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Effects of habitat type, vegetation structure, and proximity to forests on bird species richness in a forest–agricultural landscape of West Java, Indonesia

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Abstract To halt biodiversity loss in the humid tropics of developing countries, it is crucial to understand the roles and effects of human-modified landscapes with fragmented forest remnants in maintaining biodiversity while fulfilling the demands of local communities and reducing poverty. To implement appropriate landscape planning for conserving biodiversity and ecosystem functioning, appropriate information is required about parameters of habitat suitability among various anthropogenic habitats with a range of distances to forests and vegetation

characteristics, but such information is limited. We examined differences in avian communities between a remnant forest and four types of man-made forest (two mature plantations and two agroforests) in a forest–agricultural landscape of West Java, and we analyzed the effects of both local and landscape factors on various types of species richness in this landscape. The results from non-metric multidimensional scaling revealed avifauna in the two types of agroforest was clustered separately from that in the remnant forest, mainly because drastic declines in the abundance of forest specialists (including IUCN red-listed species) and their replacement with open-habitat generalists. The mixed-tree agroforests were colonized by 30 % of forest specialists and forest-edge species found in the remnant forest, and maintained the highest richness of species endemic to Indonesia among man-made forests, implying that some forest specialists and endemics might have adapted to ancient landscape heterogeneity. High proportion of insectivorous birds was found in the remnant forest (more than 50 %) and drastically decline in man-made forests, although the species richness of insectivores did not decline significantly in broad-leaved plantations. We concluded that protection of remnant forests should be prioritized to conserve forest bird diversity. However, as different environmental factors affected the richness values of different ecological groups, appropriate landscape design and habitat management could improve functional diversity in forest–agricultural landscapes in the tropics.

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Introduction

An urgent goal of the Convention on Biological Diversity (CBD)—to halt global biodiversity decline by 2010—has reportedly failed, particularly in Asian humid tropical regions (Secretariat of CBD 2010). Biodiversity loss in this region is caused mainly by the conversion of primary forests (Sodhi et al. 2004), which is still occurring at high rates (FAO 2010). Although the area of forests designated for biodiversity conservation has increased (FAO 2010), the coverage is still <10 % of the entire area of tropical forest worldwide, as well as in the South Asian subcontinent and Southeast Asia (Schmitt et al. 2009). In addition, most protected areas in tropical regions are embedded within a matrix of human-modified landscapes; this makes biodiversity in such regions likely to be influenced by surrounding human activities (Chazdon et al. 2009). Much attention has therefore been paid recently to understanding the roles and effects of human-modified landscapes surrounding tropical forests in the conservation of forest biodiversity within and beyond protected areas (Chazdon et al. 2009; Gardner et al. 2009).

Conservation of forest biodiversity in human-modified landscapes is crucial in humid tropics. Especially on the island of Java, Indonesia, here the opportunity to add forest protection areas has been exhausted and the current protection areas or national parks are highly fragmented. Agroforests in human-modified landscapes play an important role to conserve biodiversity (Jose 2012; Bardhan et al. 2012). Java, which is part of the Sundaland biogeographic region, is a biodiversity hotspot (Myers et al. 2000). Its flora and fauna are characterized by a high degree of endemism (Sodhi et al. 2004). The bird fauna of Java is unique. Although the island is lowest in bird species richness compared with other Sundaland islands such as Borneo and Sumatra (likely because of its limited forest area), there are 30 bird species found only in Java, but not in Borneo or Sumatra (MacKinnon et al. 2010). Conservation concern has been focused on the latter two areas because of their high rates of

deforestation and rapid loss of forest biodiversity, and there is less information about the state of biodiversity—particularly among birds—in the highly fragmented tropical forests of Java and their adjacent human-modified habitats, which have a relatively long history of human disturbance (FWI and GFW 2002). According to Balmford et al. (2001), rural areas with high human population densities still have high levels of biodiversity, especially endemic species. This makes conflicts between conservation and developments are not easily avoided. In addition, the population density of rural poor living in or near protected forest areas is high in Java (FWI and GFW 2002). Therefore, it is crucial to understand what sorts of human-modified landscapes with fragmented forest remnants can maintain biodiversity while fulfilling the demands of local communities and reducing poverty.

Many studies have examined the roles and effects of human-modified tropical landscapes in the conservation of forest biodiversity. In many cases, avian communities are used as indicators because they are taxonomically well identified, easy to observe, sensitive to changes in habitat quality, and among the key players in ecosystem functioning by acting as pollinators, predators, seed dispersers, scavengers, and ecosystem engineers (Sekercioglu 2006; Tscharntke et al. 2008). Previous studies have revealed that high levels of biodiversity, including among forest species, are maintained in human-modified habitats such as plantations (Beukema et al. 2007; Sheldon et al. 2010) and shaded cacao and coffee agroforests (Harvey et al. 2006; Jose 2012), although these habitats often have different species assemblages than those of the original forests (Naidoo 2004; Walther et al. 2005; Harvey and Gonzalez Villalobos 2007). Among man-made forests, tropical agroforests that have vegetation structures similar to those of the original forests have been highlighted as alternative forest habitats since the 1990s. Agroforests can support high levels of forest bird diversity if they are close to remnant forests (Naidoo 2004; Beukema et al. 2007), but less so if there is an absence of forests nearby (Thiollay 1995; Greenberg et al. 2000). Apart from anthropogenic habitat type and proximity to natural forests, vegetation structure is also considered to be an important environmental factor determining bird diversity and composition (Sekercioglu 2002; Walther 2002). In agroforestry systems, shaded cacao and coffee agroforests representing a complexity of vertical

