Biological Conservation 142 (2009) 1032–1041

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry

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ARTICLE INFO

Article history:
Received 17 October 2008
Received in revised form 13 December 2008
Accepted 21 December 2008
Available online 28 February 2009

Keywords:
Agriculture
Avifauna
Functional groups
Rainforest
Sulawesi

ABSTRACT

Large-scale intensification of smallholder cacao management is currently affecting the agroforestry landscapes of Sulawesi (Indonesia), the world's third largest cacao producer. Little is known about how this shift from diverse plantations to full-sun cacao will affect functionally important biodiversity within the agroecosystem, and how this is related to landscape-wide patterns in land-use and natural ecosystems. We recorded birds in 43 cacao plots differing in woody and herbaceous vegetation as well as distance to forest in two valleys around the Lore Lindu National Park in Central Sulawesi. Species richness of frugivores and nectarivores decreased with increasing distance to forest, whereas granivorous birds increased in richness. Forest specialists, but not habitat generalists, responded positively to forest edge proximity. Species richness of all functional groups except seed eaters increased at higher density of tall shade trees. Greater species richness of shade trees was associated with higher species richness of frugivores and nectarivores, while herbaceous vegetation did not have a strong impact on the avifauna. The positive effect of shade trees was independent of distance to forest. In conclusion, our study shows the relative importance of local and landscape effects on bird diversity with shade trees being critical for bird conservation in cacao agroforestry landscapes.

1. Introduction

Current transformations of ecosystems and landscapes by human activities are probably the largest source of global change on earth (Sala et al., 2000). Land-use intensification has led to rapid changes in communities of plants and animals, which in turn affects ecosystem services and ultimately human well-being (Tilman et al., 2001). Conservation of biodiversity and ecosystem services in agricultural systems requires a landscape perspective, because the local-regional interplay means that landscape species pools influence local diversity and functioning of organisms (Kareiva and Wennergren, 1995). Hence, management effects should be evaluated separately from landscape effects (Batáry et al., 2007; Clough et al., 2005; Koh, 2008; Luck and Daily, 2003), with which they are often confounded (Reitsma et al., 2001).

Southeast Asian rainforests are suffering the highest deforestation rates worldwide, with minimum estimates around 0.75 percent yearly losses, not including forest degradation (Achard et al., 2002). Significantly, deforestation rates are rising within the region while they are decreasing in other parts of the world (Matthews, 2001). Deforested areas are converted to a mixture of annual crops, tree crops, mines and settlements, drastically changing the habitat for a large number of species (Sodhi et al., 2004). The Indonesian island of Sulawesi is part of the Wallacean biogeographic region, a biodiversity hotspot (Myers et al., 2000). Its flora and fauna is characterised by a high degree of endemicity (Whitten et al., 2002). Sulawesi and the smaller islands surrounding it still harbour a relatively large rainforest cover, about 49% of the total area (FWI/GFW, 2002), but agricultural expansion, mining and commercial logging are also threatening the integrity of those forests (FWI/GFW, 2002; Trainor, 2007). Since the 1980s, landscapes in the southern, central and eastern provinces of the island are being transformed by the cacao boom which placed Indonesia on the 3rd rank of the largest cocoa producers in just 25 years. 80% of the Indonesian cacao is grown on Sulawesi, almost exclusively by smallholders, and most of it on land formerly occupied by forest or coffee agroforests. Even though they offer habitat to only part of the original forest fauna and flora, diverse, shaded cacao agroforests are relatively species rich (Estrada et al., 1997; Schulze et al., 2004; Steffan-Dewenter et al., 2007; Waltert et al., 2004). However, rapid and widespread intensification of management practices, including removal of shade trees and frequent weeding, is underway (Belsky and Siebert, 2003; Siebert, 2002). Consequently, the current situation in smallholder cacao is one of widely differing types of vegetation structure, from forest-like environments to

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0006-3207/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2008.12.027

full-sun cacao. How these different cacao habitats differ in their fauna and flora, and how this affects functionally important species groups and ecosystem functioning is largely unknown.

