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Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species

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Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species

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Abstract: Studies on temporal changes of tropical bird communities as response to habitat modification are rare. To evaluate the sustainability of current land-use practices, we quantified changes in bird assemblages at the forest margin of Lore Lindu National Park, Central Sulawesi for a period of six years. Therefore, standardized bird counts were conducted in the years 2001/2002 and 2008 at 15 census points representing natural forest, secondary forest, agroforestry system and openland sites. Although overall species richness remained nearly identical, different species groups were affected unequally by habitat modification within the forest margin landscape. The mostly endemic forest species declined in abundance (72.0 % of forest species) and were counted at a smaller number of census points in 2008 (81.8 %). In contrast, 81.8 % of the solely widespread open-land birds became more abundant and 63.6 % of the species were recorded at al larger number of census points. Hence, recent human activities in the forest margin ecotone negatively affected species of high conservation value and contributed to the ongoing process of biotic homogenization. Species richness turned out to be a poor indicator of habitat change, and our results underline the importance of considering species identities. Small-scale disturbance and land-use change at the margin of Lore Lindu National Park had surprising negative impacts on bird community structure and endangered species, but not overall biodiversity, even within few years. Biotic homogenization as result of habitat conversion and modification is a global phenomenon. The winners, such as in our study, are widespread open land species, while the losers are endemic forest birds. Further monitoring of temporal changes of biodiversity is an important precondition to adequately valuate effects of human activities on species assemblages within sensitive transition zones such as forest margin areas, which are particularly exposed to anthropogenic disturbance.

Keywords: biotic homogenization, Sulawesi, deforestation, endemism, forest birds, land-use change, rainforest margin, temporal dynamic

Zusammenfassung: Untersuchungen über die zeitlichen Veränderungen von Vogelgemeinschaften in Folge von Habitatveränderungen sind selten. Um die Nachhaltigkeit gängiger Landnutzungspraktiken einzuschätzen, untersuchten wir Änderungen der Vogelgemeinschaften in der Waldrandzone des Lore-Lindu Nationalparks (Zentralsulawesi) über einen Zeitraum von sechs Jahren. Dazu wurden standardisierte Punktzählungen in den Jahren 2001/2002 und 2008 an 15 Standorten durchgeführt, welche relativ ungestörte Waldstandorte, Sekundärwälder, Kakaoplantagen und Offenlandstandorte repräsentierten. Obwohl sich der Gesamtartenreichtum nur unwesentlich änderte, zeigt sich, dass einzelne Vogelgruppen unterschiedlich auf Habitatveränderungen im Bereich der Waldrandzone reagierten. Die überwiegend endemischen Waldarten nahmen in ihrer Häufigkeit ab (72.0 % der Waldarten) und wurden 2008 an weniger Standorten nachgewiesen (81.8 %). Im Gegensatz dazu wurden 81.8 % der ausschließlich weit verbreiteten Offenlandarten häufiger, und 63.6% der Arten wurden an mehr Standorten festgestellt. Demnach wirkte sich der anhaltende anthropogene Einfluss auf das Ökoton Waldrandzone v.a. auf naturschutzrelevante Arten negativ aus und trägt daher zur einer fortschreitenden biotischen Homogenisierung bei. Artenreichtum scheint demnach als Indikator für Habitatveränderungen unzureichend zu sein. Vielmehr betonen unsere Untersuchungen die Notwendigkeit, Effekte auf einzelne Arten getrennt zu beurteilen. Kleinräumige Störungen und Landnutzungsänderungen im Waldrandgebiet des Lore Lindu Nationalparks hatten innerhalb nur weniger Jahre einen in dieser Form unerwarteten, deutlich negativen Einfluss auf die Struktur der Vogelgemeinschaft, wobei besonders gefährdete Arten stark betroffen waren. Der Gesamtartenreichtum blieb hingegen überraschend stabil. Biotische Homogenisierung in Folge von Habitatumwandlungen ist ein globales Phänomen. Die „Gewinner“ sind, so wie auch in unserer Studie, meist weit verbreitete, an anthropogene Störungen angepasste Offenlandarten. Im Gegensatz dazu ist die Gruppe der „Verlierer“ überwiegend durch endemische Waldarten gekennzeichnet. Tropische Waldrandzonen sind besonders stark von anthropogener Störung betroffen. Das Monitoring der zeitlichen Veränderungen von Biodiversität in diesen empfindlichen Übergangsbereichen ist eine unabdingbare Voraussetzung, um die Auswirkungen menschlicher Aktivitäten auf die betroffenen Artengemeinschaften adäquat beurteilen zu können.

Introduction

Deforestation in tropical regions contributes substantially to global biodiversity loss (Balmford & Long 1994; Pimm et al. 2006) and has thereby become a major issue in conservation biology (Sekercioglu & Sodhi 2007). An increasing number of studies have focused on the effects of habitat disturbance and land-use intensification on tropical biodiversity, generally reporting a negative impact (Bawa & Seidler 1998; Lawton et al. 1998; Marsden et al. 1998; Brooks et al. 2002; Lambert et al. 2002; Donald et al. 2004; Schulze et al. 2004; Waltert et al. 2004, 2005; Tscharntke et al. 2005; Veddeler et al. 2005; Aratrakorn et al. 2006; Peh et al. 2006). However, many predictions of species loss caused by habitat modifications have been criticized because the potential of human-dominated habitats and secondary forests to maintain biodiversity over the long term is largely unknown (Waltert et al. 2004). Furthermore, estimated rates of loss of populations in tropical areas due to land-use changes are much higher than species extinction rates but have received relatively little attention (Hughes et al. 1997, Marsden et al. 1998).