vegetation structures have species richness and compositions that are strikingly similar to those of the adjacent forests (Schroth et al. 2004). Sheldon et al. (2010) revealed that mature plantations—even those containing exotic timber species—maintain half of their primary forest species because of their greater structural complexity. Therefore, habitat types, variations in vegetation structure within and among habitat types, and proximity to forests may interact to determine bird species composition and diversity in human-modified landscapes. Although some studies have quantified the combined effects of habitat-type differences and vegetation structure (Waltert et al. 2004; Sekercioglu 2006; Harvey and Gonzalez Villalobos 2007) and of proximity to forests and vegetation structure (Clough et al. 2009), to our knowledge there have been no comparisons of different kinds of anthropogenic habitat simultaneously with vegetation structure and proximity to forests in a gradient from forest to agricultural landscapes. This sort of integrated information would help to implement landscape planning for forest biodiversity conservation while producing foods and fiber (Schroth et al. 2004). The responses of bird species and functional groups to human disturbance could also be variable (Martin et al. 2012). It is therefore worth further investigating to what extent different groups of bird species or different functional groups respond differently to local and landscape factors in environments.

We attempted to assess the influences of all three environmental factors (habitat type, vegetation structure, and proximity to forests) simultaneously on total bird species richness and the species richness of various ecological groups by comparison with these factors in the adjacent forest remnant. By using the case of a human-modified landscape with a highly fragmented forest remnant in West Java, Indonesia, we set detailed objectives (1) to investigate general patterns of bird species composition and diversity in a fragmented forest remnant and its surroundings, consisting of various types of man-made forests such as plantations and agroforests; and (2) to determine whether habitat type, vegetation structure, and proximity to forests affect the species richness of the total bird species, endemic species, habitat specialization types, and functional groups. We expected that by combining these three determinant factors we could obtain a better understanding of the ability of anthropogenic habitats to maintain species and functional

diversity. We also hoped to elucidate environmental conditions in terms of habitat characteristics and proximity to forests in order to suggest appropriate landscape designs and habitat management strategies in forest–agricultural landscapes.

Materials and methods

Study site

The study was conducted in a forest–agricultural landscape in West Java, Indonesia (lat 06°45′28′ to 06°47′53″S, long 107°04′18″ to 107°07′39″E). The site is located at an elevation of 600–1,300 m above sea level on Neogene hills. The mean daily temperature is about 22 °C and the daily maximum temperature ranges from 25 to 30 °C. The annual precipitation is approximately 2,000 mm, with a rainy season (October–June) and short dry season (July–September).

The remnant forest was located mainly on hilltops and covered an area of about 280 ha. It was not protected, but was conserved under the management of the Regional State-owned Forest Enterprise (*Perum Perhutani*) of Cianjur. The forest vegetation was typical Javanese lowland and montane forest dominated by *Schima wallichii*, *Dysoxylum* sp., and *Sterculia coccinea*, to a height of over 30 m (Table 1). The dominant species in the mid- and understory were mainly *Calliandra calothyrsus*, an exotic species planted as a buffer to protect the forest and provide fuelwood for local residents, and *Oreocnide rubescens*, a species representative of secondary forests. This indicated that the forest had been influenced by human activities such as selective logging and exotic species invasion from the forest edge. Nevertheless, the forest still seemed to function as a native forest habitat, as indicated by the presence of many primates, such as the silvery gibbon (*Hylobates moloch*), Javan surili (*Presbytis comata*), and Javan lutung (*Trachypitecus auratus*), and other large mammals such as the Javan leopard, leopard cat, Java mouse-deer, and black giant squirrel, all of which were found during our field observations in the forest; most of these are listed as critically endangered or near-threatened species (IUCN 2012) and are protected by Indonesian government regulation No. 7/1999. Therefore, we considered the forest as a quasi-natural remnant forest.

Table 1 Vegetation characteristics based on means (\pm standard deviations) per sampling plot for bird observation in each habitat type (F remnant forest, BP broad-leaved plantation, NP

needle-leaved plantation, MT mixed-tree agroforest, BT bamboo-dominated agroforest)

Variable	Habitat type				
	F (n = 22)	BP (n = 13)	NP (n = 11)	MT (n = 13)	BT (n = 13)
% vegetation cover					
Understory (<4.5 m high)	28.0 \pm 9.0	41.9 \pm 8.1	40.0 \pm 8.1	32.7 \pm 7.0	32.7 \pm 6.0
Midstory (4.5–15 m high)	32.9 \pm 6.5	29.6 \pm 9.5	29.1 \pm 10.4	47.3 \pm 10.3	60.4 \pm 9.9
Canopy (15–30 m high)	59.3 \pm 7.6	48.9 \pm 8.9	47.7 \pm 9.8	22.3 \pm 15.8	3.9 \pm 6.8
Emergent (>30 m high)	4.6 \pm 8.4	–	–	–	–
Tallest tree height (m)	29.2 \pm 2.5	26.8 \pm 1.8	26.8 \pm 1.8	22.9 \pm 4.1	16.9 \pm 2.3

Outside the remnant forest there were four types of man-made forest. Two types were mature plantations (mostly more than 15 years old) managed by the Regional State-owned Forest Enterprise of Cianjur. One type was a broad-leaved plantation dominated by *Altingia excelsa* and *Maesopsis eminii* and the native tree *S. wallichii* for timber production. The other type was a needle-leaved plantation dominated mainly by pine (*Pinus merkusii*) for timber use, but also for turpentine collection. However, broad-leaved tree species were sometimes planted in this type of plantation. Because the two plantations were mature and managed extensively, the mid- and understory vegetation was well developed (Table 1), but similar to the case of the remnant forest they were dominated by *C. calothyrsus*, with other secondary-grown trees such as *Macaranga rhizinoides*.