The bird fauna of Sulawesi is truly unique: one third of its 224 species are found nowhere else (Stattersfield et al., 1998) and as such attract birdwatchers from all over the world. More importantly though, birds are key players in ecosystems, both natural and managed: not only are they sensitive to changes in habitat quality, they maintain important ecosystem functions by acting as pollinators, predators, seed dispersers, scavengers and ecosystem engineers (Sekercioglu et al., 2004; Sekercioglu, 2006; Whelan et al., 2008). In agroforests of Latin America, predation of herbivorous pests has been repeatedly and directly linked to the species richness of the avifauna (Van Bael et al., 2008; but see Perfecto et al., 2004). A recent study demonstrated economical benefits due to effective reduction by birds of crop losses due to berry borers in Jamaica (Kellermann et al., 2008). The contrast between forest and disturbed habitats including agroforestry systems has been the subject to many avian ecological studies (Abrahamczyk et al., 2008; Sodhi et al., 2005), and general patterns in the impact of land-use change on functional diversity of birds have emerged (Sekercioglu, 2006; Tscharntke et al., 2008). However, the extent to which the management of Southeast Asian cacao agroforests, with respect to the shade tree density, species richness of the shade trees and the extent of the herbaceous vegetation, may provide valuable habitat and improve ecosystem functioning has barely been investigated, despite the global role now played by Indonesian cocoa. Studies from the neotropics abound, but it has convincingly been argued that these results cannot simply be transferred to Southeast Asia (Philpott et al., 2008). Consequences of management, be it shade or other, need to be known so that the consequences of agricultural intensification can be predicted and incentives to conservation-friendly, ecologically complex, sustainable agroforestry systems can be appropriately designed (Bhagwat et al., 2008; Gove et al., 2008; Philpott et al., 2007). In addition, attention needs to be paid that management effects are evaluated while controlling for landscape effects (Koh, 2008; Laube et al., 2008), because landscape context can influence contrasts between local management (Holzschuh et al., 2007).

To increase our knowledge of the contribution of landscape and habitat scale variables affect the avifauna, we studied birds in cacao plantations situated along independent gradients of shading, shade composition, herb layer structure and distance to natural forest. We used the avifauna data collected from 43 cacao plots in two valleys in Central Sulawesi, Indonesia, to answer the following specific questions:(1) which local and landscape-scale variables affect bird species richness? (2) Is species richness of forest specialists and generalists determined by different variables? (3) How do different functional groups respond to habitat and landscape variables? (4) Which variables affect bird community composition?

2. Material and methods

2.1. Study sites

Our study took place in Palolo and Kulawi valleys respectively on the northern and the western border of the Lore Lindu National Park, Central Sulawesi, Indonesia (Fig. 1). The elevation in these valleys range from 400 m to about 1000 m asl. Natural vegetation is lowland to submontane rainforest, although there is virtually no lowland forest remaining (Whitten et al., 2002). Being close to