Several studies have reported a significant decrease of forest bird species at various localities within Southeast Asia as a result of deforestation (Castelletta et al. 2000; Brook et al. 2003; Peh et al. 2006). Considering the enormous species richness and endemism within this region, which is characterized by one of the highest deforestation rates (Achard et al. 2002), it should be a primary focus for conservation biology research (Brooks et al. 1997; Riley et al. 2001; Lambert & Collar 2002; Waltert et al. 2004; Sodhi et al. 2005; Peh et al. 2006). Also Sulawesi, a global biodiversity hotspot (Myers et al. 2000), is known for its alarming rate of deforestation (Sodhi et al. 2004). The island is one of the globally most important endemic bird areas (Stattersfield et al. 1998). Mainland Sulawesi hosts 10 endemic bird genera and a resident avifauna of 224 land and freshwater species of which 41 (18%) are endemic (Coates et al. 1997). Based on data from two survey periods, the aim of this study was to quantify the impact of recent land-use changes and small scale deforestation on the bird fauna at the margin of Lore Lindu National Park in Central Sulawesi within six years.

Particularly, we addressed the following questions:

(1) Did species richness change within a time period of six years as response to ongoing human activities at the forest margin?

(2) Did land-use change facilitate species turnover or alter species composition?

(3) Did groups of species characterized by different range size (endemic vs. widespread species), habitat affiliation (understorey vs. canopy species) or feeding mode respond differentially to habitat modification?

(4) What are the consequences of forest margin modification for conservation?

One can expect the ongoing exploitation of the forest margin, particularly by illegal small-scale logging activities, to have a negative effect on the entire bird assemblage in the transition zone between closed forest and the adjacent human-dominated landscape. Endemic species and understorey birds are known to respond particularly sensitively to habitat modification (Waltert et al. 2004; Abrahamczyk et al. 2008; Schulze & Riedl 2008). Although a substantial number of forest species are able to utilize land-use systems such as agroforests (Greenberg et al. 1997), the value of the human-dominated countryside for forest birds may have additionally been altered due to an intensification of agroforestry system management. This could result in an increasing dominance of disturbance-tolerant birds, often represented by widespread species (Schulze & Riedl 2008). Results of this study will help evaluate the sustainability of current land-use practices at the forest margin transition zone with respect to maintaining bird diversity within a complex mosaic of habitats at the margin of Lore Lindu National Park.

Methods

Study area and study sites

The study area is located in Central Sulawesi, Indonesia, approximately 75 km southeast of the province capital Palu, at the eastern margin of Lore Lindu National Park (LLNP). The area was declared a UNESCO Man and Biosphere Reserve in 1977; the national park was established in 1993 and covers an area of 229,000 ha (Adiwibowo 2005). LLNP is an exceptionally species-rich area harboring approximately 78% of Sulawesi´s endemic birds (Coates et al. 1997).

The forest margin landscape outside the closed block of near-primary forest is characterized by a mosaic of secondary forests, young fallows, and several land-use systems with cocoa, coffee, maize and rice as the main crops (Schulze et al. 2004). Our study sites were situated at the northern tip of Napu Valley between 1,100 and 1,200 m asl. This area comprises the elevational range of the lower montane forest zone (Whitten et al. 1987) with a mean annual precipitation of over 3,000 mm (Schweithelm et al. 1992).

In 2008, bird counts were conducted at 15 census points (Fig. 1), at which birds were already surveyed in 2001/2002 (Schulze et al. 2004; Waltert et al. 2004). At that time, anthropogenic disturbance such as illegal selective logging or uncontrolled collection of rattan was already visible at the forest margin (Waltert et al. 2004). Waltert et al. (2004) selected four replicate sites 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). However, only three YSF sites were used for further analyses because one site (YSF2) was logged during the first survey period in 2001/2002 before the bird census could be finished.

