Alitupu situated at the margin of the large closed forest block represented by the Lore Lindu National Park. The elevation of the selected sites is between 1100 and 1200 m, therefore covering an altitudinal range that belongs to the lower montane forest zone (Whitten et al. 2002).

Four replicate sites were selected for all five studied habitat types, near-primary forest (NF1–4), old secondary (OSF1–4) and young secondary forest (YSF1–4), agroforestry system (AF1–4), and annual culture (AC1–4). The term “near-primary forest” was used instead of “primary forest” because the whole forest at the interior margin of the Lore Lindu National Park is already affected to a certain extent by human disturbance. Some illegal selective-logging activity already took place in the vicinity of our study sites and in the whole area uncontrolled rattan collecting can be observed. The old and young secondary-forest sites were represented by small 1–3 ha patches with a closed canopy. Forests with a closed upper canopy layer at 20–30 m aboveground were categorized as “old,” and forests with a closed upper canopy layer at 5–8 m as “young” secondary forests. Cacao plantations shaded by *Gliricidia sepium* (Leguminosae) trees were chosen as the agroforestry system. The annual cultures were maize fields. The size of both land-use systems ranged between 1 and 2 ha. All sites outside the closed forest (OSF, YSF, AF, and AC) were located <1 km from the forest margin. The prerequisite that the proximity of sites to one another should be at least 0.5 km could not be realized for all site combinations. In six cases, sites were located significantly closer to each other (AC4–AF4, 150 m; AC2–AF3 and YSF2–OSF4, 200 m; NF3–NF4, YSF1–AC2, and AF3–AC1, 300 m).

METHODS

Particularly in extremely species-rich tropical plant and animal communities, the number of species detected depends strongly on the number of collected individuals (e.g., Southwood 1978, Taylor 1978, Schulze 2000, Willott 2001) and there is still a debate on how to compare samples appropriately, avoiding results biased by size of sampling area, sampling effort, and

sample size (e.g., Moreno and Halffter 2001, Willott 2001). To standardize the size of surveyed plots (trees) and sampling effort (= days; butterflies), we used Shinozaki rarefaction (e.g., Shinozaki 1963, Achtziger et al. 1992). Hurlbert rarefaction method (Hurlbert 1971) was used to standardize the sample size (= number of specimens; fruit-feeding butterflies) in case the sample effort differed and data can be related to a definite number of specimens. Additionally, we used the first-order jackknife method to estimate (from the non-complete data as typically found in field studies) the “true” species richness (see Colwell and Coddington 1994, Chazdon et al. 1998) for all studied plant and animal groups. This species-richness predictor already performed well in other studies (e.g., Boulinier et al. 1998, Hughes et al. 2002).

At all sites one 100-m transect was established. At the forest sites 1–2 m wide paths, which were cut in advance, were used as transects. Surveys of understory plants, butterflies, fruit-feeding butterflies, and dung beetles were conducted exclusively along these transects. Also bird observations were done from one point located on the transect or close by. The transect line additionally crossed the plots selected for the assessment of tree species richness.

Due to a different time effort not all surveyed plant and animal groups could be sampled or observed on all selected plots. A summary of the sampling framework can be found in Table 1.

Trees

The tree survey was conducted in the years 2001 and 2002. At near-primary forest sites 50 × 50 m plots, separated into 25 10 × 10 m subplots, were established. Plots of 20 × 40 m were sampled at young secondary forest containing eight 10 × 10 m subplots. At agroforestry sites and annual-culture sites six subplots of 10 × 10 m were established. For all subplots, all trees more than 10 cm in diameter at a height of 1.3 m were counted and identified at least to morphospecies level. Trees were labelled with a subplot and a tree number. Samples were identified later at the National Herbarium of the Netherlands (Leiden), Herbarium Celebense,

Palu (Indonesia), or Herbarium Bogoriense, Bogor (Indonesia).

To standardize the plot size, we interpolated to a largest shared sampling area of six 10×10 m subplots by the Shinozaki rarefaction method (Shinozaki 1963, Achtziger et al. 1992). Additionally, the total number of species was estimated by first-order jackknife based on the 10×10 m subplots as sampling units.

Understory plants

Understory plants were collected between June and September 2001 at all study sites in ten 1×1 m plots along a 100-m transect. These plots, one every 10 m, were situated within ~ 5 m of the transect, alternating from one side of the transect to the other. Within the sampling plots, all vascular plants less than 1.30 m tall were identified to species level or sorted to morpho-species (Beattie and Oliver 1994). This method yields only a coarse (under-) estimate of species richness, but this "taxonomic minimalism" seems to be sufficient to provide meaningful information on plant species richness of the herb layer (see Schulze 2000, Beck et al. 2002). Reference specimens were deposited in the Herbarium Celebense, Palu (Indonesia).