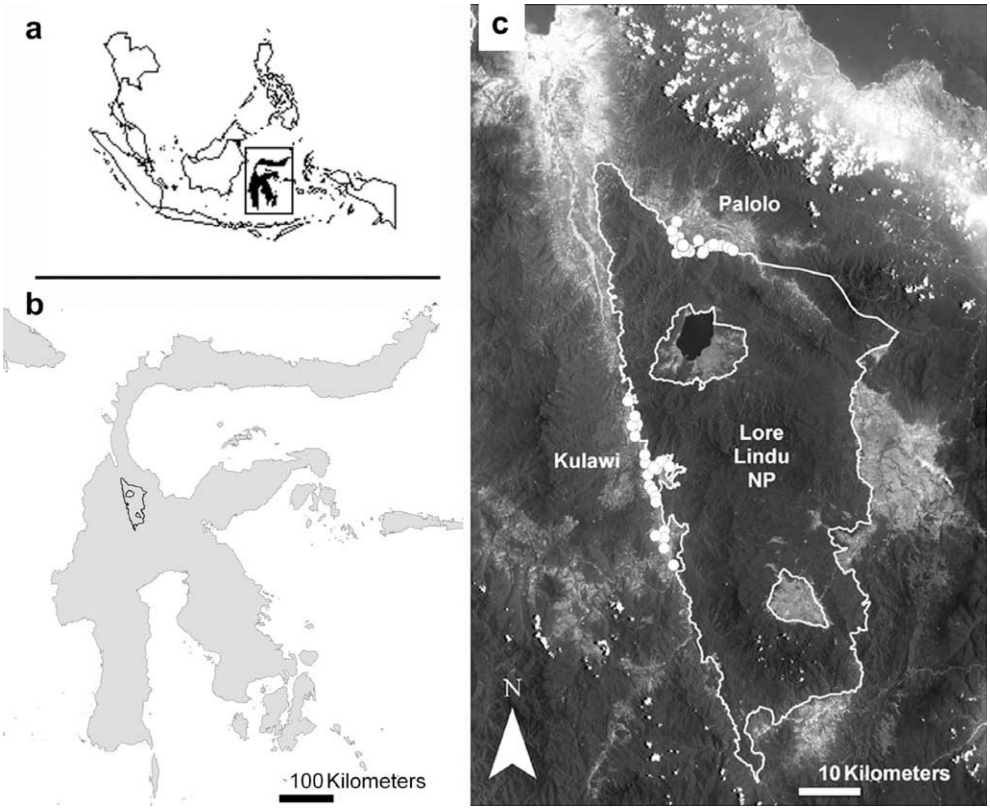

Fig. 1. Map of the study area: (a) Sulawesi within the Indo–malay region (b) Location of Lore Lindu National Park within Sulawesi (c) Lore Lindu National Park with its two populated enclaves (white lines) and the location of the 43 research plots (white dots) in Palolo and Kulawi valleys.

the equator, the seasonality is not very marked. Humidity is generally between 77% and 85%, with minimum values between 70% and 75%. Minimum temperature ranges between 12 and 17 °C, maximum between 26 and 35 °C. Rainfall is very variable and may range between 84 and 2110 mm per month (The Nature Conservancy, 2004).

Our objective was to obtain a dataset that did not contain strong correlations between the environmental variables shading, shade tree composition and distance to forest, to allow their effects to be detected separately when considered jointly in statistical models. Random selection of plots was not used as it would have caused multiple collinearity between explanatory variables. For example, natural forest shade trees tend to be more frequently found close to the forest edge, while plots with planted shade or without shade are more common further away; for our aims however it was necessary to include both plots with planted, natural shade as well as without shade at different distances from the forest. Our approach was to select 35 cacao plantations (15 in Palolo, 20 in Kulawi) differing in shade intensity and shade tree diversity, as well as distance to forest and altitude (Fig. 1) from a subset of 80 plantations for which YC recorded environmental data in 2006. Full gradient range cover was achieved for all environmental factors in both valleys. We used additional data such as plot history, management history, and farmer characteristics to avoid introducing systematic bias due to non-random plot selection. In each plantation we established a plot of 40 × 40 m, which was rented from the farmers and managed by local assistants. All but four between-plot distances were greater than 1000 m, with the absolute minimum distance being 850 m.

Common planted shade tree species in the plots are the leguminous trees *Gliricidia sepium* (Jacq.) Walp. and *Erythrina subumbrans* Merr., candlenut *Aleurites moluccana* (L.) Willd., rambutan *Nephelium lappaceum* L., avocado *Persea americana* Mill., langsat (=longan) *Lansium domesticum* Correa, durian *Durio zibethinus* Merr. Species that are both planted and naturally occurring are sugar palm *Arenga pinnata* (Wurmb) Merr. and sago palm *Metroxylon sagu* Rottb. Common remaining forest tree species are *Ficus* sp., *Pterospermum celebicum* Miq. and *Bischofia javanica* Blume. Many other species occur infrequently: 150 species of trees were recorded in total. In addition to the shade trees, other crops, such as coffee *Coffea* sp., or chili *Capsicum annuum* L. are grown within the cacao plots, however, in all our plots cacao was the most numerous crop tree.

2.2. Environmental variables

Table 1 gives an overview of environmental variables used, as well as their range.

Trees either standing in, or with the crown overlapping a 50 × 50 m plot containing the 40 × 40 m plot were identified to species level and measured for total height by RP. Percentage shade tree canopy cover was based on the computer-based analysis of hemispheric pictures obtained by 5.80 m above the soil, i.e. above the cacao canopy, with a digital camera fitted with a remote-control shutter release placed on heavy-duty tripod. Distance to forest is based on satellite pictures of the study area displayed and managed with ArcGIS 9.2 (ESRI). Distance to nearest forest was measured as the distance from the edge of the plot to the rainforest edge. Half of the plots were weeded every second month, the other half every six months, a fixed treatment which interacts with plot shading in producing differences in the herbaceous layer. Height of the herbaceous vegetation in the cacao was measured monthly between October 2007 and June 2008 at 5 random points in the plot. While these measurements do not cover the whole bird survey period, their mean is a good measure for the weediness as experienced by the bird fauna as weeding frequency is constant and seasonality very limited. In October 2007, herb cover and species richness was recorded in two 5 × 5 m quadrats within each plot by D. Cicuzza (unpublished data).

