Effects of Land Use on Bird Species Richness in Sulawesi, Indonesia

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Abstract: *There is still much debate over the potential value of land-use systems for the maintenance of tropical biodiversity. An increasing number of studies indicate that much forest biodiversity can also be found in the agricultural landscape matrix. Because there is little information on the potential value of land-use systems for tropical forest bird species, we conducted repeated point counts in near-primary forest, adjacent young secondary forest, modernized cacao agroforestry systems, and annual cultures at submontane elevations in central Sulawesi, Indonesia. Species richness decreased from natural forest and young secondary forest to agroforestry systems and annual cultures. Although species richness was similar between natural and young secondary forest, the number of endemic bird species was significantly lower in second-growth forest. Species composition gradually changed as the habitat changed from natural to secondary forest, agroforestry systems, and annual cultures. Despite close proximity to near-primary forest, the agroforestry systems studied supported only a few small frugivorous-nectarivorous species. Our results suggest that secondary forest could play an important role in the conservation of many Sulawesi bird species, but, although suitable for colonization, its potential to sustain populations over the long term is unknown. Improvement of the landscape matrix for biodiversity conservation through secondary habitats therefore seems desirable to enlarge the ranges of forest species, but the fight against land conversion within protected areas of the region should be of much higher importance, at least at present.*

Key Words: birds, endemism, Indonesia, land use, rainforest, Sulawesi, Wallacea

Efectos del Uso de Suelo sobre la Riqueza de Especies de Aves en Sulawesi, Indonesia

Resumen: *Aun hay debate sobre el valor potencial de los sistemas de uso de suelo para el mantenimiento de la biodiversidad tropical. Un creciente número de estudios indica que mucha de la biodiversidad del bosque también se encuentra en la matriz agropecuaria del paisaje. Debido a que hay poca información sobre el valor potencial de los sistemas de uso de suelo para especies de aves de bosque tropical, realizamos conteos por puntos repetidos en bosque casi primario, bosque secundario joven adyacente, sistemas agroforestales modernizados de cacao y cultivos anuales en elevaciones sub-montanas en Sulawesi central, Indonesia. La riqueza de especies decreció del bosque natural y bosque secundario joven a los sistemas agroforestales y cultivos anuales. No obstante la cercanía de bosque casi primario, los sistemas agroforestales estudiados soportaron solo a unas cuantas especies frugívoro-nectarívoras. Nuestros resultados sugieren que el bosque secundario podría jugar un papel importante en la conservación de muchas especies de aves de Sulawesi pero, aunque adecuado para colonización, se desconoce su potencial para sostener poblaciones a largo plazo. Por tanto, parece deseable un mejoramiento de la matriz del paisaje para la conservación de biodiversidad mediante hábitats secundarios para ampliar los rangos de las especies forestales, pero la lucha contra la conversión de suelos dentro de áreas protegidas de la región pudiera ser mucho más importante – por lo menos en el presente.*

Palabras Clave: aves, bosque lluvioso, endemismo, Indonesia, Sulawesi, uso de suelo, Wallacea

Introduction

Ten years after the Rio Declaration, Agenda 21 of the 1992 Earth Summit in Rio, rates of natural forest loss appear to have worsened in all tropical regions except Latin America. In absolute terms, more natural forest may have been lost in the 1990s than in the 1980s (Matthews 2000). Predictions of species loss from deforestation rates in the tropics have been made several times (e.g., Brooks et al. 2002) but have been criticized partly because of a failure to acknowledge the ability of many tropical forest species to survive in agricultural production areas (Budiansky 1994).

Recently, several researchers have examined the conservation value of agricultural landscapes by using species-richness data from various taxonomic groups. In several cases, studies showed that a relatively high number of individuals and species can still be found in land-use systems and that a major proportion of these species are part of the natural forest fauna (e.g., Hughes et al. 2002). Species composition can be quite different between sampled habitat types, however, and species with certain ecological characteristics seem more affected than others. A cautious interpretation of abundance and species richness data is necessary because deforestation is a relatively recent phenomenon, intensification of agricultural land is still ongoing, and so far little information on population viability or population development is available.