Species richness of understory plants was quantified as total number of species recorded within all ten 1×1 m plots established. The total number of expected species was estimated by first-order jackknife method using the ten 1×1 m plots as sampling units.

Birds

The survey of birds was conducted between November 2001 and January 2002. Point counts located at the center of each site were used to record all birds within a radius of 50 m from the observer. Because most land-use types studied were of a small size (< 2 ha), it was necessary to sample birds at this scale regardless of the fact that bird point diversity in tropical forest might only reflect a minor proportion of overall within-habitat diversity (see Terborgh et al. [1990] and discussions of tropical plot sizes therein). Points were visited between 0600 and 0900 hours and all birds detected visually and acoustically within 20 min were recorded. A digital rangefinder was used to measure and estimate distances, and all observations beyond 50 m were discarded for analysis. Sites were visited alternately; a total of eight visits were carried out. Field work was done exclusively by the second author (M. Waltert), who acquired identification skills during five months experience in submontane areas of Lore Lindu National Park where he had been assisted by various locals and members of NGOs. Field identification was facilitated by bird recordings (Steve Smith 1991, unpublished data ["Bird recordings from Sulawesi" and "Bird recordings from the Moluccas"], R. Thomas and S. Thomas 1994, unpublished data ["Birds of Sulawesi,

Lesser Sundas and Sabah"]⁷) and the excellent voice descriptions in Coates et al. (1997). Out of a total of 828 detections within the 50-m circle, 65 (8%) remained unidentified; these, and those for which no distance estimate could be obtained, were discarded before the analysis. Bird species richness was quantified as total number of bird species recorded per site because all sites were surveyed with the same sampling effort except YSF2, which was logged before the study could be finished. Therefore, this site was excluded from the calculation of the mean number of bird species recorded at young secondary forest sites as well as from the conducted ANOVA for analyzing the effect of habitat on species numbers. Also the total number of bird species was estimated by the first-order jackknife method for all sites.

The guilds of insectivorous and frugivorous/nectar-feeding birds were analyzed separately. Information on feeding behavior was extracted from Coates et al. (1997). Because a high proportion of nectar-feeding birds also use fruits (e.g., *Loriculus*, *Trichoglossus*) and several fruit feeders also take nectar to an unknown extent (e.g., Dicaeidae), the two groups were defined as belonging to one guild.

Butterflies

Butterflies were surveyed by the transect count method that proved to be an adequate tool also capable of detecting differences in species richness of tropical butterfly communities (Schulze and Fiedler 1998, Walpole and Sheldon 1999). Transect walks were conducted between May 2001 and January 2002 and were evenly distributed over the whole time period. Each sampled transect had a length of 100 m. All specimens observed in a corridor of 3 m to each side of the transect were noted. Due to previous butterfly studies in other parts of Southeast Asia by the first author (C. H. Schulze), who conducted the field work, and because, additionally, a 1.5-mo survey of the study area was done in advance to produce a preliminary species inventory, many specimens could be identified on the wing. Just unfamiliar species and species that cannot be identified properly in the field (like most lycaenids and skippers) were caught and identified later on. Reference specimens of most species will be deposited at the Zoological Museum at Cibinong (Indonesia). Each butterfly count lasted 15 min. Transects were surveyed just between 9:30 and 15:30 on days without rain and a cloud cover of less than $\sim 50\%$. The sites were visited alternately. At least nine transect walks were conducted per site. Because one old secondary forest site was cleared after seven transect counts, for comparison the number of conducted transect walks was standardized by interpolating on the number of expected species after seven transect walks by Shinozaki rarefaction (e.g., as in Schulze and Fiedler [1998]). Additionally,

⁷ Available online: <www.nhbs.com>

the total number of butterfly species was estimated by the first-order jackknife method.

Fruit-feeding butterflies

Fruit-feeding butterflies were caught alive in traps baited with rotten bananas (e.g., Beck and Schulze 2000, Schulze et al. 2001; trap design: e.g., Sourakov and Emmel 1995) between May and September 2001. The traps were controlled every day while active, the bait being replaced when it was dried out or lost (presumably due to squirrels). Only specimens of difficult taxa (e.g., *Lohora* sp., Nymphalidae: Satyrinae) were killed for identification. Reference specimens will be deposited at the Zoological Museum at Cibinong (Indonesia). Released specimens were marked with numbers to recognize recaptured individuals. Five traps were set up per site along the transects, at intervals of ~15 m. At least 11 trap days were conducted per site. At sites where bait trapping was less efficient (e.g., bait was frequently removed by squirrels or monkeys), more trap days were necessary.