2.3. Survey

Each plot was visited once in 2007 (Kulawi: April–May, Palolo: August–October) and a second time in 2008 (Kulawi: April–May, Palolo: May–July). At each visit, a plot was surveyed continuously from 05:30 am to 10:30, resulting in a total of 10 h of observation per plot. Shorter, but more often repeated observation periods would have reduced the variability between plots, but would have increased disturbance in the relatively small plots. No rain events ever occurred during that time of the day. Birds were recorded visually and acoustically, and by systematic tape recordings (Parker, 1991), which allowed a posteriori confirmation when necessary. Individuals flying above the canopy were excluded from the analysis. For taxonomy we followed Coates et al. (1997).

We are aware that point count data do not deliver any information on survivability, fitness and productivity effects of a habitat on the birds using it (Komar, 2006). However our method provides an overview of the species of birds using these plantations, which is our prime focus in this study.

2.4. Ecological groups

We separated bird species according to three criteria: distribution, habitat specialisation and primary diet based on Abrahamczyk et al. (2008), which we use as a proxy for ecological function (Tscharntke et al., 2008). Data for additional species was obtained from Coates et al. (1997), with weight class being extrapolated from similar sized, closely related species (Table 2).

2.5. Data analysis

We first tested for bicollinearity between explanatory variables. Not surprisingly, correlation between number of tall trees and

Table 1
Explanatory variables used in general linear models to explain bird diversity in smallholder cacao plantation in Central Sulawesi (transformed values in parentheses). Variables included in the full models are in bold.

Variable name	Description	Minimum	Mean	Maximum
Region	Factor with two levels, Palolo and Kulawi regions	–	–	–
Altitude	In meters above sea level, untransformed	400	663	950
Forest distance	Distance to nearest forest patch over 2 ha in area; square-root transformed	0 (0)	390 (16)	2400 (49)
Number of tall trees	Trees > 10 m height, untransformed	2	15	32
Tree species richness	Number of shade tree species	3	10.6	26
Shade above canopy	In percent, measured 5.80 m above soil	23.4	57.3	81
Mean weed height	In centimetres, untransformed	11	26	59
Weed cover	In percent, untransformed	5	66.7	100
Weed species richness	Untransformed	2	14.1	24
Shade above canopy	In percent, measured 5.80 m above soil	23.4	57.3	81

Table 2
List of 57 bird species detected in cacao plantations in the highlands of Central Sulawesi, species codes used in NMDS ordination and ecological characteristics (Distribution: E = endemic, R = residents, V = vagrant; Diet: C = carnivores, F = frugivores, G = granivores, I = insectivores, N = nectarivores, O = omnivores; Weight: 1 = 0–10 g, 2 = 11–20 g, 3 = 21–40 g, 4 = 41–80 g, 5 = 81–160 g, 6 = 161–320 g, 7 = 321–640 g, 8 = 641–1280 g, 9 => 1280 g; Stratum G = ground & understory, M = midstory, C = canopy; Habitat: F = forest species, G = generalist; based on Abrahamczyk et al. (2008) and Coates et al. (1997)).