General findings concerning birds have been that traditional agroforests, with a mix of cultivated and natural shade trees, can support a high number of species, including many forest specialists, especially in close proximity to natural forest (e.g., Greenberg et al. 1997*b*). In contrast, agroforests with planted shade trees, even if composed of many tree species, support only a few forest-specialist birds in the absence of nearby primary forest (Greenberg et al. 1997, 2000). Annual cultures generally do not support high numbers of bird species in forest regions, but the picture can be different if groups of tall trees and forest fragments are left in the agricultural landscape (Daily 2001; Hughes et al. 2002).

Most information on bird species richness in tropical land-use systems is available from America (Greenberg et al. 1997*a*, 1997*b*). Only a few studies exist from Africa (Kofron & Chapman 1995), South and Southeast Asia (Thiollay 1995), or Australasia (Poulsen & Lambert 2000). Our objective was to document patterns of species richness and abundance of birds in near-primary forest, young secondary forest, and two types of land use—agroforestry systems and annual cultures—representing major components of the agricultural habitat mosaic in tropical landscapes world-wide.

We carried out our study in Sulawesi, an island well known for its exceptional endemism (Whitten et al. 1988). Forty-one (18%) of the 224 land birds of mainland Sulawesi are endemic to the core island, and a further 56 species (25%) are confined to Sulawesi or its satellite islands (Coates et al. 1997). As many as 11 endemic genera can be found, which makes Sulawesi one of the most important endemic bird areas of the world (Stattersfield et al. 1998) and largely contributes to Wallacea being a global biodiversity hotspot (Myers et al. 2000).

Study Area

The study area is located in central Sulawesi, Indonesia, approximately 75 km southeast of the province capital Palu, at the eastern margin of the Lore Lindu National Park. Information on weather conditions, geology, and prominent soil types of the area is available from Whitten et al. (1988). As in our study area, the margin of the national park is in most parts characterized by a mosaic of secondary forests, young fallows, and several land-use systems with cacao, coffee, maize, and paddy as main crops.

All study sites were located in the northern part of Napu Valley in the vicinity of the villages Kaduwaa, Wuasa, Watumaeta, and Alitupu, situated at the margin of the large closed-forest block of the Lore Lindu National Park. Selected sites were between 1100 and 1200 m above sea level, within the elevational range of the lower montane forest zone (Whitten et al. 1988).

Four replicate sites were selected for each of the four studied habitat types, near-primary forest (NF1-4), young secondary forest (YSF1-4), agroforestry system (AF1-4), and annual culture (AC1-4). All sites outside the closed forest (YSF, AF, and AC) were located in the vicinity of the forest edge. The term "near-primary forest" was used instead of "primary forest" because the entire forest at the interior margin of the Lore Lindu National Park is affected by some (small-scale) human disturbance. Illegal selective logging has already taken place close to our study sites, and uncontrolled rattan collecting is widespread. The young secondary forest sites were represented by small 1- to 3-ha patches with a closed canopy. We chose cacao plantations shaded by *Gliricidia sepium* Jacq. (Leguminosae) trees as a representative agroforestry system. The annual cultures were maize fields. The size of both land-use systems ranged between 1 and 2 ha. Table 1 provides further details on each habitat type.

Methods

The survey 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. Points were visited between 0600 and 0900 hours, and all birds detected visually and acoustically within 20 minutes were recorded. A digital

Table 1. Description of study sites in Sulawesi, Indonesia.

Site codes	Habitat type	Description
NF1–NF4	near-primary forest	mature closed-canopy forest; multilayered canopy; canopy height 25–30 m; emergents up to 40 m; sparse to dense foliage at midstory and understory level; Rubiaceae-dominated herb layer 1 m high; some selective logging in the vicinity of all sites
YSF1–YSF4	young secondary forest	5- to 6-year-old patches of secondary forest of approximately 1–1.5 ha; canopy layer 7–8 m high, mainly shrubs such as *Pipturus* sp. (Urticaceae); understory only developed at YSF4; herb layer mainly composed of Rubiaceae and ferns; single trees and Arenga (Palmae) up to 15 m; distance to closed-forest margin 50–200 m
AF1–AF4	agroforestry systems	approximately 5-year-old cacao plantations of 1–2 ha with a sparse cover of *Gliricidia sepium* (Leguminosae) as shade trees; cacao trees up to 3–3.5 m high; *Gliricidia sepium* 9–10 m high; single Arenga palms and other trees up to 15 m
AC1–AC4	annual culture	maize fields; solitary *Gliricidia sepium* trees up to 5 m high and young cacao trees 1 m high at one site; only sparse grass and herb layer; presence of recently felled logs