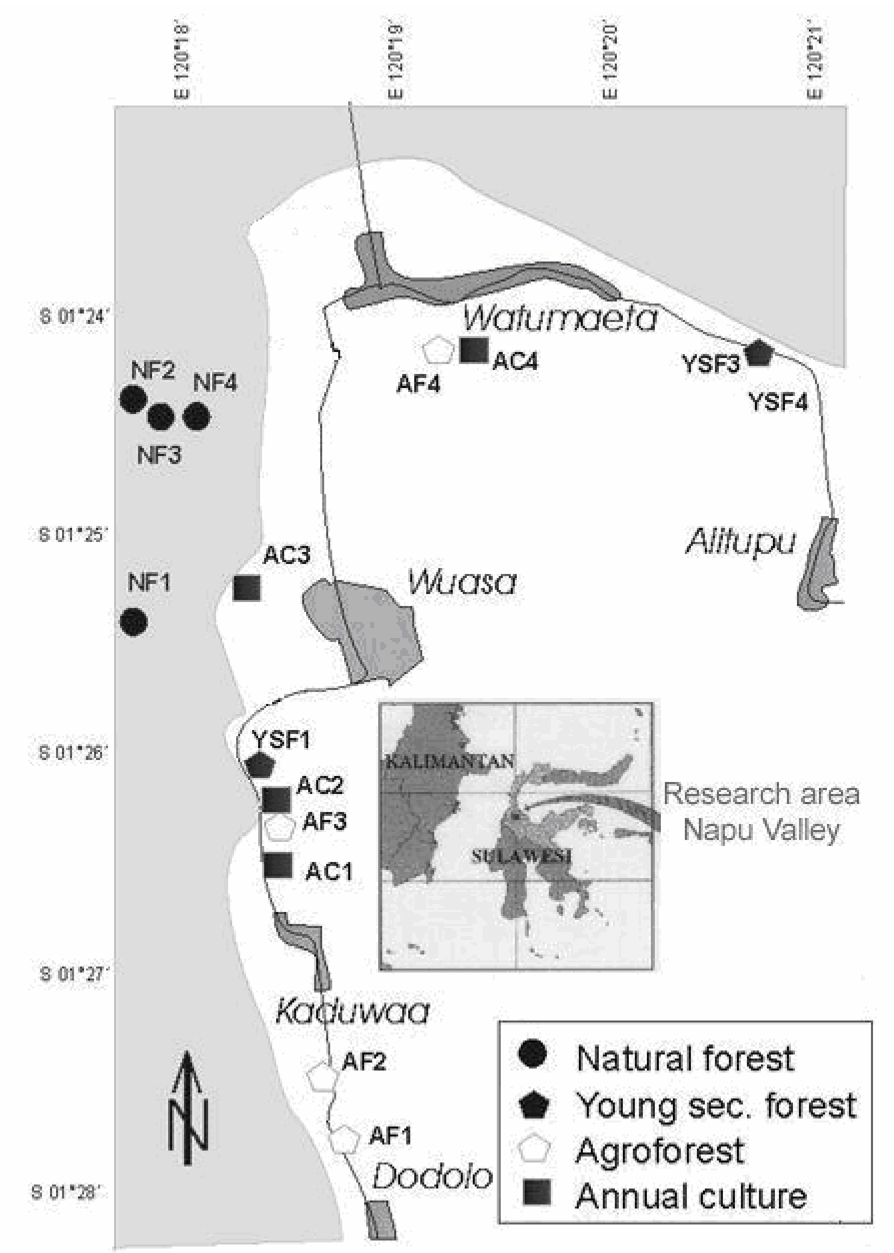

Fig. 1. Bird census points at the margin of LLNP in the vicinity of the villages Wuasa, Watumaeta, Alitupu and Kaduwaa which are connected by a well established road which provides relatively easy access to the forest area (indicated in grey). The white area represents several types of land use systems (e.g. rice fields, cacao plantations, coffee plantations).

Only few sites remained in a similar condition compared to the first bird census period in 2001/2002. Habitat changes, which occurred between the first bird survey (Waltert et al. 2004) and the re-survey in 2008, are summarized in Table 1. Sites were relocated using GPS and the field experience of the last author who was involved in the initial site selection in the years 2000–2001.

Tab.1. Description of study site changes.

Habitat type in 2001/2002	**Habitat changes until 2008**
Primary forest sites (NF1-4)	Due to a shift of the forest margin towards the park's interior caused by logging activities two former natural forest sites (NF4, NF3) were clear-cut. NF4 was converted to an annual culture; NF3 was in the stage of a young secondary forest. NF2 and NF1 were not affected by recent logging activities and appeared to be even less influenced by human disturbance than in 2001/2002.
Secondary forest sites* (YSF1, YSF 3-4)	This habitat type was most dramatically affected by human activities. YSF3 and YSF4 were converted into cacao plantations. YSF1 was in a similar condition than in 2001/2002 indicating that it was logged 3-4 years ago.
Cacao agroforestry systems (AF1-4)	All agroforestry systems still existed. However, shade trees which were still present during the studies in 2001/2002 were removed in all plantations.
Annual cultures (maize) (AC1-4)	Except of one site (AC2), all sites can be still described as annual cultures but are obviously going to be converted into agroforestry systems as noticeable by numerous recently planted small cacao and shade trees (*Gliricidia sepium*). AC2 already is an agroforestry system with cacao and a dense layer of shade trees of ca. 7 m height.

* YSF2 was already logged in 2001 before the first bird survey could be finished.

Bird survey

We used the same survey method, which is described in Waltert et al. (2004). To reduce seasonal effects, our second survey was conducted during a time frame (January–February 2008) similar to the first survey (December 2001–February 2002; Waltert et al. 2004). During point counts, all birds detected visually and acoustically within a radius of 50 m from the observer were recorded within 20 minutes. We tried to ensure that the same individual was not counted more than once. A digital rangefinder was used to measure and estimate distances. All observations beyond 50 m, including those individuals that flew over the canopy, were discarded from analysis. Census points were visited in succession between 06:00 and 09:00 am with a total of eight visits per site. Field work was conducted by the first and second author. Identification of birds was facilitated by voice recordings (Steve Smith 1993

[”Bird recordings from Sulawesi”], and 1994 [“Bird recordings from Java, Bali and Sumatra”]) and the voice descriptions in Coates et al. (1997). Because our study focused on the temporal change of the native breeding bird community, three migrant species (*Motacilla cinerea*: 1 bird in 2001/2002 and 5 birds in 2008; *Motacilla flava*: 2 birds in 2001/2002; *Anthus novaehollandiae*: one bird in 2008) and the introduced *Passer montanus* (one flock of four in 2001/2002*)* were excluded from all analyses.

Endemic species

Birds were classified as endemic (Appendix S1) when restricted to the Sulawesi subregion as defined by Coates et al. (1997). Aside from Sulawesi and its smaller satellites, the region also comprises the Banggai and Sula Islands.

Habitat affiliation

Species were classified as (1) forest species (FO), (2) open land species (OL) or (3) species frequently observed in forest and open land habitats (F+O) (Appendix S1). Furthermore, we analyzed forest understorey and forest canopy birds separately (Appendix S1). Information on habitat preferences and preferred forest stratum were extracted from Coates et al. (1997).

Analysis of data

To estimate total species richness as well as the completeness of our samples, we used the Chao 2 richness estimator, which was identified as the best overall richness estimator by Walther & Moore (2005). Chao 2 estimates and species accumulation curves were calculated using the software EstimateS version 8 (Colwell 2006). Samples were randomized 100 times. Bird species richness was estimated separately for both survey periods. Species lists for individual census points were used as sample units.