NMDS	Species	Distribution	Diet	Weight	Stratum	Habitat
1	*Haliastur indus*	R	C	7	G	G
2	*Hieraaetus kienerii*	R	C	8	G	F
3	*Macropygia amboinensis*	R	F	5	GMC	F
4	*Chalcophaps stephani*	R	I	*7*	GMC	G
5	*Treron griseicauda*	R	F	5	C	F
6	*Ptilinopus subgularis*	E	F	5	MC	G
7	*Ptilinopus melanospila*	R	F	5	C	F
8	*Ducula radiata*	E	F	6	MC	F
9	*Ducula forsteni*	E	F	7	MC	G
10	*Trichoglossus ornatus*	E	N	5	C	G
11	*Loriculus stigmatus*	E	F	3	C	F
12	*Loriculus exilis*	E	F	2	C	G
13	*Cuculus saturatus*	V	I	5	MC	F
14	*Cacomantis merulinus*	R	I	3	C	G
15	*Cacomantis sepulcralis*	R	I	3	GMC	G
16	*Chrysococcyx russatus*	R	I	2	GM	G
17	*Surniculus lugubris*	R	I	3	MC	F
18	*Eudynamys melanorhyncha*	R	F	6	MC	F
19	*Phaenicophaeus calyorhynchus*	E	I	*6*	GMC	F
20	*Tyto rosenbergii*	E	C	7	GMC	G
21	*Eurostopodus macrotis*	R	I	*5*	G	G
22	*Hemiprocne longipennis*	R	C	4	G	G
23	*Halcyon chloris*	R	I	1	MC	G
24	*Penelopides exarhatus*	E	F	7	C	F
25	*Dendrocopos temminckii*	E	I	3	MC	G
26	*Mulleripicus fulvus*	E	I	*6*	GMC	F
27	*Coracina morio*	E	I	4	MC	F
28	*Lalage leucopygialis*	R	I	4	MC	G
29	*Pycnonotus aurigaster*	R	F	4	GMC	G
30	*Dicrurus hottentottus*	R	I	4	MC	G
31	*Oriolus chinensis*	R	I	4	C	G
32	*Corvus enca*	R	O	7	GMC	G
33	*Gerygone sulphurea*	R	I	1	MC	G
34	*Muscicapa griseisticta*	V	I	2	GMC	G
35	*Muscicapa dauurica*	V	I	2	GMC	G
36	*Cyornis rufigastra*	R	I	2	GM	F
37	*Hypothymis azurea*	R	I	2	GMC	G
38	*Culicicapa helianthea*	R	I	1	MC	G
39	*Aplonis minor*	R	F	4	MC	F
40	*Basilornis celebensis*	E	F	5	MC	F
41	*Streptocitta albicollis*	E	F	4	C	G
42	*Scissirostrum dubium*	E	F	4	C	G
43	*Myzomela sanguinolenta*	R	N	1	MC	G
44	*Anthreptes malacensis*	R	N	2	MC	G
45	*Nectarinia aspasia*	R	N	1	GMC	G
46	*Nectarinia jugularis*	R	N	1	GMC	G
47	*Aethopyga siparaja*	R	N	1	GMC	G
48	*Dicaeum aureolimbatum*	E	F	1	GM	G
49	*Dicaeum nehrkorni*	E	F	1	C	G
50	*Dicaeum celebicum*	E	F	1	C	G
51	*Zosterops atrifrons*	R	I	2	GMC	G
52	*Zosterops chloris*	R	I	2	GMC	G
53	*Passer montanus*	R	G	3	GMC	G
54	*Lonchura molucca*	R	G	2	G	G
55	*Lonchura punctulata*	R	G	2	G	G
56	*Lonchura malacca*	R	G	2	G	G

shade above cacao was relatively high (Pearson's $r = 0.60$). Shade cover was left out of the analyses because tree cover on the plot is a direct structural parameter and can be manipulated while shade cover also depends on variables such as the proximity of slopes. All other variable pairs were not strongly correlated (Pearson's $r < 0.5$). To characterise the herbaceaous layer we selected weed cover as it correlated well with mean herb height and herb species richness (Pearson's $r = 0.51$ and 0.57, respectively).

We analysed species richness of total bird species richness and of the distribution, habitat specialisation and feeding groups separately using generalised linear models. To allow for uncertainty in the choice of the best model, we opted for multi-model inference and model averaging, based on Burnham and Anderson (2002). We started by checking the appropriateness of the full generalised linear model (maximum-likelihood) by checking diagnostic plots (a plot of residuals against fitted values, scale-location plot of $\sqrt{|\text{residuals}|}$ against fitted values, a Normal Q–Q plot and a plot of Cook's distances against leverage/(1-leverage)). If necessary we used a Poisson distribution with log-link function, otherwise a normal distribution with identity link function. We did not have any case of overdispersion. For each analysis, the full model, the null model and models with all valid combinations of the explanatory variables including first-order interactions were generated, and delta AICc values computed. AICc is the Akaike Information Criterion corrected for small sample sizes and deltaAICc is the difference between the values for the best model and the remaining models. All models within 2 deltaAICc entered the best-model-subset. Model-averaged estimates were obtained by computing means and standard errors of the estimates weighted by the model weights.

To visualise the dependency of the species composition of the bird fauna on environmental variables, we conducted indirect gradient analysis by non-metric multidimensional scaling (NMDS, also called NMS or principal coordinate analysis) on the presence–absence site-species matrix. This type of ordination can be described as unconstrained, because it is based solely on the species data and is not constrained by environmental variables. NMDS is a computational-intensive iterative optimization method that searches for the best positions of n entities (samples) on k dimensions (axes) that minimizes the departure from monotonicity in the relationship between the original dissimilarity data of the n samples and the reduced k-dimensional ordination space of these samples (Mc Cune and Grace, 2002). It is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin, 1987).

We used NMDS to ordinate plots and species in species space. We superimposed computed vectors for the environmental variables onto the ordination diagrams. The significance of the fitted vectors was assessed using 1000 permutations of environmental variables. The goodness of fit statistic is the squared correlation coefficient r^2.

All analyses were conducted in *R* (R Development Core Team, 2007), with additional functions provided by the *R* package *vegan* (Oksanen et al., 2007) for NMDS, and original unpublished *R* code for the multi-model inference procedure (available on request from the corresponding author).