rangefinder was used to measure and estimate distances, and all observations beyond 50 m were discarded from analyses. Sites were visited alternately, with a total of eight visits per site. Field work was done exclusively by the first author, who acquired identification skills during 5 months of experience in submontane areas of Lore Lindu National Park with the assistance of locals and members of nongovernmental organizations. Field identification was facilitated by recording bird calls. Voice descriptions provided by Coates et al. (1997) also facilitated identification. Out of 1267 individuals recorded within the 50-m circle, 71 (6%) remained unidentified. These individuals and those for which no distance estimate could be obtained were discarded. For all but one site (YSF2), which unfortunately was illegally logged during survey work, bird species richness was quantified as the total number of recorded bird species per site, and analysis of variance (ANOVA) was performed to determine the effect of habitat type on bird species richness.

To obtain information on the completeness of our samples, we used the first-order jackknife method to estimate (from the incomplete data typically found in field studies) the total species richness (Colwell 2000). We chose this method because it performed well in comparable studies (e.g., Hughes et al. 2002).

We analyzed all bird species and endemic species separately. Birds were categorized as endemic when restricted to the Sulawesi region (a biogeographical subregion of Wallacea) as defined by Coates et al. (1997). Aside from the main island of Sulawesi (formerly Celebes), this region covers the Talaud, Nenusa, and Sangihe islands in the north, the southern-most Flores Sea Islands, and the Togian, Banggai, and Tukangbesi islands. Geographical distribution of birds is provided by Coates et al. (1997).

We analyzed the guilds of insectivorous and frugivorous/nectar-feeding birds separately and extracted information on feeding behavior 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), we combined the two guilds into a single group.

Species-Level Analysis

For each study site and species, we calculated a measure of relative abundance as the maximum number of individuals detected at each study site. We used one-way ANOVA to detect significant responses of bird species to variation in habitat. According to varying results from post hoc tests (Tukey's HSD test), species were assigned to response categories. The proportions of endemic species and species from different feeding guilds were determined with a chi-square goodness-of-fit test to see how they differ from their overall representation within the sampled bird community.

Statistical Analysis

To calculate the first-order jackknife and beta diversity between bird assemblages per site, we used the computer program of Colwell (2000). We randomized samples 50 times but did not shuffle individuals among samples within species. To compare means, we performed one-way ANOVA, and we used Tukey's honest-significance-difference test for multiple comparisons of means. We conducted a two-dimensional ordination of study sites, analyzing abundance data in a correspondence analysis to depict faunal similarity between habitat types.