Similarities of bird species composition between survey periods and census points within each of the two survey periods were quantified by Sørensen’s similarity index, which is regarded as one of the most effective similarity measures (e.g. Southwood &

Henderson 2000). In addition to the classic Sørensen index we used Chao's Sørensen Raw Abundance-Based Similarity Index (Colwell 2006). According to Chao et al. (2005) this estimator for the total number of shared species is considerably less biased than the classic similarity indices, in situations where species assemblages are incompletely sampled (Chao et al. 2005).

To quantify changes in abundance of individual bird species between both survey periods, we calculated for each survey period the sum of the maximum numbers of individuals counted at census points during individual counts. The total number of census points, at which an individual bird species was recorded, was defined as the occurrence frequency. Again, this measure was calculated for both survey periods separately. Both measures were used to quantify if individual species increased or decreased from 2001/2002 to 2008. Furthermore, we calculated the changes in relative abundance for the 41 most abundant species (n >7 individuals counted during both survey periods) as the differences between their relative abundances (proportion of total number of birds observed in 2001/2002 and 2008, respectively) in 2008 and 2001/2002. All statistical analyses to test for differences of bird assemblages or selected groups of bird species between the two survey periods were performed using Statistica 6.0 (StatSoft 2002).

Results

A total of 69 breeding bird species belonging to 35 families were recorded at the 15 census points. The number of species was very similar in both survey periods with 54 species in 2001/2002 and 56 in 2008 (Appendix S1). Very similar species richness is also indicated by the similar progression of the species accumulation curves of each survey period and the total species richness predicted by the Chao 2 estimator (Fig. 2). The performance of both estimator curves indicates that the expected total bird richness of 60 species in 2001/2002 and 67 species in 2008, respectively, represent reliable estimates. According to the Chao 2 estimates, the completeness of species inventories reached 90.51 % for the survey period 2001/2002 and 84.03 % for 2008.

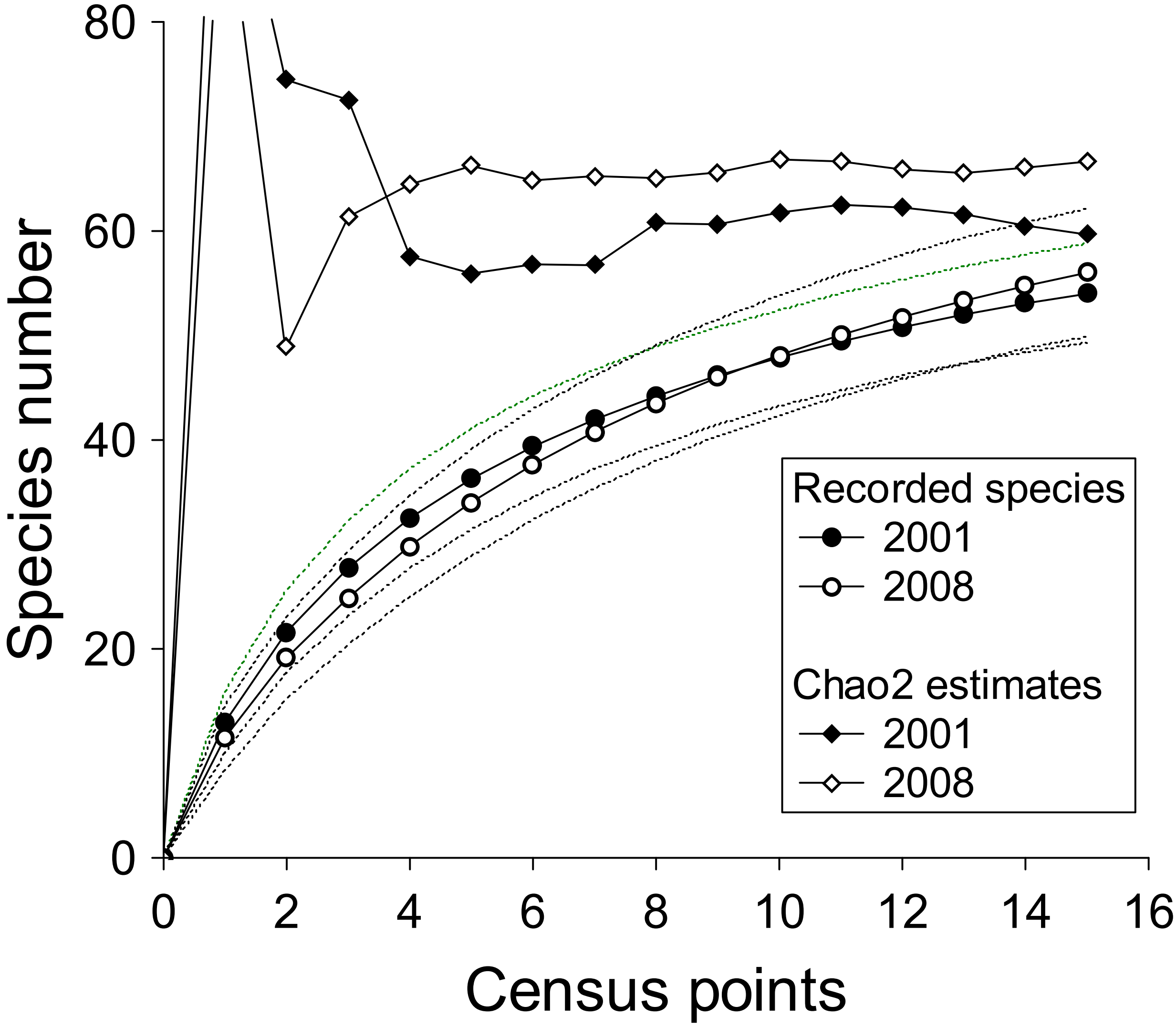

Fig. 2. Species accumulation curves (± 95% confidence intervals) for bird assemblages recorded in 2001/2008 and 2008 as well as the expected total species richness estimated by the Chao2 Mean estimator (Colwell 2006) for both survey periods.