3. Results

3.1. Cacao agroforest bird community

We recorded 56 species of birds within the cacao plantations, which represents between 63.9% and 82.2% of commonly-used estimators for species richness (Chao: 74 ± 11.2; first-order jacknife: 73.5 ± 5.9, second order jacknife 82.2, bootstrap 63.9 ± 3.2). Thus the total inventory of the species is relatively complete, even though the species richness per site is likely to have been underestimated. An overview of the species and their ecological characteristics is given in Table 2. One third of the species are endemics to the Sulawesi subregion. Only three of the species recorded were vagrants, the others were all non-endemic residents.

3.2. Species richness: endemics vs. non-endemics

The multi-model inference approach for the analysis of total species richness and species richness split into habitat specialisation groups was justified by the relatively large number of candidate models, i.e. where deltaAICc < 2 (Appendix A). Explanatory power of models in the best-subset models was relatively good, with 31% to 35% of the variance explained for all species and non-endemic residents, and 34% to 42% for endemics. Multi-model-averaged estimates are summarised in Table 3. Estimated total species richness per plot increased with number of tall trees and tree species richness. Species richness of endemics was increased at higher altitudes and close to the forest edge, but also increased with number and species of shade trees. While the number of non-endemic resident species also responded positively to an increase in both shade variables, it increased at lower altitudes (Table 3).

3.3. Species richness: habitat generalists vs. forest specialists

While both forest specialist and habitat generalist species richness responded positively to shade-tree-related variables, only the forest-specialist-bird community was richer closer to the edge of the natural forest. Multi-model-averaged estimates are summarised in Table 3.

3.4. Species richness of different functional groups

The analysis of functional groups also revealed several likely models for each group (Appendix B). Proportion of variance explained differed between groups, with values from 28% to 31% for insectivores, 15% to 32% for frugivores, 51% to 59% for nectarivores and 41% to 50% for granivores. Multi-model averaged parameters (Table 4) show that frugivores and nectarivores had lower species richness at increasing distances from the forest, while in the granivores the opposite trend was found. Both nectarivore and granivore communities were richer at lower altitudes, while insectivores and frugivores are slightly richer at higher altitudes. Granivores were the only group which did not respond positively to either higher number of tall trees or increased tree species richness. Less species of frugivores and nectarivores were found in plantations with a high weed cover, and for nectarivores that effect increased with increasing distance to forest. The changes in the functional composition of the communities along the environmental gradients are shown in Fig. 2.

3.5. Species community composition

The non-metric multidimensional scaling enabled us to plot sites and species in a two-dimensional species space (Fig. 3; con-

Table 3

Multi-model averaged estimates for coefficients of environmental parameters determining bird species richness; R: region, A: altitude, FD: forest distance, NTT: number of tall trees, TSR: tree species richness, WC: weed cover, ":" denotes two-way interaction.

	All species	Endemic species	Non-endemic resident species	Forest specialists	Habitat generalists
Intercept (Kulawi)[a]	6.342 ± 2.124	−0.740 ± 2.048	4.792 ± 1.519	−0.575 ± 0.638	6.583 ± 1.237
Region (Palolo)	–	0.926 ± 0.624	−0.911 ± 0.954	0.834 ± 0.394	–
Altitude[a]	0.004 ± 0.005	0.006 ± 0.002	−0.003 ± 0.003	–	–
FD	–	−0.042 ± 0.026	–	−0.048 ± 0.016	–
NTT	0.297 ± 0.087	0.089 ± 0.037	0.215 ± 0.061	0.065 ± 0.028	0.253 ± 0.068
TSR	0.172 ± 0.120	0.060 ± 0.050	0.107 ± 0.085	–	0.113 ± 0.096
WC	–	–	–	–	–
FD:NTT	–	–	–	–	–
FD:TSR	–	–	–	–	–
FD:WC	–	–	–	–	–

[a] Coefficient for Kulawi is the intercept, for Palolo it is the difference the intercept and the value indicated in the table.

Table 4
Multi-model averaged estimates for coefficients of environmental parameters determining of four bird diet groups species richness. Carnivores and omnivores (2 and 1 species recorded, respectively) were omitted. Frugivore and granivore model coefficients are raw coefficients from generalised linear models using a log-link; R: region, A: altitude, FD: forest distance, NTT: number of tall trees, TSR: tree species richness, WC: weed cover, ":" denotes two-way interaction.