For analysis, specimens from all five traps along one transect were pooled. Species richness was quantified by calculating the number of expected species for a largest shared sample size of 42 specimens using the Hurlbert rarefaction method. The total number of expected species was estimated by the first-order jackknife method based on single trap days as sampling units.

Dung beetles

Ten pitfall traps, as described by Davis et al. (2001), were used to collect dung beetles. The traps were established along each 100-m transect, one trap every 10 m. The traps were baited with cattle dung and exposed six times at every site between May and July 2002 for three days before dung beetles were removed from the traps. Reference specimens were deposited at the Department for plant pests and diseases, Tadulako University Palu (Central Sulawesi, Indonesia) and the Museum Zoologicum Bogoriense (Java, Indonesia).

Endemic species

Bird and butterfly species were categorized as endemic when they are restricted to the Sulawesi region (a biogeographical subregion of Wallacea) as defined by Coates et al. (1997). In addition to the main island of Sulawesi (formerly Celebes), this region covers the Talaud, Nenusa, and Sangihe Islands in the north, the southernmost Flores Sea Islands, and the Togian, Banggai, and Tukangbesi Islands. Because the distribution of the two butterfly families Lycaenidae and Hesperidae is still not accurately known for all species, only endemism in Papilionidae, Pieridae, and Nymphalidae butterflies was evaluated, as already done in other studies (e.g., Spitzer et al. 1993). Information on geographical distributions was provided by Coates et al. (1997) for birds and from a manuscript on the butterfly fauna

of Sulawesi by R. I. Vane-Wright and R. de Jong. Knowledge of the geographical distribution of understory plants, trees, and dung beetles is not reliable enough to classify them as Sulawesi endemics.

Statistical analysis

The Shinozaki rarefaction method—used to calculate the number of species expected for a largest shared number of sampling units (identical number of subplots for trees, identical number of transect walks for butterflies)—was performed by a program provided by Roland Achtziger (see Achtziger et al. 1992). Hurlbert rarefaction was computed by the program “rarefact” (Krebs 1989). To calculate first-order jackknife estimates, we used the computer program of R. K. Colwell (EstimateS, version 6.0b1 [available online])⁸ by randomizing samples 50 times.

Pearson correlations and one-way ANOVA were performed using Statistica 5.1 (StatSoft 1997). Means are given with 1 SD if not mentioned otherwise. Tukey’s honest significance difference test was used for multiple comparisons of means.

Although we are aware of the problem of the statistical nonindependence of the pairwise comparisons between species richness of subgroups and higher taxonomic levels (in particular when species richness of both levels can only be extracted from identical samples), Pearson correlations were also conducted for these pairs. However, they were not taken into account for calculating the mean Pearson’s *r*.

RESULTS

Species richness of all studied plant and animal groups showed a significant response to habitat type (one-way ANOVA; trees: $F_{3,10} = 35.33$, $P < 0.0001$; understory plants: $F_{4,15} = 18.28$, $P < 0.0001$; birds: $F_{3,12} = 40.76$, $P < 0.0001$; butterflies: $F_{4,15} = 12.52$, $P < 0.001$; fruit-feeding butterflies: $F_{3,12} = 26.85$, $P < 0.0001$; dung beetles: $F_{3,12} = 9.47$, $P < 0.01$). This also counts for endemic birds ($F_{3,12} = 104.20$, $P < 0.0001$) and butterflies ($F_{4,15} = 7.92$, $P < 0.01$) and for the analyzed guilds of birds (insectivorous: $F_{3,12} = 20.98$, $P < 0.0001$; frugivorous and nectar-feeding combined: $F_{3,12} = 15.79$, $P < 0.001$). In general, plant and animal groups or guilds showed a pronounced decline of species richness with increasing habitat modification (Fig. 1). In most cases highest species richness could be documented for the near-primary forest sites, while a significantly lower richness was reported for secondary forests and the land-use systems. Understory plants were most diverse in the old secondary forest fragments, a habitat type that was not surveyed for all groups (see Fig. 1).