The other two types of man-made forest were agroforests, which are common agroforestry systems in West Java, Indonesia, and are locally called *talun* or *kebon tatangkalan* (Parikesit et al. 2005). In general, Javan agroforests consist of trees that produce fruits, vegetable crops, industrial crops such as coffee and cloves, timber, and bamboos used for various purposes, including as construction materials, fuel, and support for climbing crops (Okubo et al. 2010). In accordance with the definition of Okubo et al. (2010), the agroforests in our study area were classified into bamboo-dominated and mixed-tree agroforests on the basis of plant species composition. The bamboo-dominated agroforests were dominated by mostly bamboos (*Gigantochloa apus* and *Gigantochloa verticillata*) and some timber and fruit trees (*M. eminii* and *Artocarpus heterophylla*), whereas the mixed-tree agroforests were dominated by fruit trees

(*Parkia speciosa*, *Durio zibethinus*, *Nephelium lappaceum*, *Persea americana*), fast-growing timber trees (*Paraserianthes falcataria* and *M. eminii*), and industrial crops such as cloves and coffee. The vegetation structure of the bamboo-dominated agroforests was relatively simple, and the vegetation height was the lowest among all the habitat types (Table 1).

Bird survey

Bird surveys were performed from 10 October 2011 to 28 March 2012 in accordance with a standardized observation method using point counts proposed by Bibby et al. (2000). We defined 72 sampling plots of point counts arbitrarily from a map derived from an orthorectified QuickBird satellite image (0.6 m resolution in pan-sharpen image) taken on 9 September 2011, and we aimed to sample all habitat types in proportion to their actual occurrences in the forest–agricultural landscape. The sampling plots were at least 200 m apart from each other. Admittedly, a distance of 200 m to the nearest sampling plot may not have always been sufficient to ensure data independence. We therefore recorded only birds within a radius of 50 m of the center of each sampling plot, and we ensured that we did not double-count birds that were identifiable as moving between two plots. We surveyed a total of 22 plots in the remnant forests (hereafter referred to as F), 13 in the broad-leaved plantations (BP), 11 in the needle-leaved plantations (NP), 13 in the mixed-tree agroforests (MT), and 13 in the bamboo-dominated agroforests (BT).

All bird surveys were conducted from 06:00 to 09:30 h, but only when the weather was fine (e.g. no precipitation or strong wind). All bird samplings were

conducted by the same two experienced bird experts and the first author (D. Muhamad) with the help of local villagers. For each plot, all visual and acoustic detections within a period of 20 min were recorded. A digital rangefinder was used to measure and estimate distance, and all observations beyond 50-m radius were discarded in the analysis of each site. To avoid hour-counting bias in the sampling (Leyequién et al. 2009), we alternated the order of the point counts at every visit, with a total of six visits to every plot. The observers did not count birds that were flying over or through the count areas. The bird nomenclature followed that of MacKinnon et al. (2010) and Sukmantoro et al. (2007).

Environmental data

We measured vegetation cover and structure within circles of the same radius as the bird-sampling plots (50 m). Within these areas, we visually estimated the overhead percentage foliage covers of emergent layers (>30 m high), canopy (30–15 m), midstory (4.5–15 m), and understory (<4.5 m) by following the methods in Daubenmire (1959) and Simons et al. (2006). At the sampling points we visually estimated foliage cover by making an imaginary circle divided into quadrants representing the four cardinal directions (i.e. north, south, east, and west); the readings from each quadrant were averaged for each sampling plot. We also measured the height of the tallest tree in each plot, and we inventoried the dominant species in each point count.

We used the QuickBird map mentioned above to measure the proximity to the nearest forest margin as the distance from the edge of each sampling plot to the nearest remnant forest margin. In the case of sampling plots in the remnant forest, we measured the distances to the nearest forest margin as negative values to account for any edge effect. The range of proximities to the nearest forest margin was −1.0 to −0.1 km for the sampling plots in F, 0.1–2.0 km for BP, 0.2–1.8 km for NP, 0.2–2.9 km for MT, and 0.4–1.6 km for BT.

Ecological groups of bird species

We classified the observed bird species into several ecological groups on the basis of biogeographical distribution, habitat specialization, and primary diet

(feeding guild). To assign the bird species to these ecological groups, we extracted the information from a bird field guidebook by MacKinnon et al. (2010) and a list of birds in Indonesia by Sukmantoro et al. (2007). For biogeographical distribution, we extracted data on the species endemic to Indonesia in order to assess the conservation value of quasi-natural (the remnant forest) and man-made forests. For habitat specialization, we classified all species into forest specialists (primarily preferring forest interiors), forest-edge species (preferring forest edges, gaps, or woodlands), forest generalists (preferring forests, forest edges, and woodlands, and often visiting cultivated areas), and open-habitat generalists (primarily preferring open areas, grasslands, shrubs, cultivated areas, or settled areas). For feeding guilds, we classified all species into carnivores, frugivores, granivores, nectarivores, insectivores, or omnivores. Because the number of insectivorous bird species was much higher than that of other feeding guilds and included many different functional groups (as determined by behavior when foraging), we further classified insectivores into subgroups, namely bark-gleaning, canopy-foliage-gleaning, understory-foliage-gleaning, ground-gleaning, and sallying insectivores.

Data analysis

For each sampling plot, we merged the data from six observation times by summing the abundance of each species. We calculated the abundance and species richness of all observed birds, species endemic to Indonesia, each habitat specialization group, and each feeding guild, as well as of each subgroup of insectivores. We also calculated Simpson's diversity index for all species in each plot (Hurlbert 1971), as follows:

$$\text{Simpson's diversity index} = 1 - \sum_{i=1}^N P_i^2$$

where P_i is the relative individual density (the proportion of the total number of individuals accounted for by a species) for species i in a sampling plot, for a total of N species.