	Insectivores	Frugivores	Nectarivores	Granivores
Intercept (Kulawi)[a]	0.958 ± 1.654	0.291 ± 0.578	3.210 ± 1.098	2.470 ± 1.098
Region (Palolo)[a]	–	0.356 ± 0.211	−0.536 ± 0.290	–
Altitude	0.003 ± 0.003	0.001 ± 0.001	−0.002 ± 0.001	−0.005 ± 0.002
FD	–	−0.012 ± 0.008	−0.030 ± 0.022	0.024 ± 0.014
NTT	0.172 ± 0.047	0.024 ± 0.013	0.062 ± 0.024	–
TSR	–	0.024 ± 0.016	0.048 ± 0.026	–
WC	–	−0.004 ± 0.003	−0.012 ± 0.007	–
FD:NTT	–	–	−0.002 ± 0.002	–
FD:TSR	–	–	–	–
FD:WC	–	–	−0.001 ± 0.001	–

[a] Coefficient for Kulawi is the intercept, for Palolo it is the difference the intercept and the value indicated in the table.

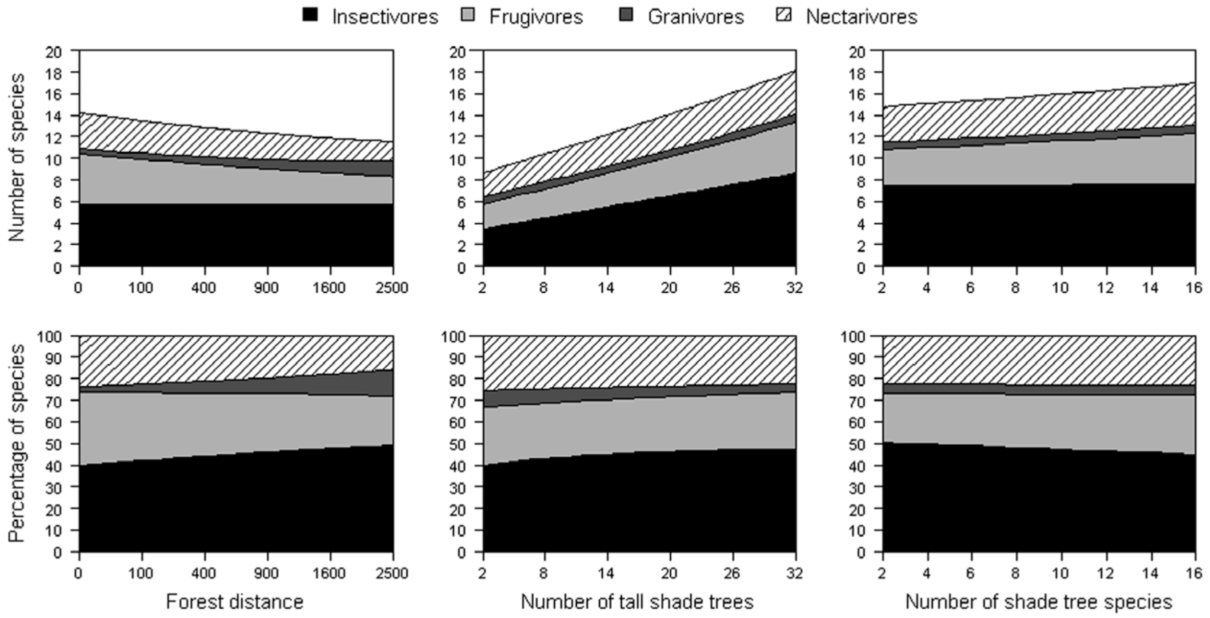

Fig. 2. Functional richness of bird communities in cacao agroforests: effect of distance to forest, number of tall trees and tree species richness based on model averaged estimates (Table 4). Average values of undisplayed explanatory variables are used in the calculation of the predicted values.

vergent solutions found, two dimensions, stress = 21.842). Fitting environmental variables as vectors into this space revealed that distance to forest, altitude, number of tall trees and tree species richness were useful in explaining gradients (goodness-of-fit: distance to forest, $r^2 = 0.35$, $p < 0.001$; altitude, $r^2 = 0.31$, $p = 0.001$; number of tall trees, $r^2 = 0.24$, $p = 0.011$, tree species richness, $r^2 = 0.17$, $p = 0.043$). Species situated towards the left-lower left of the multidimensional scaling plot tend to occur further away from the forest and at lesser altitudes. Examples are the tree sparrow *Passer montanus*, the chestnut munia *Lonchura malacca.* On the upper left-upper left part of the plot, one finds species such as Stephan's dove *Chalcophaps stephani*, which occur further away from the forest but in plantations with a large number of tall shade trees. On the right side of the scaling plot are species that occur close to the forest and with a diverse shade tree cover, such as the citrine flycatcher *Culicicapa helianthea* and the ornate Lorikeet *Trichoglossus ornatus*, which need both proximity to forest edge and diverse shade tree cover. Several montane species such as the crimson-crowned flowerpecker *Dicaeum nehrkorni*, only occur at higher altitudes in the proximity of lower montane forest.