Although the species assemblages of most studied animal groups were not completely recorded, the expected species totals estimated by first-order jackknife

⁸ (<http://viceroy.eeb.uconn.edu/estimates>)

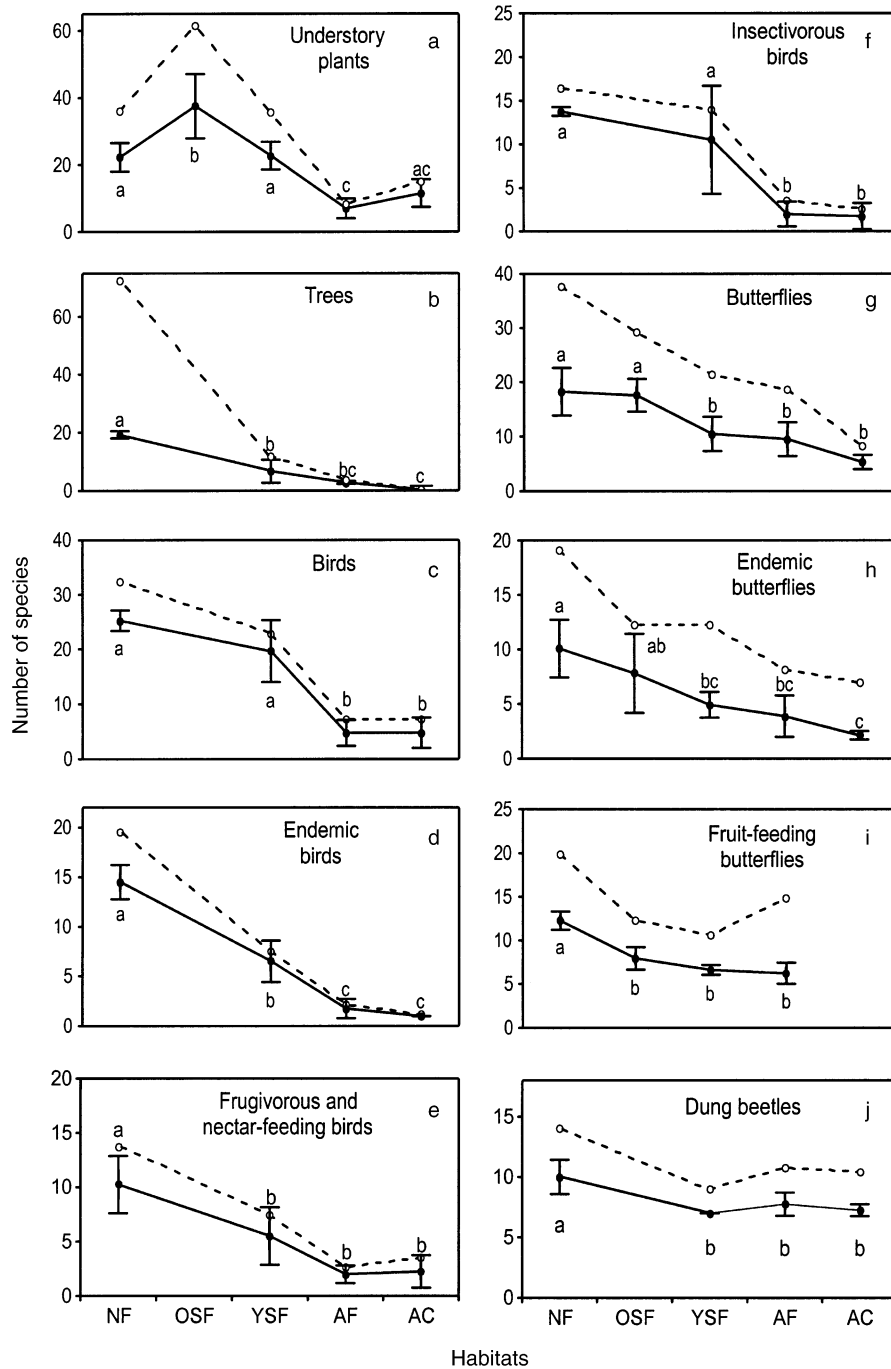


FIG. 1. Species richness (solid circles) given as the true number of recorded species (b, c, d, e, f, j) or (when sampling effort or sample size differed) interpolated by Shinozaki rarefaction to a standardized sampling area (a) or sampling effort (g, h) or interpolated by Hurlbert rarefaction to an identical sample size (i). Data are means with 95% CI. Additionally, the total species richness as estimated by first-order jackknife method (open circles) is presented. Within each panel, data points with the same letter are not significantly different at $P < 0.05$ (Tukey's honest significant difference test) between mean recorded or interpolated species richness. Key to abbreviations for habitats: NF, near-primary forest; OSF, old secondary forest; YSF, young secondary forest; AF, agroforestry systems; AC, annual culture. For the sampling framework, see Table 1.