To determine the general status of bird diversity, we first compared the species richness and Simpson's diversity index of the total number of species and the species richness values of ecological groups among all habitat types by using the Kruskal–Wallis test

followed by a Wilcoxon pairwise test. Because there were limitations on the sampling, some species were not observed. We thus estimated the true species richness for the whole study site and for each habitat type by using three different non-parametric species estimators, namely first- and second-order jackknifes and a bootstrap (Palmer 1990).

Second, we performed a non-metric multidimensional scaling (NMDS) by using a table of species and sampling plots with the abundances in each in order to investigate the general patterns of bird species composition in the remnant forest and its surrounding four man-made forests. The NMDS is considered to be the most effective ordination method for ecological community data, whereby sample units are positioned according to the association among species and are not constrained by previously selected environmental variables (McCune and Grace 2002). We used random starting configurations and the Sørensen (Bray–Curtis) dissimilarity index as a distance measure.

To quantify the simultaneous effects of all three determinant factors (habitat type, vegetation cover and structure, and proximity to forest margins) on bird species richness of the total and each ecological group, we chose generalized linear models (GLMs) with a logarithmic link function that followed a Poisson distribution. We set richness values for all species, species endemic to Indonesia, forest specialists, open-habitat generalists, and each of six feeding guild groups as response variables separately. Explanatory variables were habitat type as a nominal variable; proximity to the nearest forest margin (km); percentage vegetation covers in the canopy, midstory, and understory layers; and height of the tallest tree (m).

To incorporate spatial autocorrelations, we applied a trend surface analysis in the GLM. In accordance with the method of Lichstein et al. (2002), we added all nine third-degree polynomial terms of the geographic coordinates (x , y , x^2 , y^2 , xy , x^3 , y^3 , x^2y , and xy^2 , where x and y are longitude and latitude, respectively) of each sampling plot as explanatory variables in the GLM, together with environmental variables. Before the analysis, the geographic coordinates of longitude and latitude for each sampling plot were centered on their respective means to reduce collinearity with higher order terms (Lichstein et al. 2002).

To allow for uncertainty in the choice of the best model, we opted for multi-model inference and model averaging based on the Akaike information criterion

corrected for small sample bias (AICc; Burnham and Anderson 2002). For each analysis, the full model, the null model, and models with all valid combinations of the explanatory variables were generated, and ΔAICc values that showed the difference between the values for the best model (i.e. with the smallest AICc) and those for the remaining models were computed. Model-averaged estimated coefficients (AECs) for the explanatory variables were obtained by computing the means and standard errors of the estimates weighted by the Akaike weight of each plausible model. The Akaike weight is an indicator of the strength of evidence that the selected best model is convincingly the best. The sum of the Akaike weights of models that included a particular parameter was used as the weight of evidence of the relative importance of that variable (IoV). To identify the effect of multicollinearity we also calculated VIF (variance inflation factor) values for each explanatory variable included in the model. If a variable showed a VIF of >10 in a model, the models including the variable were excluded from model averaging.

All the numerical analyses were performed with R software version 2.15.1 (R Development Core Team 2012), with additional function provided by the R package *vegan* for NMDS, and *MuMIn* and *DAAG* for GLM, and multi-model inference and model averaging.

Results

General description of bird community

A total of 1,083 point-count records (single detection of individual birds or groups) was obtained in the 72 plots from observations on six occasions; this figure represented 115 bird species and 2011 individuals from 32 families. Nine additional species, namely three migratory raptors (*Accipiter soloensis* or Chinese sparrowhawk, *Accipiter gularis* or Japanese sparrowhawk, and *Butastur indicus* or grey-faced buzzard), three swifts (*Collocalia linchi* or cave swiftlet, *Rhaphidura leucopygialis* or silver-rumped swift, and *Apus nipalensis* or house swift), and three swallows (*Hirundo rustica* or barn swallow, *Hirundo tahitica* or Pacific swallow, *Hirundo striolata* or striated swallow) were observed only in flight over the survey sites. These species were thus excluded from further analysis. There were 22 species endemic

to Indonesia, including 14 species endemic to Java and the surrounding islands; the latter accounted for 43.8 % of all species endemic to Java and surrounds. Five species were registered on the IUCN Red List: four as near-threatened and one (*Spizaetus bartelsi* or Javan hawk-eagle) as endangered (IUCN 2012). The latter species is a species regional-endemic only to Java and is currently found only in West and East Java.

The most commonly observed bird species were forest generalists (40 species), followed by forest-edge species (39 species), forest specialists (31 species), and open-habitat generalists (five species). In the guild classification, the majority of birds were insectivores (64 species), followed by frugivores (18 species). Carnivores, nectarivores, and omnivores represented less than 8 % of the total number of species observed. Among the five subgroups of insectivores, sallying and understory-foliage-gleaning insectivores were the most common, accounting for 22 and 19 species, respectively, followed by ground-gleaning (11 species), canopy-foliage-gleaning (eight species), and bark-gleaning (four species) insectivores.

When we compared species richness, diversity, and abundance among the five habitat types (Table 2), species richness and Simpson's diversity index based on the mean values for the sampling plots in each habitat type differed significantly between F (highest) and BT (lowest). The values of BP, NP, and MT were intermediate between those for F and BT and did not differ significantly from each other. For total abundance in each sampling plot there were no significant differences among the five habitat types. The results of the species richness estimation based on the first- and second-order jackknife and bootstrap methods revealed that the bird community in the surveyed plots was not yet completely recorded. However, the

whole samples' completeness, as expressed by the mean percentage of the three estimators, seemed acceptable (85.1 %). When calculated for each habitat type, it was lowest in F (70.4 %) followed by the two types of plantation (74.5 %), MT (76.5 %), and BT (77.9 %), indicating that the observed species richness in F was underestimated compared with those of the other habitat types. The mean numbers of species in sampling plots in each habitat type for each feeding guild group and each subgroup of insectivores indicated that the species richness of insectivores declined along a gradient from F to BT, whereas that of granivores increased, particularly in the two agroforests (Fig. 1a). Among the subgroups of insectivores, a large decline in the species richness of understory-foliage gleaners was obvious between F and all the man-made forests (Fig. 1b).