Although similar bird species richness was found in both survey periods, 21.7 % (28 species) of all recorded species were only recorded in one survey period. Chao's Sørensen Raw Abundance-Based Similarity Index, which reached a value of 0.89 for the comparison of species composition between the two survey periods, indicates that a certain proportion of bird species did not occur during both surveys even if bird assemblages had been recorded completely.

The mean Sørensen similarity of pairwise comparisons (n = 105) of species assemblages recorded at all 15 sites was 0.31 in 2001/2002 and 0.36 in 2008. A more pronounced increase of similarity is indicated by Chao's Sørensen Raw Abundance-Based Similarity Index. According to this measure the mean similarity between sites increased from 0.36 in 2001/2002 to 0.55 in 2008.

Depending on their habitat affiliation, bird species responded differentially to land-use changes. When considering only bird species recorded during one of both survey periods, a significant difference was found between species numbers of FO birds and all others (F+O and OL) recorded during individual surveys (Fisher's exact test: p = 0.016). While 8 FO species were only observed in 2001/2002, only 2 FO species were exclusively recorded in 2008. In contradiction, the total number of F+O and OL species, which were recorded only in one survey period, increased from 2001/2002 (5 species) to 2008 (13 species). As a result the total number of recorded FO species declined from 23 in 2001/2002 to 17 in 2008, and total numbers of OL and F+O species increased from 6 to 10 and from 26 to 29 species, respectively.

Also, changes in abundance and occurrence frequency of individual bird species differed depending on their habitat affiliation. While no significant overall change in abundance was found for the entire bird assemblage (Tab. 3), the group of FO birds proved to be negatively affected by habitat changes. The majority showed a decline in total abundance (72.0 % of all FO species) and occurred at a smaller number of plots (56.0 % of all FO species) than six years previously (Tab. 2). This overall decline of FO species was significant, irrespectively of which measure was used (abundance or occurrence frequency) (Tab. 3). In contrast, the abundance (but not the occurrence frequency) of OL species increased significantly (Tab. 3). In total, 81.8 % of the OL species were more abundant in 2008 and 63.6% were recorded at more census points during the second survey period (Tab. 2). No clear response was found for F+O species (Tab. 3). A similar number of species increased and declined from 2001/2002 to 2008 (Tab. 2).

Tab. 2. Response of species with different habitat affiliation (FO, OL and F+O), vertical stratification (understorey and canopy; only forest birds considered) and range size (endemic and widespread) to land-use changes, measured as change of (1) total number of individuals counted at all sites (value for individual sites: maximum number of individuals counted during single census) and (2) total number of plots at which the respective species was recorded. The number of bird species which increased (+), decreased (−) or did not show a change (=) between 2001/2002 and 2008 are provided for all defined groups of species. Values in brackets represent the proportion of the total species number within the respective group.

Group of species	**Response**	**Species number (% of respective group)**	
		Response measurement	
		Individuals	**Plots**
Habitat affiliation			
FO (n = 25)	+	4 (16.00)	3 (12.00)
	=	3 (12.00)	8 (32.00)
	−	18 (72.00)	14 (56.00)
OL (n = 11)	+	9 (81.82)	7 (63.64)
	=	0 (0.00)	3 (27.27)
	−	2 (18.18)	1 (9.09)
F+O (n = 33)	+	13 (39.39)	16 (48.48)
	=	1 (3.03)	1 (3.03)
	−	19 (57.58)	16 (48.48)
Vertical stratification			
Understorey (n = 9)	+	1 (11.11)	1 (11.11)
	=	2 (22.22)	2 (22.22)
	−	6 (66.67)	6 (66.67)
Canopy (n = 16)	+	3 (18.75)	2 (12.50)
	=	4 (25.00)	6 (37.50)
	−	9 (56.25)	8 (50.00)
Range size			
Endemic (n = 31)	+	7 (22.58)	7 (22.58)
	=	2 (6.45)	7 (22.58)
	−	22 (70.97)	17 (54.84)
Widespread (n = 38)	+	19 (50.00)	19 (50.00)
	=	2 (5.26)	5 (13.16)
	−	17 (44.74)	14 (36.84)

Although the majority of forest canopy species declined (Tab. 2), the response was not significant (Tab. 3). The decline of understorey species was more pronounced. Two thirds of the species showed lower abundances and occurrence frequencies in 2008 (Tab. 2). The decrease of understorey bird abundances proved to be significant (Tab. 3).

A comparison of endemic and widespread species indicated a weak opposite response to habitat changes. While the number of endemic species declined from 27 species in 2001/2002 to 23 in 2008, widespread species increased from 27 to 33 species. The negative response of endemic species to habitat changes at the forest margin zone is confirmed by the comparison of their abundances and occurrence frequencies between both survey periods. The abundance of most endemics (71.0 % of all endemic species) decreased and more than half (54.8 %) of the endemic species were recorded at a smaller number of census points in 2008 (Tab. 2). Although both measures, abundance and occurrence frequency, indicated a decline of endemics, only the first, however, proved to be significant (Tab. 3). For widespread species our data did not indicate a significant change of abundance or occurrence frequency from 2001/2002 to 2008 (Tab. 3).

Tab. 3. Results (*p* values) of paired Wilcoxon tests for changes in abundance (number of individuals) and occurrence frequency (number of plots) of all bird species, bird species with different habitat affiliation (FO – forest, F+O – forest and openland, OL – openland), different vertical stratification (only FO understorey and canopy species included) and different range size between the years 2001/2002 and 2008. *p* values printed in bold indicate statistical significance. N = number of species.