Results

Bird Diversity within Habitat Types

We recorded 59 bird species in 31 families. Bird species richness differed significantly between habitat types. For all species combined, endemic birds and the analyzed guilds showed a pronounced decline in species richness when increasing habitat modification was visible
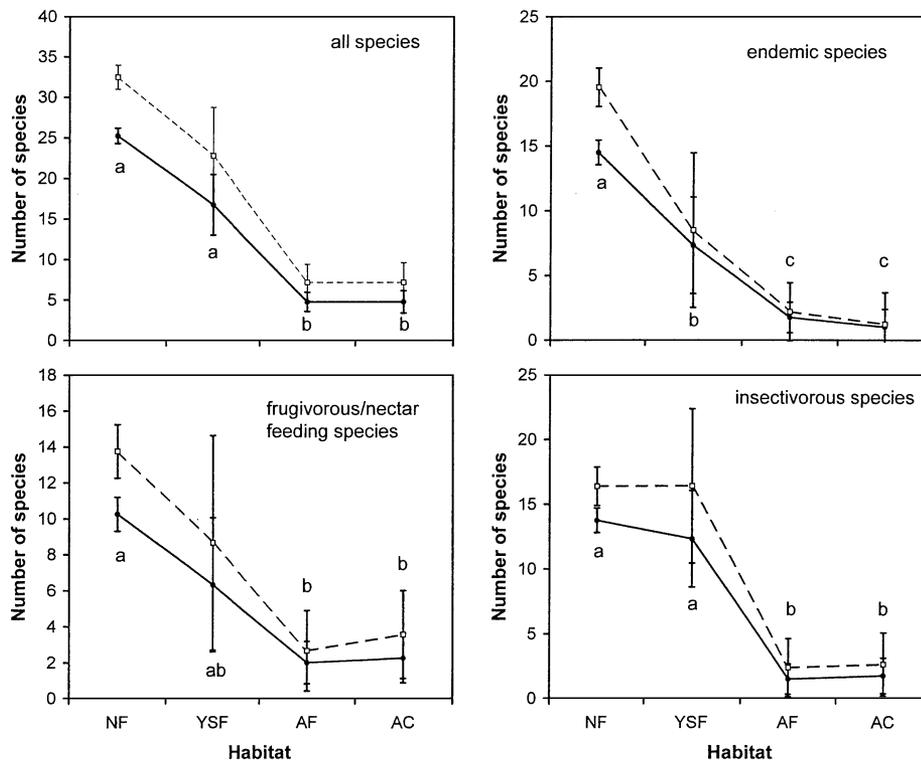
Figure 1. Mean number of observed species (filled dots) and total species estimated by the first-order jackknife method (open squares) of birds in 50-m-radius point count stations after eight repeat visits in near-primary forest, young secondary forest, and two land-use systems. Variance measures are standard deviations. Different letters (a, b) indicate significant differences on the 5% level (one-way analysis of variance). Habitats are ranked in order of increased forest modification: NF, near-primary forest; YSF, young secondary forest; AF, agroforestry systems; AC, annual culture (see also Schulze et al. 2004b).

(one-way ANOVA, $p < 0.001$ in all cases; Fig. 1). Species richness was highest in near-primary forest. In secondary forest sites, the species richness of endemic birds was significantly lower (Tukey's HSD test, $p < 0.001$). Overall species richness and richness in insectivorous and frugivorous/nectar-feeding birds did not differ significantly between the near-primary forest and the secondary forest (Tukey's HSD tests; for all species, $p = 0.167$; insectivorous species, $p = 0.910$; frugivorous/nectar-feeding species, $p = 0.095$). Species richness in land-use systems was lower than in near-primary and secondary forest for all birds (Tukey's HSD, $p < 0.001$), endemic birds ($p < 0.001$), and insectivorous birds ($p < 0.001$ and 0.002) and did not differ between the annual culture and the agroforestry sites ($p = 0.999$). Species richness of frugivorous/nectar-feeding birds was lower in the agroforestry system and the annual culture than in the near-primary forest ($p < 0.001$), but was intermediate in and did not differ significantly from the young secondary forest (for annual culture, $p = 0.079$; for agroforestry, $p = 0.998$).

Based on the jackknife index, completeness of the inventories at single sites ranged between 60 and 100% for all birds and separate guilds (74.8 ± 12.3%, min. 60.4%, max. 100%). Complete inventories (100%) were only obtained in annual culture or agroforestry sites.