Bird species composition in habitat types

The whole dissimilarity in species composition was summarized into two dimensions by using NMDS analysis (Fig. 2), although the stress value that represented the inverse degree of correspondence against the original distances among sampling plots was still high (0.27). Sample score plots with habitat-type differences in ordination revealed strong grouping of plots by habitat type (Fig. 2a). Plots of F and the two types of agroforest (MT and BT) were distinguishable, as they were clustered separately and were much closer to one another, with almost no overlap. However, plots of the two types of plantation (BP and NP) were scattered among those of F and the agroforests. Some plots of BP were very close to those of F. Examination of the ordination plots of the scores of species in different ecological groups revealed that

Table 2 Species richness, abundance, and Simpson's diversity index based on means (\pm standard deviations) per sampling plot for bird observation in each habitat type (F remnant forest, BP broad-leaved plantation, NP needle-leaved plantation, MT

mixed-tree agroforest, BT bamboo-dominated agroforest), with Kruskal–Wallis comparisons (*H*) followed by Wilcoxon pairwise test

Variable	Habitat type					<i>H</i> value
	F (<i>n</i> = 22)	BP (<i>n</i> = 13)	NP (<i>n</i> = 11)	MT (<i>n</i> = 13)	BT (<i>n</i> = 13)	
Species richness	17.9 \pm 4.9a	15.0 \pm 4.0ab	14.6 \pm 4.2ab	14.2 \pm 4.0ab	11.5 \pm 2.4b	17.36**
Abundance	28.2 \pm 10.2a	35.3 \pm 15.2a	24.3 \pm 7.9a	25.1 \pm 9.7a	26.0 \pm 8.5a	5.55
Simpson's diversity	0.92 \pm 0.03a	0.87 \pm 0.06ab	0.89 \pm 0.05a	0.89 \pm 0.03a	0.81 \pm 0.11b	19.71***

Different letters within the same row indicate significant differences ($P < 0.05$)

** $P < 0.01$, *** $P < 0.001$

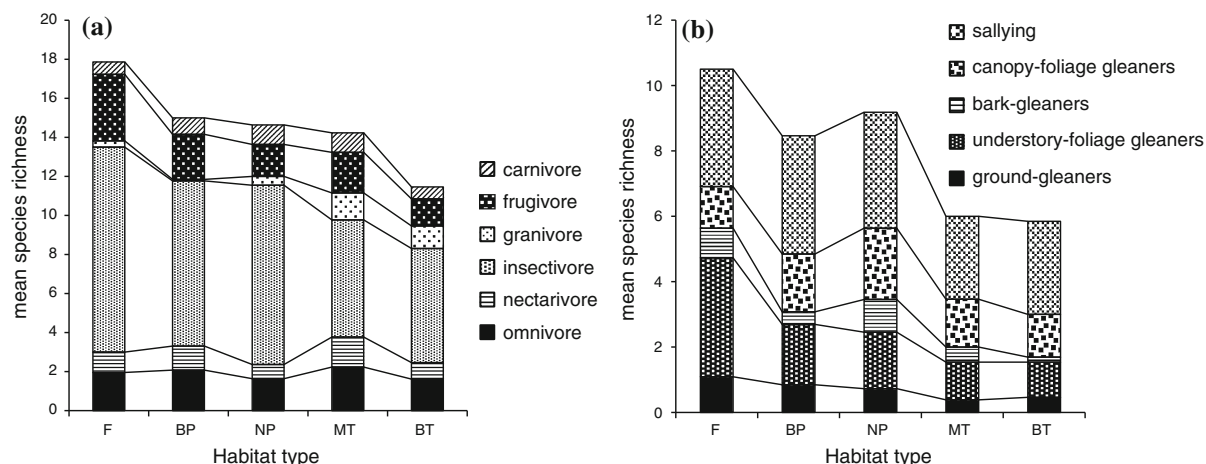


Fig. 1 Functional richness of bird communities, based on the mean number of species per sampling plot in each habitat type (*F* fragmented forest remnant, *BP* broad-leaved plantation, *NP* needle-leaved plantation, *MT* mixed-tree agroforest, *BT*

bamboo-dominated agroforest), using **a** six primary dietary (feeding guild) groups and **b** subgroups of insectivores classified on the basis of foraging activities

the scores of species of each habitat-specialization type represented well the differences in habitat type ordination (Fig. 2b). Forest specialists and forest-edge species were each clustered in negative scores on the first axis; open-area specialists were clustered in positive scores on the first axis, whereas forest generalists were distributed widely. This implies that the first axis can be interpreted as an environmental gradient from forest interior to open habitat.

Differences in factors determining various richness values

The results of a multi-model inference approach using the GLM revealed that environmental factors affected various richness values differently (Tables 3, 4). Among environmental factors, habitat type differences tended to be more important than other factors in explaining many of the richness values in each ecological group, as well as in all species combined.

For total species richness, the nominal variable of habitat type was always chosen in the best models ($\Delta\text{AICc} < 2$) (Table 3). Compared with remnant forest (*F*) as a baseline, all four man-made forests had a significant negative influence on total species richness. *BT* contributed to the decrease more than did the others. The richness of species endemic to Indonesia was also strongly determined by habitat type, but compared with the case of total species richness different habitat types were important: the

richness value was significantly and negatively influenced by *NP*, *BT*, and *BP*, but not by *MT*.