	N	**Individuals**	**Plots**
All species	69	0.170	0.296
Habitat affiliation			
FO	25	**0.004**	**0.020**
F+O	33	0.454	0.416
OL	11	0.120	**0.036**
Preferred forest stratum			
Understorey	9	**0.043**	0.063
Canopy	16	0.114	0.065

Range size			
Widespread	38	0.962	0.986
Endemic	31	**0.020**	0.076

Although effects of habitat changes on birds with different habitat affiliations and range sizes were analyzed separately, the conclusions which can be drawn from these results are partly redundant because both classifications are not completely independent from each other. While the majority (68.0 %) of FO species is represented by endemic birds, the groups of OL and F+O species are dominated by widespread species representing 100.0 % and 63.6 % of the species, respectively. Hence, it is not surprising that a comparison of species´ relative abundances in both survey periods shows that the majority of species with decreasing relative abundances belong to the group of endemic forest birds (Fig. 3). Relative changes in abundance were calculated for the 41 most abundant species (n > 7 observed individuals per species) as the differences of their relative abundances (= proportion of total number of counted birds in the respective survey period) between both years (2001/2002: total of 978 individuals, 2008: total of 1,058 individuals). While none of the species with the highest increases of relative abundance was a FO species (Fig. 3a), there is one remarkable exception for endemic species (Fig. 3b). The highest increase of its relative abundance was found for an endemic bird, *Dicaeum celebicum* (Fig. 3b: bar on top).

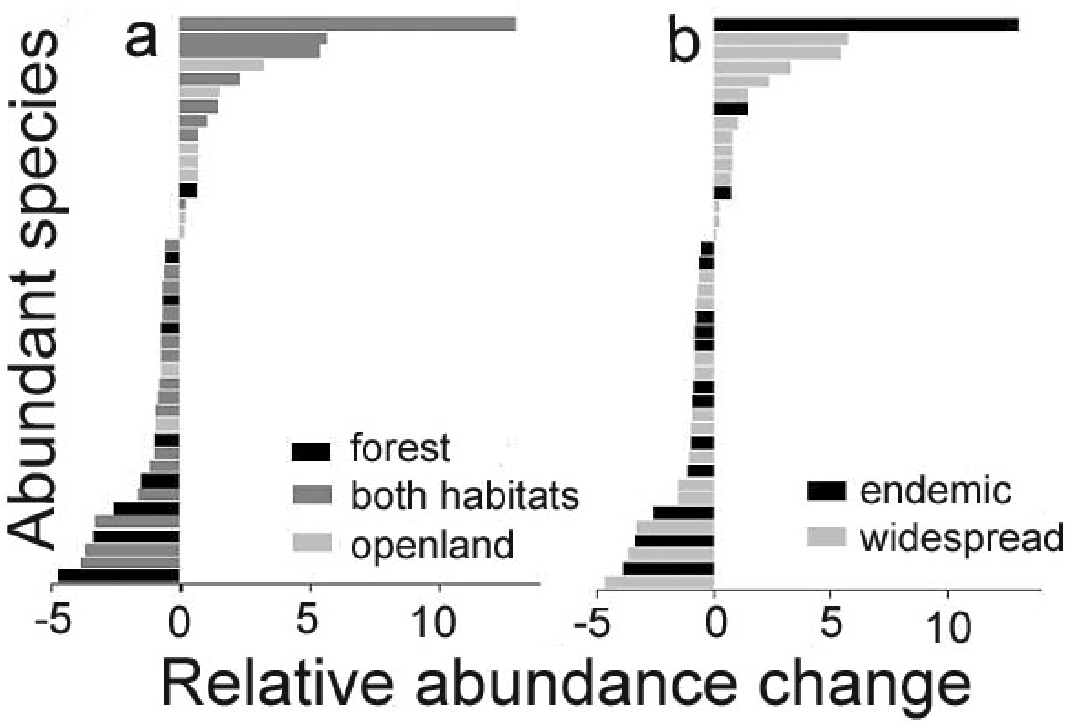

Fig. 3. Changes in relative abundance of abundant species (N > 7 individuals) between 2001/2002 and 2008; graphs indicate habitat affiliation (a) and range size (b), respectively. Habitat affiliations: forest, openland and both habitats. Birds are ranked from species with the highest increase (top) towards the highest decrease (bottom) of their relative abundance from 2001/2002 to 2008.

Discussion

The rapid loss and degradation of tropical forests means that an understanding of the general patterns of species' responses to habitat disturbance is urgently needed (Hill & Hamer 2004) and it has to be shown whether species occurring in modified forests and land-use systems can maintain viable populations (Waltert et al. 2004). So far the loss of biodiversity caused by forest conversion has mostly been studied by comparing different habitat types ranging from primary forest to disturbed forest types (e.g. secondary forests of different age, forest with different timber exploitation practices) and land-use systems (e.g. agroforests, plantations, annual cultures) (Lawton et al. 1998; Schulze et al. 2004). Here, we focused on the effects of forest disturbance and land-use changes on the regional bird assemblage on a landscape scale.

At our study sites at the margin of the Lore Lindu National Park (LLNP), the obvious habitat modification and conversion caused by land-use intensification and small-scale forest clearance did not result in a significant overall change of bird species richness over the time period of six years. However, the conclusion that a more or less constant overall species richness of the forest margin bird assemblage indicates a high tolerance against human disturbance would be a fallacy. In fact, bird assemblages of the forest margin zone suffered a dramatic species turnover and species groups with different conservation value were affected differentially. Birds with more specific ecological requirements, such as forest birds and understorey birds, responded negatively to habitat modification. Traits of forest species sensitive to deforestation and land use, such as specialized foraging strategies (Lindell & Smith 2003), have been identified in several previous studies (Waltert et al. 2005). The loss of this part of the avifauna, which proved to respond very sensitively to habitat changes, was “compensated” by an increase of widespread open land species, which obviously profited from habitat changes within the forest margin zone. The contrasting responses of these bird groups resulted in similar species richness, but the observed species turnover of the forest margin avifauna most likely contributes significantly to an overall homogenization of the regional avifauna. Such biotic homogenization as result of habitat conversion and modification is a global phenomenon (Mc Kinney et al. 2006; Olden et al. 2006; Olden 2006; Crooks et al. 2004; Clough et al. in press). The winners, such as in our study, often are widespread open land species, the losers are endemic forest birds. Only few range-restricted species are able to profit from increased forest disturbance such as the Sulawesi endemic *Dicaeum celebicum* which prefers disturbed secondary habitats (Coates et al. 1997; own unpublished data).