for birds, butterflies, fruit-feeding butterflies, and dung beetles did not indicate any change of the general picture. In all studied groups the absolute numbers of recorded species (understory plants, birds, dung beetles) or the number of species calculated for a standardized plot size (trees), sampling effort (butterflies), or sample size (fruit-feeding butterflies) were significantly correlated with the estimates (understory plants: $r > 0.99$, $N = 20$, $P < 0.0001$; trees: $r = 0.96$, $N = 14$, $P < 0.0001$; birds: $r = 0.99$, $N = 16$, $P < 0.0001$; butterflies: $r = 0.99$, $N = 20$, $P < 0.0001$; fruit-feeding butterflies: $r = 0.98$, $N = 16$, $P < 0.0001$; dung beetles: $r = 0.90$, $N = 16$, $P < 0.0001$). Only in fruit-feeding butterflies the species richness of agroforests ranked more highly by first-order jackknife estimates than the expected number of species predicted by Hurlbert rarefaction for a largest shared sample size (Fig. 1).

Estimates—based on total species richness estimated by first-order jackknife—of the completeness of the inventories at single sites ranged between 59.03% and 100% for the surveyed groups of organisms and guilds (understory plants: $69.67 \pm 9.8\%$ [mean ± 1 SD] of the species recorded, minimum 59.03%, maximum 88.61%; trees: $74.73 \pm 13.87\%$, min. 59.97%, max. 100%; birds: $74.80 \pm 12.34\%$, min. 60.38%, max. 100%; butterflies: $67.80 \pm 5.38\%$, min. 56.66%, max. 76.73%; fruit-feeding butterflies: $75.37 \pm 6.06\%$, min. 67.70%, max. 90.60%; dung beetles: $73.24 \pm 8.08\%$, min. 61.51%, max. 89.06%). Complete inventories were only achieved in annual cultures.

With one exception (correlation between estimates for fruit-feeding butterflies and understory plants), in all cases changes in recorded or interpolated and estimated total species richness showed a positive relationship between taxonomic groups and guilds (Table 2). In total, 89.5% of all calculated pairwise correlations of recorded and/or interpolated species richness reached a significant level of $P < 0.05$; a total of 68.4% was reached for comparisons between estimated total species richness of groups. Also the relatively high mean correlation coefficients (for recorded and/or interpolated species numbers: $r = 0.69$, see Table 2; for first-order jackknife estimates: $r = 0.56$) underlined that most studied groups responded in a very similar way to habitat modification.

However, only few taxonomic groups or guilds turned out to be good predictors for others, for example, trees for fruit- and nectar-feeding birds (88% explanation) (Fig. 2a) and fruit-feeding butterflies (83%) (Fig. 2b), endemic birds for endemic butterflies (72%) (Fig. 2c), and fruit-/nectar-feeding birds for fruit-feeding butterflies (67%) (Fig. 2d). All these relationships had a Pearson's r of higher than 0.81, reached a level of significance of 0.001 or lower, and can be described sufficiently by a linear regression model. Although most of the other relationships (graphs not shown) also proved to be able to predict the change in species richness of another taxon or guild in general, they are not

able to forecast accurately the species richness of other plant and animal groups at a single sampling site. In most cases species richness of other taxonomic groups or guilds would be severely over- or underestimated.

DISCUSSION

Response to habitat modification

Species richness of plant and animal groups surveyed at the margin of the Lore Lindu National Park (Central Sulawesi [Indonesia]) decreased significantly with increasing habitat modification, a pattern already documented by previous studies for other geographical regions and a wide spectrum of taxonomic groups (e.g., Bowman et al. 1990, Gradstein 1992, Marshall and Swaine 1992, Estrada et al. 1994, Hill et al. 1995, Thiollay 1995, Lawton et al. 1998, Raman et al. 1998, Greenberg et al. 2000, Schulze 2000, Acebey et al. 2002, Beck et al. 2002). Species richness and diversity do not always decrease steadily with increasing habitat modification (e.g., Kappelle et al. 1996, Johns 1997, Beck et al. 2002, Costa and Magnusson 2002). As was documented by our study, understory plants did not reach the highest species numbers at the near-primary forests sites. However, our data underline the common opinion that old-growth forests hold the highest species richness in most cases. Forest disturbance can also cause an increase of species numbers on a small-scale in insects. Davis et al. (2001) showed that small-scale species richness of dung beetles in logged forests may be higher than in primary forest due to the presence of overlapping species ranges that are usually spatially separated in primary forest. Trap-nesting bees and wasps may even become more diverse with increasing land-use intensity (Klein et al. 2002). Secondary forests and agroforestry systems may help to maintain a certain portion of diversity (e.g., Lawton et al. 1998, Schulze 2000, Beck et al. 2002), but not of all taxonomic groups. In particular, species richness of trees is certainly suffering seriously from forest modification.