Species richness of forest specialists was not affected by habitat type, but instead by proximity to the nearest forest margin and percentage canopy cover: distance from the forest edge had a negative effect and percentage canopy cover had a positive effect (Table 3). In contrast, the richness of open-habitat generalist species was determined again by habitat type, with a weak positive effect of proximity to the nearest forest margin. Compared with remnant forest, all man-made forests contributed to an increase in richness of open habitat generalists, but the two types of agroforest (*MT* and *BT*) had significantly larger coefficient values than did the plantations (*BP* and *NP*).

For species richness of carnivores, nectarivores, and omnivores, the best model for each feeding guild group was the model that included only a three-dimensional polynomial trend surface. Although some environmental variables were chosen in the subset of competing models in the case of carnivores and nectarivores, the coefficient values were not significant and their relative IoVs were small (Table 4). In the case of other groups of feeding guilds, different environmental factors affected the richness values. For the frugivores, the influential variables were only those of vegetation structure (i.e. percentage canopy cover and tallest tree height), with weak positive effects. For granivores, only habitat type influenced species richness: the two types of

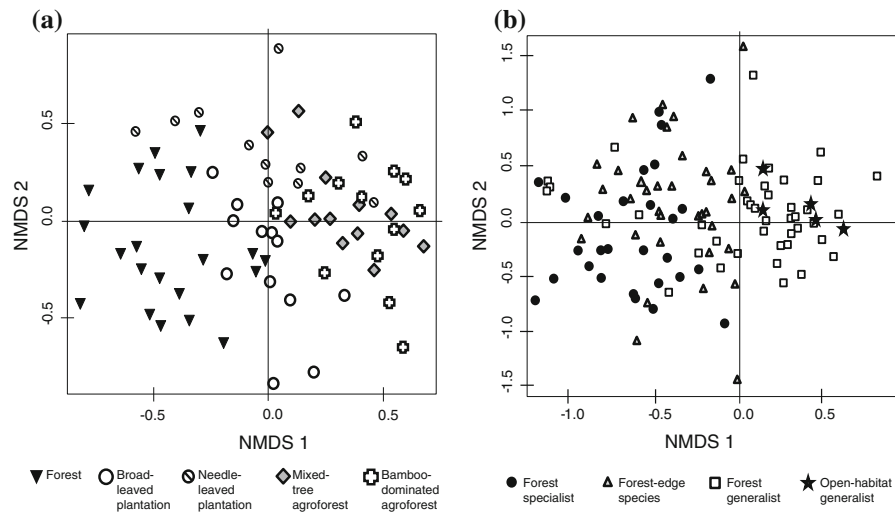


Fig. 2 Two-dimensional ordination plots derived from non-metric multidimensional scaling (NMDS) of **a** site scores with habitat types and **b** species scores with habitat specialization types

Table 3 Multi-model averaged estimates of coefficients (AECs) and relative importance of variables (IoVs) for environmental factors determining bird species richness of all

(total) species, species endemic to Indonesia, forest specialists, and open-habitat generalists

	Total species richness		Endemic to Indonesia		Forest specialist		Open-habitat generalist	
	AEC	IoV	AEC	IoV	AEC	IoV	AEC	IoV
Proximity to forests	–	–	–	–	$-1.419 \pm 0.304^{***}$	1.00	0.435 ± 0.278	0.09
Habitat type ^a		1.00		1.00		–		1.00
BP	$-0.317 \pm 0.110^{**}$		$-0.662 \pm 0.238^{**}$		–		0.706 ± 0.975	
NP	$-0.374 \pm 0.108^{***}$		$-0.580 \pm 0.241^{*}$		–		1.569 ± 0.895	
MT	$-0.332 \pm 0.101^{**}$		-0.134 ± 0.186		–		$2.704 \pm 0.834^{**}$	
BT	$-0.630 \pm 0.110^{***}$		$-0.608 \pm 0.219^{**}$		–		$2.499 \pm 0.813^{**}$	
% canopy cover	–	–	–	–	$0.035 \pm 0.009^{***}$	1.00	–	–
% midstory cover	–	–	–	–	-0.016 ± 0.011	0.36	–	–
% understory cover	-0.004 ± 0.004	0.23	-0.007 ± 0.004	0.30	-0.011 ± 0.012	0.16	–	–
Tallest tree height	–	–	–	–	–	–	–	–

Data are not shown for the nine third-degree polynomial terms of the geographic coordinates

BP broad-leaved plantation, NP needle-leaved plantation, MT mixed-tree agroforest, BT bamboo-dominated agroforest. As the baseline for the nominal variable of habitat type, remnant forest (F) does not appear

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

agroforest (MT and BT) contributed to an increase in granivorous bird species richness compared with especially BP and the remnant forest (F). The richness of insectivorous bird species was influenced by many environmental factors (Table 4). Because there were significant positive effects of percentage canopy cover and tallest tree height and significant negative effects of proximity to the nearest forest margin and of all man-made forests except BP, it appeared that interior forest environments were suitable for insectivores.