Bird Diversity between Habitat Types

Pairwise similarity of bird species composition (mean Sörensen ± SD) was highest between the four near-

primary forest samples (0.69 ± 0.07), intermediate between young secondary forest samples (0.56 ± 0.02), and low between the agroforestry system (0.32 ± 0.10) and annual culture sites (0.28 ± 0.12). Two-dimensional ordination of study sites based on abundance data in a correspondence analysis did not show overlap between the four habitat types (Fig. 2). A one-way multiple analysis of variance of sample scores extracted from the two-dimensional ordination revealed a significant difference
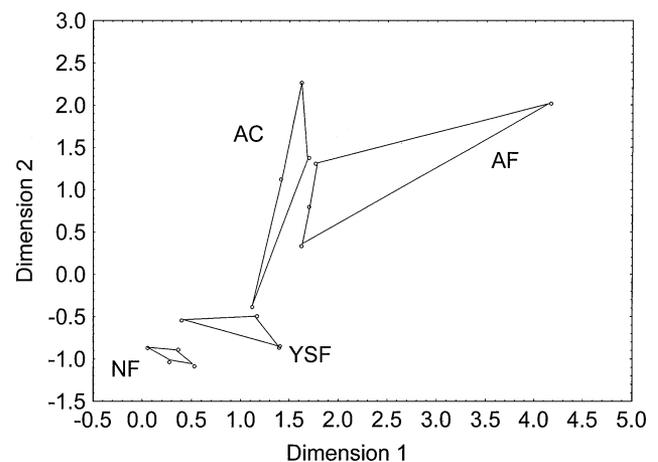

Figure 2. Correspondence-analysis plot of avifaunal similarity between different study sites based on abundance data. Study sites belonging to the same habitat category are connected by lines. Habitats: NF, near-primary forest; YSF, young secondary forest; AF, agroforestry systems; AC, annual culture.

Table 2. Summary of significant effects of habitat type on relative abundance of 17 bird species.[a]

| Family and species | Habitat type[b] | | | | $F_{3,12}$ | p | Response. category[c] | Geographic range[d] | Feeding guild[e] |
	NF	YSF	AF	AC					
Columbidae									
Macropygia amboinensis	1.50	0.75	0.00	0.00	14.14	0.000	2	4	F
Ptilinopus melanospila	1.75	0.25	0.25	0.00	13.67	0.000	1	3	F
Ducula forsteni	1.25	0.00	0.00	0.00	25.00	0.000	1	2	F
Psittacidae									
Loriculus stigmatus	1.00	0.25	0.00	0.00	14.33	0.000	1	2	N
Cuculidae									
Cacomantis sepulcralis	0.75	0.50	0.00	0.00	3.86	0.038	2	4	I
Bucerotidae									
Rhyticeros cassidix	0.75	0.00	0.00	0.00	9.00	0.002	1	2	F
Picidae									
Dendrocopus temminkii	0.75	0.50	0.00	0.00	3.86	0.038	2	2	I
Oriolidae									
Oriolus chinensis	1.25	0.50	0.00	0.00	9.57	0.002	2	4	I
Timaliidae									
Trichastoma celebensis	1.75	1.25	0.00	0.00	10.86	0.001	2	2	I
Muscicapidae									
Eumyias panayensis	2.00	1.50	0.00	0.25	25.57	0.000	1	4	I
Cyornis omissus	1.25	1.00	0.00	0.00	7.55	0.004	2	2	I
Monarchidae									
Hypothymis azurea	1.25	0.50	0.00	0.00	9.57	0.002	2	4	I
Rhipiduridae									
Rhipidura teysmanni	1.00	0.00	0.00	0.00	6.00	0.010	1	2	I
Petroicidae									
Culicicapa helianthea	1.25	0.50	0.00	0.00	9.57	0.002	2	4	I
Pachycephalidae									
Pachycephala sulfuriventer	1.25	0.50	0.00	0.00	9.57	0.002	2	1	I
Dicaeidae									
Dicaeum aureolimbatum	1.00	0.75	0.25	0.00	6.67	0.007	2	2	F
Zosteropidae									
Zosterops atrifrons	1.75	1.50	0.00	0.25	14.80	0.000	2	4	I

[a]*Data are means calculated from maximum numbers of individuals observed per 20-minute point, with F and p values from one-way analysis of variance.*

[b]*Abbreviations: NF, near-primary forest; YSF, young secondary forest; AF, agroforestry systems; AC, annual culture.*

[c]*Response category: 1, clear preference for near-primary forest, steady decline with increasing habitat modification; 2, preference for natural and secondary forest and lower abundance in agroforestry systems and annual culture.*

[d]*Geographic range: 1, endemic to Sulawesi Island; 2, endemic to Sulawesi subregion; 3, endemic to Wallacea; 4, range extending from Wallacea (Coates et al. 1997).*

[e]*Feeding guild: F, frugivorous; N, nectar-feeding; I, insectivorous (Coates et al. 1997).*

between the four groups of sites (Rao's $R_{6,22} = 5.33$, $p = 0.002$).