The disturbed-forest sites and land-use systems of our study were situated close to the margin of the Lore Lindu National Park. Therefore, this large forest block can still act as an important source for frequent recolonization processes. It can be expected that species richness of all studied groups may further decline with increasing isolation from remaining areas of old-grown forest (as shown for bees and wasps in the study area, Klein et al. 2003, 2004). This also counts for other studies reporting changes of species richness across a gradient of habitat modification, which surveyed sites in close vicinity to remaining near-primary or primary forest (e.g., Lawton et al. 1998, Willott 1999, Schulze 2000, Willott et al. 2000, Beck et al. 2002). Site independence should change contingent on the investigated taxa and guilds. For some groups (e.g., understory plants) the distances between plots may have been sufficient to reach high site independence in commu-

TABLE 2. Relationships among the nine plant and animal groups surveyed across sites; the top and right portion of the table presents correlations of species richness (Pearson's r), a level of significance, P (in parentheses; P -values <0.05 are printed in bold), along with the number of sites available for pairwise comparison, N (in square brackets). Values in the bottom and left portion of the table (below the diagonal) represent pairwise correlations of species numbers estimated by first-order jackknife method.

Group	Group			
	Understory plants	Trees	Birds	Endemic birds
Understory plants	...	0.40 (0.066) [14]	0.75 (0.001) [16]	0.81 (< 0.001) [16]
Trees	0.44 (0.111) [14]	...	0.86 (< 0.001) [14]	0.95 (< 0.001) [14]
Birds	0.78 (< 0.001) [16]	0.74 (0.002) [14]	...	0.95 (< 0.001) [16]
Endemic birds	0.69 (0.003) [16]	0.96 (< 0.001) [14]	0.90 (< 0.001) [16]	...
Insectivorous birds	0.84 (< 0.001) [16]	0.54 (0.006) [14]	0.94 (< 0.001) [16]	0.77 (0.001) [16]
Fruit-/nectar-feeding birds	0.59 (0.017) [16]	0.87 (< 0.001) [14]	0.88 (< 0.001) [16]	0.90 (< 0.001) [16]
Butterflies	0.59 (0.006) [20]	0.65 (0.011) [14]	0.75 (0.001) [16]	0.75 (0.001) [16]
Endemic butterflies	0.45 (0.048) [20]	0.67 (0.009) [14]	0.66 (< 0.005) [16]	0.70 (0.003) [16]
Fruit-feeding butterflies	-0.12 (0.668) [16]	0.52 (0.125) [10]	0.39 (0.211) [12]	0.61 (0.034) [12]
Dung beetles	0.11 (0.679) [16]	0.81 (< 0.001) [14]	0.49 (0.055) [16]	0.64 (0.008) [16]

Notes: When all sites were surveyed with an identical sampling effort (understory plants, birds, dung beetles) the true numbers of recorded species were used for pairwise comparisons. In case the sampling effort was different, species numbers were interpolated by Shinozaki rarefaction (Shinozaki 1963) to an identical sampling area (trees) or an identical sampling effort (= identical number of transect counts for butterflies). Samples of fruit-feeding butterflies were rarefied to a largest shared number of specimens by the Hurlbert rarefaction method (Hurlbert 1971). Values printed in italics account for correlations between subgroups and higher taxonomic levels and were not taken into account (because of their nonindependence) for calculating mean Pearson's r (see *Methods: Statistical analysis*).

nity structure (Tschamtko et al. 2002). In contrast, for highly mobile organisms (e.g., birds, some butterfly species) most of our sites are within home ranges.

Potential of taxa or guilds to predict species richness of other groups

The only published study covering a diverse spectrum of taxonomic groups across a similar land-use gradient (in Cameroon) also reports a general trend of decreasing species richness with increasing habitat modification (Lawton et al. 1998). However, there were no strongly pronounced relationships of change in species richness among the eight different animal groups surveyed. The mean correlation coefficient among species richness of the studied animal groups was 0.33, much lower than the one documented by our study ($r = 0.69$). Additionally, just the minority of pairwise correlations reached a significant level, while in our study species richness of most taxonomic groups and/or guilds was significantly correlated. Furthermore, in contrast to our study with almost no negative correlations among species richness (except between understory plants and fruit-feeding butterflies), 25% of all correlations among species richness of taxa surveyed by Lawton et al. (1998) reached a negative value,

one correlation even proved to be significantly negative (as in Klein et al. 2002).