Ongoing anthropogenic disturbance and habitat modification in our study area obviously represent a major threat to many species with a high conservation status, thereby confirming studies from other regions (Brooks et al. 1997; Lambert et al. 2002; Sodhi 2002; Schulze et al. 2004; Waltert et al. 2004; Sodhi et al. 2005; Aratrakorn et al. 2006; Peh et al. 2006). The overall decline of forest birds and endemic species may not only be caused by forest degradation, but could be additionally related to a decreasing habitat quality of certain land-use systems formerly representing an important secondary habitat for a substantial fraction of these species. Another study from Central Sulawesi reported that cacao plantations, if managed to maintain a high and diverse cover of forest trees, can harbor up to 60% of forest specialists and endemic bird species (Abrahamczyk et al. 2008). Particularly, remnant large trees can provide important breeding niches and food resources for many birds (Sodhi et al. 2005; Van Bael et al. 2007; Abrahamczyk et al. 2008). In our study area the management of most cocoa agroforestry systems was significantly intensified during the last six years. Consequently, many shade trees were removed, thereby decreasing the structural habitat complexity and the availability of suitable feeding and nesting sites for forest birds. Furthermore, remaining disturbed forest at the margin of LLNP may have lost its former importance as source area responsible for the occurrence of forest species in adjacent land-use systems, which itself may not have been able to maintain stable populations of such species (Schulze et al. 2004; Waltert et al. 2004). This combination of factors will finally result in a decrease of population densities and an increased local extinction risk of forest birds.

One of the most important conclusions which can be drawn from our study is that, negative effects would not have been detectable without taking into account species identities. The fact that species richness only weakly differed between the two survey periods could have led to the wrong assumption of a low negative impact of recent land-use changes on the forest margin avifauna. Species richness certainly does not always decrease steadily with increasing habitat modification (e.g. Beck et al. 2002). In general, responses of species to continually changing ecosystems and related changes of interactions with other species are often complex, nonlinear, and difficult to predict on the basis of ecological theory or short-term empirical studies (Brown et al. 2001). As documented in our study, distribution and habitat affiliation can act as reliable indicators, revealing the impact of disturbance and helping to understand temporal patterns of biodiversity within dynamic landscape matrices such as the forest margin of LLNP.

The persistence of the Southeast Asia’s highly endemic forest avifauna in degraded habitats depends on extrinsic factors such as disturbance history, quality and quantity of remaining forest (Hughes et al. 2002), food supply (Sodhi 2002) and intrinsic factors such preferred microhabitats, dispersal abilities, and feeding and nesting habits (Sekercioglu et al. 2002). However, the spectrum of unknown factors influencing the occurrence of individual bird species certainly remains large and poses a challenge to future research. The identification of threats to biodiversity and endangered species is necessary for providing information on which to base management and conservation decisions (Raven & Wilson 1992; Scott et al. 1993; Pimm et al. 2001; Olson & Dinerstein 2002). Forest loss and fragmentation are recognized as two of the most important drivers of biodiversity loss and can cause local avian extinctions (Ford & Davison 1996; Brooks et al. 1999; Castelletta et al. 2000; Brook et al. 2003; Clough et al. 2008). Given the rapid human population growth and ensuing demands for forest resources, this threat is likely to persist. The results of our study quantifying temporal changes of a bird community at the margin of a protected area are alarming. Protected forest areas provide one of the last glimmers of hope for the survival of forest species. However, the replacement of traditional land-use systems formerly acting as buffer zone habitats at the margin of established reserves and the enormous pressure on the forest margin itself may devalue forest margin habitats thereby negatively affecting the status of entire conservation areas. In the short term, the implementation of measures preventing further illegal logging activities and slowing down the rapid degradation of forest margin habitats have to be of high priority to halt the ongoing decline of biodiversity.

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Appendix S1

List of bird species recorded in 2001-2002 and 2008. Understorey birds are indicated by “u”, abundant species (n > 7 individuals) by asterisks (*).