Discussion

Roles of man-made forests in conservation of birds

The results showed that total species richness and diversity were maintained in man-made forests except bamboo-dominated agroforests (BT), although these factors were highest in the remnant forest (F). These findings are similar to those of previous studies examining bird diversity in tropical forests and

Table 4 Multi-model averaged estimates of coefficients (AECs) and relative importance of variables (IoVs) for environmental factors determining bird species richness of six feeding guilds

	Carnivore		Frugivore		Granivore		Insectivore		Nectarivore		Omnivore	
	AEC	IoV	AEC	IoV	AEC	IoV	AEC	IoV	AEC	IoV	AEC	IoV
Proximity to forests	–	0.04	–	–	–	–	–0.149 ± 0.070*	0.48	0.678 ± 0.467	0.44	–	–
Habitat type ^a	–	–	–	–	–	1.00	–	0.18	–	–	–	–
BP	–	–	–	–	–1.475 ± 1.076	–	–0.278 ± 0.140	–	–	–	–	–
NP	–	–	–	–	0.279 ± 0.140	–	–0.305 ± 0.136*	–	–	–	–	–
MT	–	–	–	–	1.373 ± 0.471**	–	–0.560 ± 0.143***	–	–	–	–	–
BT	–	–	–	–	1.184 ± 0.483*	–	–0.653 ± 0.146***	–	–	–	–	–
% canopy cover	0.007 ± 0.007	0.13	0.010 ± 0.004*	0.62	–	–	0.007 ± 0.002**	0.75	–0.019 ± 0.016	0.06	–	–
% midstory cover	–	–	–0.008 ± 0.010	0.15	–	–	–0.007 ± 0.004	0.07	–	–	–	–
% understorey cover	–0.014 ± 0.016	0.04	–0.015 ± 0.01	0.41	–	–	–	–	–	–	–	–
Tallest tree height	0.039 ± 0.033	0.19	0.044 ± 0.018*	0.27	–	–	0.023 ± 0.010*	0.04	0.056 ± 0.051	0.36	–	–

Data are not shown for the nine third-degree polynomial terms of the geographic coordinates

^a BP broad-leaved plantation, NP needle-leaved plantation, MT mixed-tree agroforest, BT bamboo-dominated agroforest. As the baseline for the nominal variable of habitat type, remnant forest (F) does not appear

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

surrounding anthropogenic habitats (Thiollay 1999; Naidoo 2004; Waltert et al. 2005; Harvey and Gonzalez Villalobos 2007; Martin et al. 2012). However, the important role of remnant forest in conserving forest biodiversity was emphasized by the NMDS results. The avian species compositions in all of the man-made forests differed dramatically from that in the remnant forest, mainly because of a decline in abundance of forest specialists and their replacement with open habitat generalists. This finding is consistent with those of other studies (Thiollay 1995; Naidoo 2004; Waltert et al. 2004, 2005; Harvey and Gonzalez Villalobos 2007). Although dense canopy cover was fragmented in the remnant forest because of selective logging, this forest may still provide suitable habitats for forest species that feed on dense and high canopy (e.g. *Pericrocotus flammeus* or scarlet minivet, *Rhyticeros undulatus* or wreathed hornbill). The GLM results showed that species richness of forest specialists decreased with increasing distance from forest and with decreasing density of canopy cover; this is consistent with the results of previous studies (see Greenberg et al. 2000 and references therein). This result is not surprising, because forest specialists are highly dependent on forest interior environments and do not enter cultivated open areas (Waltert et al. 2005). Therefore, the protection of tropical natural forests should be prioritized to conserve forest bird diversity (Abrahamczyk et al. 2008; Zurita and Bellocq 2012).

Our two types of agroforest did not appear to have a strong ability to maintain forest specialists, although the conservation roles of agroforests (mostly shaded cocoa and coffee agroforests) have been emphasized (Schroth et al. 2004; Abrahamczyk et al. 2008; Clough et al. 2009). This inconsistent finding is likely attributable to differences in the definition of forest-dependent species, as most studies include not only forest specialists, but also forest-edge species. Combining both forest specialists and forest-edge species reveals that the agroforestry systems were colonized by 30 and 21 % of the total numbers of forest-dependent species (the total combination of forest specialists and—edge species) in the mixed-tree and bamboo-dominated agroforests, respectively; these values are similar to those in coffee agroforests in Sumatra (27 %) (Philpott et al. 2008).

Likewise, the richness of species endemic to Indonesia was also negatively influenced by man-made habitats, although mixed-tree agroforests had

the least influence. In general, endemic species of birds are more sensitive to forest change and fragmentation than are widespread species (Waltert et al. 2004) and are reported to decline in species richness in anthropogenic habitats (Waltert et al. 2005; Arriaga-Weiss et al. 2008), but high species richness and abundance of endemic species in human-modified land uses have also recently been reported from a tropical island off the Gulf of Guinea (Dallimer et al. 2012) and in a traditional mosaic landscape of agriculture in Madagascar (Martin et al. 2012). The 22 species endemic to Indonesia that were observed at our study site consisted of seven forest specialists, seven forest-edge species, six forest generalists, and two open-habitat generalists. Eleven species, consisting of five forest-edge species, four forest generalists, and two open habitat generalists, were recorded in mixed-tree agroforests. Our finding that many species in this study that were endemic to Indonesia were not strictly confined to forest interior environments (unlike the case in Sulawesi; Abrahamczyk et al. 2008) could be an indication of the possibility of ancient landscape heterogeneity, to which endemic species may have adapted over centuries (Martin et al. 2012). Long-cultivated agroecosystems such as the mixed-tree agroforests of Java (Parikesit et al. 2005; Okubo et al. 2010) might have provided suitable habitat for many narrowly distributed endemic species. Notably, one forest-edge species (*Megalaima javensis*) among 11 endemic species found in the agroforest is listed as a near threatened species (IUCN 2012), emphasizing that further attention should be paid to conserving such species in agricultural mosaic landscapes under rapid biotic homogenization and agricultural intensification.

Different responses of various ecological groups

Overall, the high proportion of insectivorous species in the remnant forest and the drastic decline in this proportion from remnant forest to man-made forests is consistent with previous studies (Harvey and Gonzalez Villalobos 2007; Martin et al. 2012). The GLM results revealed that different environmental factors affected the species richness of different ecological groups; the patterns were somewhat different from those in previous studies that stressed the importance of vegetation cover and proximity to forests (Harvey and Gonzalez Villalobos 2007; Clough et al. 2009).