In our study we did not include species-rich invertebrate taxa restricted to highly specific microhabitats such as the soil or the upper canopy layer as done by Lawton et al. (1998), but we did include two plant groups and diversity estimates for 2–3 times more field sites. This may be partly responsible for the different results. In addition, in our study three groups (trees, birds, and dung beetles) were not sampled in old secondary forests, a forest type featured strongly in Lawton et al. (1998), with several taxa increasing in species richness in old secondary forest relative to near-primary forest. Such a response could also be found in our study for understory plants. Furthermore, habitat fragmentation, which has a major impact on species richness (e.g., Klein 1989, Brown and Hutchings 1997, Carvalho and Vasconcelos 1999, Chiarello 2000, Laidlaw 2000, Krauss et al. 2003, Steffan-Dewenter et al. 2004), may have additionally contributed to the pronounced decrease of species richness from natural forest to young secondary forests and the land-use types documented by our study. While the last three habitat types were highly fragmented, our near-primary forest

TABLE 2. Extended.

Group					
Insectivorous birds	Fruit/nectar-feeding birds	Butterflies	Endemic butterflies	Fruit-feeding butterflies	Dung beetles
0.82 (<0.001) [16]	0.58 (0.018) [16]	0.70 (0.001) [20]	0.60 (0.005) [20]	0.16 (0.553) [16]	0.18 (0.504) [16]
0.70 (0.006) [14]	0.94 (<0.001) [14]	0.78 (0.001) [14]	0.81 (<0.001) [14]	0.91 (<0.001) [10]	0.71 (0.005) [14]
0.96 (<0.001) [16]	0.91 (<0.001) [16]	0.80 (<0.001) [16]	0.78 (<0.001) [16]	0.76 (0.004) [12]	0.55 (0.028) [16]
0.88 (<0.001) [16]	0.93 (<0.001) [16]	0.82 (<0.001) [16]	0.85 (<0.001) [16]	0.90 (<0.001) [12]	0.69 (0.003) [16]
...	0.77 (0.001) [16]	0.77 (<0.001) [16]	0.73 (0.001) [16]	0.60 (0.041) [12]	0.44 (0.091) [16]
0.69 (0.003) [16]	...	0.66 (0.005) [16]	0.71 (0.002) [16]	0.82 (0.001) [12]	0.67 (0.005) [16]
0.73 (0.001) [16]	0.56 (0.024) [16]	...	0.93 (<0.001) [20]	0.60 (0.014) [16]	0.59 (0.017) [16]
0.52 (0.040) [16]	0.67 (0.005) [16]	0.75 (<0.001) [20]	...	0.68 (0.004) [16]	0.64 (0.007) [16]
0.24 (0.449) [12]	0.40 (0.192) [12]	0.34 (0.198) [16]	0.31 (0.247) [16]	...	0.66 (0.020) [12]
0.31 (0.250) [16]	0.63 (0.008) [16]	0.51 (0.042) [16]	0.55 (0.028) [16]	0.45 (0.138) [12]	...