Overall Abundance

The maximum number of individual birds recorded per point count was significantly different between habitat types (ANOVA: $F_{3,12} = 50.97$, $p < 0.001$). Bird abundance was highest in the near-primary forest (15.75 ± 2.1 individuals or groups) and the young secondary forest (9.50 ± 2.1) and lowest in the agroforestry systems (3.25 ± 1.5) and the annual culture sites (2.75 ± 1.0). Differences were significant between each of the forest habitats (near-primary, young secondary) and each of the agroforestry system and annual culture sites (Tukey's HSD test, $p < 0.01$ in all cases), but not between the agroforestry system and the annual culture sites.

Species-Level Responses

Out of the 59 recorded species, 17 showed significant differences in relative abundance among habitat types (ANOVAs, $p \leq 0.05$) and 42 did not (Table 2). Given a maximum 5% probability of a Type I error, it is unlikely that 17 species (29%) would show significant responses to habitat by chance (chi-square test, $p < 0.001$).

Based on ANOVA and post hoc tests, there were two main categories of responses: (1) 6 species declined steadily with increasing habitat modification from near-primary to secondary forest and to both agroforestry and annual culture sites (Tukey's HSD test, $p < 0.05$, for comparison of near-primary with young secondary forest), and (2) 11 species were found in similar numbers in the near-primary and in the secondary forest but were less frequent in agroforestry and annual culture sites. None of

the species was significantly more abundant in the secondary forest than near-primary forest, and none showed significant differences in numbers between agroforestry and annual culture sites.

Feeding Guild, Geographic Range, and Responses to Habitat Type

Among the 17 species affected by habitat modification were 5 frugivores, 1 nectar-feeding psittacid, and 11 insectivorous species. The distribution of these feeding guilds in response categories did not differ significantly from the overall representation of feeding guilds in the bird community ($\chi^2 = 3.61$, df = 3, $p = 0.31$). Among the 17 affected species, there were 9 endemics (53%). This proportion was not significantly different from the overall representation of endemic species in the bird community ($\chi^2 = 0.00$, df = 1, $p = 0.95$).

Discussion

Bird Diversity in Secondary Forest and Land-Use Systems

Bird diversity in early successional forest is usually lower than in mature forest and correlates positively with vegetation complexity and food availability (Terborgh & Weske 1969; Marsden & Pilgrim 2003). The results of many studies suggest that a substantial proportion of the native bird fauna in tropical forests is still in secondary habitats, but species composition usually differs markedly in younger secondary forests (Shankar Raman et al. 1998). In Costa Rica, 46% of regional avifauna still utilizes the agricultural landscape, but this is mainly due to the availability of forest edges and fallows with trees (Hughes et al. 2002). Results of one study indicate higher (site) bird species richness in 5- to 15-year-old secondary forests than in undisturbed forest (Estrada et al. 1997). It has also been documented, however, that even extensive farm bush and second growth within agricultural areas support only a few forest species at larger distances (>25 km) from closed-forest blocks (Kofron & Chapman 1995).

Our results also indicate that young secondary forest can be used by a high number of bird species and that its species richness is not significantly lower than that of adjacent near-primary forest. Species composition in young secondary forest was clearly different from that in near-primary forest, however, and can be seen as an early transition stage to annual cultures and agroforestry systems. In our study, the bird species in second growth were mainly insectivorous, often only present in mixed flocks (e.g., *Oriolus chinensis*), and it is possible that several of them were not holding permanent territories. The near absence of larger frugivores (*Rhyticeros, Ducula, Ptilinopus*) in this habitat was most probably due to a shortage of food resources. The number of endemic species

was significantly lower in the secondary than in the near-primary forest sites, suggesting that endemic species are more sensitive to forest change and fragmentation than more widespread species, a pattern that has been shown before (e.g., Fjeldsa 1999; Renjifo 2001). Asymmetric responses of endemic and nonendemic forest fauna to habitat change have also been documented for other taxa (e.g., Fermon et al. 2000). It is difficult, however, to statistically detect such responses at the species level (this study; Marsden 1998).