Species	DIS[1]	Habitat[2]	Feeding guild[3]	Year[4]	2001/2002		2008	
					Ind.[5]	Plots[6]	Ind.[5]	Plots[6]
Accipiter trinotatus	E	FO	P	2001	3	3	0	0
Aceros cassidix	E	FO	F	both years	5	3	1	1
Aethopyga siparaja	W	F+O	N	2001	4	2	0	0
*Anthreptes malacensis**	W	F+O	N	both years	11	8	2	2
Aplonis minor	W	FO	O	both years	4	1	2	1
*Aplonis panayensis**	W	F+O	O	2001	8	2	0	0
Ardea purpurea	W	OL	P	2008	0	0	3	3
Basilornis celebensis	E	FO	F	2001	1	1	0	0
Bradypterus castaneus[U]	E	FO	I	both years	1	1	1	1
*Cacomantis sepulcralis**	W	FO	I	both years	9	5	2	2
*Centropus bengalensis**	W	OL	I	both years	2	2	10	5
*Chrysococcyx russatus**	W	F+O	I	2008	0	0	8	3
*Cisticola exilis**	W	OL	I	2008	0	0	8	2
Collacalia esculenta	W	F+O	I	both years	1	1	3	2
Corvus enca	W	F+O	O	2008	0	0	4	3
*Coracina morio**	E	FO	I	both years	6	2	14	4
Coracina temminckii	E	FO	I	both years	1	1	2	1
Corvus typicus	E	FO	O	both years	4	2	2	2
Coracias temminckii	E	F+O	I	2001	1	1	0	0
*Culicicapa helianthea**	W	F+O	I	both years	24	5	19	6
*Cyornis rufigastra**[U]	W	FO	I	both years	22	6	8	4
*Dendrocopos temminckii**	E	F+O	I	both years	11	5	6	2
*Dicaeum aureolimbatum**	E	F+O	O	both years	29	7	23	8
*Dicaeum celebicum**	E	F+O	O	both years	109	15	256	15
*Dicrurus hottentotus**	W	F+O	I	both years	3	2	6	3
Dicrurus montanus	E	FO	I	2001	5	2	0	0
Dicaeum nehrkorni	E	FO	O	2008	0	0	7	3
*Ducula forsteni**	E	FO	F	both years	18	4	9	4

Appendix S1 (continued)

Species	DIS[1]	Habitat[2]	Feeding guild[3]	Year[4]	2001/2002		2008	
					Ind.[5]	Plots[6]	Ind.[5]	Plots[6]
*Enodes erythrophris**	E	FO	O	2001	33	2	0	0
Eudynamys melanorynchа	E	FO	I	2001	3	2	0	0
*Eumyias panayensis**	W	FO	I	both years	51	8	6	2
Falco molluccensis	W	F+O	P	2001	1	1	0	0
Ficedula hyperythra[U]	W	FO	I	both years	1	1	1	1
Ficedula rufigula[U]	E	FO	I	2008	0	0	1	1
*Gallirallus torquatus**	W	OL	O	both years	7	3	9	3
Gerygone sulphurea	W	F+O	I	both years	2	1	2	2
*Halcyon chloris**	W	OL	I	both years	11	5	28	8
Hemiprocne longipennis	W	F+O	I	2008	0	0	1	1
*Hypothymis azurea**	W	F+O	I	both years	24	6	15	5
*Lalage leucopygialis**	E	F+O	O	both years	10	4	1	1
*Lonchura malacca**	W	OL	G	2008	0	0	35	5
*Lonchura molucca**	W	OL	G	both years	15	1	6	1
Lonchura punctulata	W	OL	G	2008	0	0	3	1
Lophozosterops squamiceps[U]	E	FO	I	2001	1	1	0	0
Loriculus exilis	E	FO	N	both years	1	1	1	1
*Loriculus stigmatus**	E	F+O	N	both years	22	5	12	1
*Macropygia amboinensis**	W	F+O	F	both years	38	7	2	2
Meropogon forsteni	E	F+O	I	2008	0	0	2	1
*Merops philippinus**	W	OL	I	2008	0	0	8	2
*Mulleripicus fulvus**	E	F+O	I	both years	9	2	1	1
Muscicapa dauurica	M	F+O	I	2008	0	0	1	1
*Muscicapa griseisticta**	M	F+O	I	2008	0	0	11	1
Myza celebensis[U]	E	FO	N	2001	1	1	0	0
*Nectarinia aspasia**	W	F+O	N	both years	8	7	2	1
*Nectarinia jugularis**	W	OL	N	both years	3	3	6	3
*Oriolus chinensis**	W	F+O	O	both years	22	6	7	3

Appendix S1 (continued)

Species	DIS[1]	Habitat[2]	Feeding guild[3]	Year[4]	2001/2002		2008	
					Ind.[5]	Plots[6]	Ind.[5]	Plots[6]
*Pachycephala sulfuriventer**	E	FO	I	both years	39	6	15	3
Phaenicophaeus calyorhynchus	E	F+O	I	both years	5	2	2	1
Pitta erythrogaster	W	FO	I	2001	3	1	0	0
*Ptilinopus melanospila**	W	F+O	F	both years	36	6	4	2
*Rhipidura teysmanni**	E	FO	I	both years	14	3	9	2
*Scissirostrum dubium**	E	F+O	F	both years	85	2	84	5
*Streptopelia chinensis**	W	OL	F	2001	8	2	0	0
*Treron griseicauda**	W	F+O	F	2008	0	0	61	1
*Trichastoma celebense**	E	F+O	I	both years	58	7	22	6
*Trichoglossus flavoviridis**	E	FO	N	both years	13	2	6	2
*Trichoglossus ornatus**	E	F+O	N	2008	0	0	16	2
*Zosterops atrifrons**	W	F+O	I	both years	131	8	167	9
*Zosterops chloris**	W	F+O	I	both years	89	7	154	14

[1] Distribution: Species are defined as (E) endemic to Wallacea subregion, (W) widespread and accordingly non-endemic and (M) migrants (Coates et al. 1997).
[2] Species were assigned to their habitat affiliation as defined by Coates et al. (1997): Forest species (FO), openland species (OL) and those species which use both habitat types combined (F+O).
[3] According to the descriptions in Coates et al. (1997) the following feeding guilds were defined: frugivorous species (F), nectarivorous species (N), omnivorous species (O), granivorous species (G) and predators.
[4] Years in which respective species were recorded.
[5] Total number of individuals which could be detected in 2001/2002 and 2008, respectively,
[6] Number of census sites at which each species occurred in 2001/2002 and 2008, respectively.

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Sprachkenntnisse	Deutsch	– Muttersprache
	Englisch	– sehr gute Kenntnisse (mündlich wie schriftlich)
	Indonesisch	– gute Kenntnisse (mündlich wie schriftlich)
	Spanisch	– fortgeschrittene Sprachkurskenntnisse