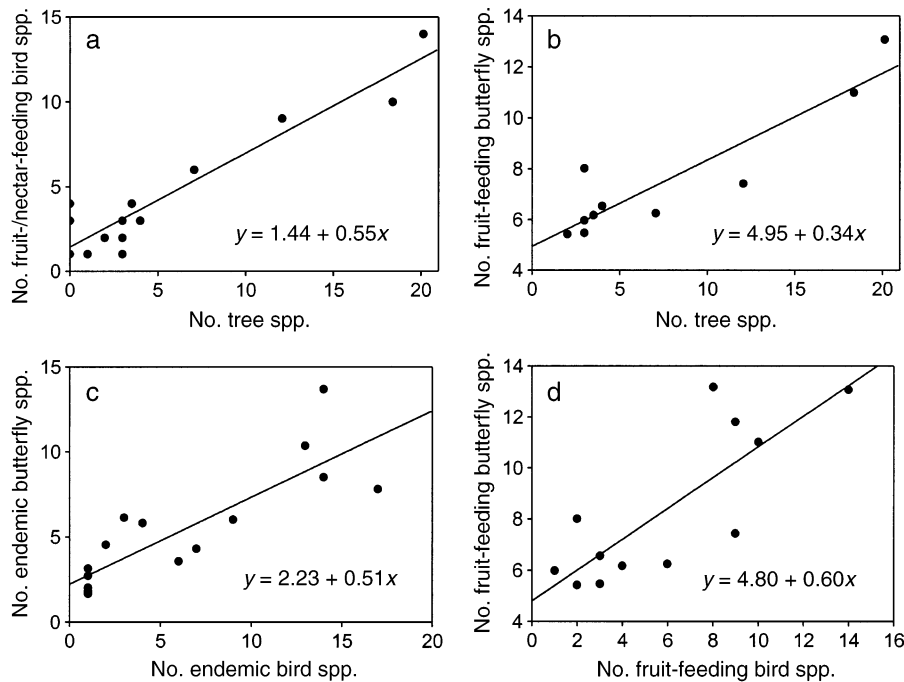


FIG. 2. Relationships between number of species of selected animal and plant taxa and/or guilds across the habitat gradient. Two examples show the relationship between two animal groups and trees: (a) fruit-feeding birds, (b) fruit-feeding butterflies. The relationship between species richness of endemic birds and butterflies is also shown (c), as well as the relationship between species richness of birds and butterflies belonging to the guild of fruit-feeders (birds also include nectar-feeders) (d). Each graph contains the linear regression curve as well as the regression function. Pearson correlations can be found in Table 2 for all relationships.

plots were integrated in a partly disturbed but still large block of forest.

A number of studies in tropical forest habitats have searched for diversity-indicator groups that are able to predict the species richness of higher (e.g., Cronk 1988, Beccaloni and Gaston 1994, Kessler and Bach 1999, Schulze and Fiedler 1999, Schulze 2000) or different taxa and guilds (Mittermeier 1988, Noss 1990, Daniels et al. 1992, Pearson and Cassola 1992, Pearson 1994, Pearson and Carroll 1997, Carroll and Pearson 1998). Although some groups proved to be good diversity indicators on a larger geographic scale, this cannot be generalized for predicting precisely local patterns of species richness across land-use gradients (e.g., Lawton et al. 1998). In general, this was also confirmed by our data. Schulze and Fielder (1999) emphasized that detailed long-term investigations and monitoring of whole species assemblages should preferably be done rather than recording only indicator taxa. However, the use of diversity indicators can be legitimate if detailed sampling of whole species communities is out of reach (Kessler and Bach 1999, Schulze and Fiedler 1999). This is the case for most tropical ecosystems because the resources to conduct complete community assessments would exceed those currently available to taxonomists and ecologists worldwide, as emphasized by Lawton et al. (1998).

Conclusions for conservation

Conservation programs should take into account that the presence of species of high conservation value is not always related to high overall diversity. For example, Holloway (1998) documented for moths and Kessler et al. (2001) for plants and birds that a high number of endemic species does not necessarily indicate a high diversity. In contrast, our data showed that the entire species richness of birds and butterflies at individual sites was closely related to the number of recorded endemic species. Although biodiversity of our land-use systems showed taxon-specific and guild-specific differences, most groups were affected in a similar way by habitat modification. Near-primary forest sites proved to be of principal importance for conservation, but land-use systems such as secondary forests (for understory plants, birds, and butterflies) and agroforestry systems (for butterflies) supported relatively high numbers of species and might—to a yet unknown extent—play a significant role for biodiversity conservation in tropical landscapes.

Even though our data on understory plants, trees, birds, butterflies, and dung beetles showed that in most cases individual plant or animal groups cannot predict the species richness of others accurately, most of them followed roughly the general pattern of change in species richness. Hence, the general conclusion of Lawton et al. (1998) that the use of popular groups like birds and butterflies as “flagship taxa” in biodiversity inventories and as indicators of changes in the diversity

of other taxonomic groups gives a highly misleading picture, is at least not valid for the groups surveyed across the studied land-use gradient in Central Sulawesi.

In conclusion, predictability of the diversity of one group by another group appears to have little reliability. Although diversity of the groups we studied tended to decrease with land-use intensity, only the species numbers of a few groups (for example, with similar resource use like the fruit-feeding birds and butterflies) were closely correlated. Our results also support the irrefutable conclusion that only old-growth forests (primary forests and old secondary forests) are capable of maintaining a substantial proportion of biodiversity. However, focusing strictly on only large and old tropical-forest habitats may not be a realistic way of conservation in most of the human-dominated tropical landscapes. Landscape management should also take small and young land-use types such as the relatively small patches of secondary forests and agroforests into account in strategies to counteract the modern trend to even more degraded, monotonous tropical regions.

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