Unlike in other studies (e.g. Greenberg et al. 2000; Waltert et al. 2005; Tschamtké et al. 2008), the numbers of nectarivorous and omnivorous species in our study were not influenced by any environmental factors. This is not surprising in the case of omnivorous species, because they were mostly forest generalists with a wide dietary range and strong ability to adapt to habitat changes and competition for food resources. In the case of nectarivores, the wide distribution in our study could be explained by the abundance of flowering resources, even in anthropogenic habitats; examples are mistletoes (*Loranthus* sp. and *Dendrophthoe* sp.) growing on trees, and wild-banana (*Heliconia* spp.) and *Erythrina* sp.

Moreover, no environmental factors explained the distribution of species richness of carnivores. It is well known that carnivores—especially raptors—are sensitive to forest fragmentation and human disturbance because of their need for large territories (Arriaga-Weiss et al. 2008). The finding that species richness of carnivores did not decline in man-made forests is likely attributed to the relatively small maximum distance from forests (about <3 km) in our study landscape.

The number of frugivores was strongly related to vegetation structure (i.e. high percentage canopy cover, with high trees); this corresponds to the results of previous studies (Greenberg et al. 2000; Arriaga-Weiss et al. 2008). Because trees and shrubs bearing fleshy fruits, such as wild berries, wild grapes, bananas, guavas, coffee, mangos, and papayas, were abundant throughout our study site, the differences in habitat type may have had no effect on species number, although the mean species number of frugivores per sampling plot was smaller in needle-leaved plantation and bamboo-dominated agroforest than other habitat types (Fig. 1a), likely because of reduced availability of food resources. Nevertheless, some medium and large frugivores, such as wreathed hornbill (*R. undulates*) depend on tree cavities for nesting and thus depend directly on the availability of larger trees (MacKinnon et al. 2010); they were rarely found outside the remnant forest (see Appendix 1).

Species richness of granivores was influenced by habitat type. The increased species richness of granivores that we found in the two types of agroforest is explained by the presence of two munias (*Lonchura leucogastroides* and *Lonchura punctulata*) only in the agroforests, together with commonly observed columbids.

Among the six feeding guilds, the species richness of insectivores (the most dominant group overall and in all habitat types) was affected by many environmental factors and declined along a gradient of human disturbance, as summarized by Tschamtké et al. (2008). However, unlike in our study, Clough et al. (2009), who compared avifauna in cacao agroforests with that in a natural forest in Sulawesi, revealed that the diversity of insectivorous birds did not depend strongly on distance to forest. This different result could have been due to the low degree of specialization of insectivores in the case of Sulawesi (Abrahamczyk et al. 2008), whereas the insectivorous birds in our study, as well as in other biogeographic regions (Waltert et al. 2005; Arriaga-Weiss et al. 2008; Leyequién et al. 2009; Martin et al. 2012), showed some degree of specialization in terms of foraging location (e.g. ground, understory, shrubs, trees, and trunks of tall trees) and strategies (e.g. gleaning and sallying).

Conclusions

Our results indicate that appropriate landscape design and management in anthropogenic habitats surrounding remnant forest could conserve forest bird communities and functional diversity to some degree. However, remnant forest as a source of bird diversity has to be prioritized to conserve regional bird diversity and forest-dependent species in forest–agricultural landscapes. Because the remnant forest in our study area is not protected for biodiversity conservation and has undergone selective logging, efforts to avoid further human disturbance and to rehabilitate complex-structured vegetation strata with a tall canopy of native trees are necessary. We found large differences in habitat characteristics and landscape quality for birds between the fragmented forest remnant and bamboo-dominated agroforest, but the two plantations and the mixed-tree agroforests exhibited moderate percentages of the forest specialists found in the remnant forest. This indicates that man-made forests with appropriate vegetation composition and structure and proximity to remnant forest could support forest biodiversity while producing foods and fibers. Despite the mixed-tree agroforests being located close to village settlements and frequently visited by farmers, this type of man-made forest maintained high species

diversity of various functional groups of birds. It should be noted that anthropogenic habitats alone may not function as alternative habitats of the original forest species, because our study landscape includes natural forests that could have spill-over effects on nearby man-made forests.

Nevertheless, man-made forests maintained the species richness of various feeding-guild groups, thus providing important ecosystem functions and services such as seed dispersal, biological pest control, and pollination. On the basis of our findings, we can recommend some appropriate habitat management and landscape arrangements to improve the ecosystem functioning of the anthropogenic habitats. Because each habitat type of man-made forest had a unique bird species composition, various types of tree composition with multistoried structure might need to be maintained. Among the anthropogenic habitat types, broad-leaved plantations with native trees used for timber production could be facilitated more to maintain an avian community similar to that in the remnant forest, provided that these plantations are located as close as possible to the remnant forest. The current types of mixed-tree agroforests, which are important in ecosystem provisioning such as the production of fruits, timbers, vegetables, fuelwoods, and industrial tree crops that generate cash income for local villagers, should be maintained to conserve some of the species endemic to Indonesia, as well as frugivores and nectarivores. High functional diversity of birds could be sustained more in the agroforest by adding pine trees over the present canopy trees, or in the needle-leaved plantation by adding various tree-crop mixtures under the sparse canopy, because the coarse bark on the pine trunks seems attractive for bark-gleaning insectivores. Bamboo-dominated agroforests, which produce materials economically important for value-added crafts (e.g. bamboo-woven walls, locally called *bilik*) for local villagers, as well as construction materials sold mainly to city markets, could be located far from the remnant forests, because the former are obviously not favored by many functional groups except granivores. This action can also be expected to reduce the pressure on forest resource extraction from the forest.

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