Tropical agroforestry systems can also be colonized by many forest species (Thiollay 1995; Estrada et al. 1997; Greenberg et al. 1997). However, distance to primary forest (see Greenberg et al. 2000 and references therein) and the availability of a dense and diverse shade-tree assemblage (Greenberg et al. 2000) are important factors. Natural shade trees in agroforestry systems can provide food resources, allowing long-lived species to persist for longer periods (Marsden & Pilgrim 2003). Artificial plantations with exotic shade trees far from natural forest usually do not support large numbers of resident forest species (Greenberg et al. 2000).

The cacao system we studied was situated close to near-primary forest and shaded only by a single species of a non-native small tree. In contrast to the relatively high number of forest butterfly species found on these sites (Schulze et al. 2004a), bird counts did not indicate the presence of large numbers of individuals and species. The assemblage was mainly composed of small forest-edge species, also present in the natural and the secondary forest. Some nonforest species such as *Streptopelia chinensis* and *Zosterops chloris* were present. It is obvious that food availability is generally limited in these artificial habitats, even for medium-sized frugivores and, possibly because of the use of insecticides, for insectivores.

Bird diversity and composition in agricultural landscapes in the wet tropics are strongly influenced by the availability of groups of trees and patches of second growth (Daily 2001; Hughes et al. 2002). Our study sites mainly consisted of larger maize fields with little or no remaining natural vegetation, and they supported few forest species. The few species present in these fields were arboreal, also occurring in secondary forest. Only some granivores and two palaearctic migrants were found exclusively in annual culture sites.

Implications for Conservation

Our results show that secondary forests could be valuable habitats for the colonization of a large proportion of central Sulawesi's forest avifauna. A mosaic of agricultural areas, alternating with sufficiently large forest patches, might therefore sustain a considerable proportion of the bird fauna within the overall landscape context.

On Sulawesi, forest cover below 400 m above sea level is already insignificant (FWI & GFW 2002). The Lore Lindu

region still holds continuous strips of natural forest at submontane level (400–1,200 m asl). These areas are exclusively used by some 60 native forest bird species (Waltert et al. 2004) but are situated along the borders of the park, being subject to further agricultural encroachment. A reduction of forest cover in these areas down to 100 km^2 of forest, a scenario that can be inferred from present deforestation patterns, could lead to the extinction of almost half these species (Waltert et al. 2003). Considerable reductions in forest cover might already be responsible for the absence of several understory birds in certain submontane valleys (M.W., unpublished data), highlighting the possibility that forests at lower montane elevations that are rich in bird species do not contribute to the population viability of many species occurring there but may in fact be population sinks (see also Poulsen & Lambert 2000).

The ability of forest birds to persist over the longer term in secondary habitats also depends on the availability of nesting sites (e.g., Marsden & Jones 1997; Marsden & Pilgrim 2003) and on several other factors such as parasitism, competition, and predation, for which we do not yet have good assessments. Results of a nest-predation study carried out at Lore Lindu suggest considerably higher predation rates than those in near-primary forest, a finding that might also be relevant for natural bird populations (Pangau-Adam 2003). Additional research and monitoring are needed to show whether species colonizing modified forest can maintain viable populations. Despite the fact that relatively high site species richness can be found in modernized agroforestry systems (e.g., for butterflies, Schulze et al. 2004a; for bees and wasps, Klein et al. 2002a, 2002b), conservation of global and regional biodiversity strongly depends on adequate areas of forest.

Considering the rate at which even protected forest is converted to agricultural areas in Indonesia, we strongly believe that conservationists should do everything possible to highlight the importance of remaining natural forest within protected areas instead of focusing on improved management of agroforestry systems in the surrounding landscape.

Acknowledgments

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