4. Discussion

While not equalling a controlled experiment, our methods of plot selection and analysis allowed us to tease apart the effects of different variables such as landscape composition and shade tree layer descriptors which are usually confounded (Reitsma et al., 2001; Greenberg, 2000). The results of both the general linear models and the NMDS ordination demonstrate that both affect the richness, species and functional composition of the avifauna. In the following, we discuss landscape and local effects separately.

4.1. Landscape context

The large spatial extent of the study enabled us to assess the contribution of landscape matrix something which is not the case with more localised studies (e.g. Reitsma et al., 2001; Waltert et al., 2004; Abrahamczyk et al., 2008). Distance to forest is a critical variable in explaining the composition of the bird communities. Predictably, the species richness of forest specialists

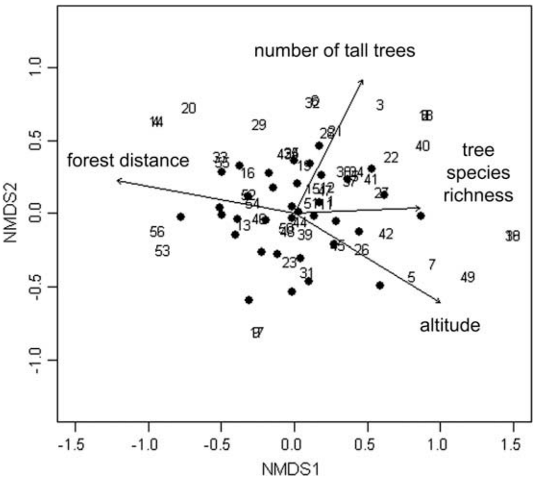

Fig. 3. NMDS ordination biplots of site scores (points) and species (numbers) with the environmental variables distance to forest (square-root transformed), tree species richness and altitude superimposed. Species codes are listed in Table 2.

– and endemic birds, most of which belong to this group (Table 2) – decreases fast as one moves away from the forest edge, similarly to findings from other agroecosystems (Raman, 2006; Laube et al., 2008; Anand et al., 2008). Many forest specialists are unlikely to be able to subsist in cacao plantations without the immediate proximity of natural forest. Frugivores and nectarivores, of which a substantial proportion are forest specialists, show a remarkable decrease in diversity away from the forest edge, as the resources offered by the cacao plots did not appear to sustain fruit and nectar feeders. The fruits of the cacao trees themselves have evolved to be mammal-dispersed and are not suitable as a food item for birds. A number of shade trees bear fruit that are eaten by birds, but shade tree species diversity is lower than in the forest and the number of tree species is limited compared to forests (Steffan-Dewenter et al., 2007), providing resources only for part of the year. The parallel increase in diversity of seed eating birds reflects the increasing availability of food items in neighbouring land-uses such as paddy rice – in which all four granivorous species recorded in cacao are considered to be pests – and possibly also of seeds from herbs within the cacao plots themselves. Interestingly, the diversity of insectivorous birds did not depend strongly on distance to forest – estimates for the effect of distance to forest are substantially lower and more uncertain for insectivores than for frugivores and nectarivores. Forest understory insectivores are considered to be disproportionately sensitive to habitat and landscape modification (Sekercioglu et al., 2002; Tscharntke et al., 2008), but more generalised insectivores, and insect feeders with a broad diet may be less affected than habitat-specialised, stenophagous insectivores (Lindell et al., 2004). It has already been noted elsewhere (Abrahamczyk et al., 2008) that the species richness of understory insectivores in Sulawesi as a whole is rather low compared to other biogeographic areas, which suggests a lower overall degree of specialisation. Only one quarter of the exclusively insectivorous species recorded in cacao are forest specialists, while the others readily use mixed-gardens and plantations. Due to a the complex vegetation structure, a relatively low usage of insecticides (YC, pers. obs.), cacao and the shade trees host a large diversity of potential insect prey (Bos et al., 2007) that is liable to attract members of this functional group. One insectivorous species, the black-naped monarch *Hypothymis azurea*, was observed nesting in cacao trees (YC, pers. obs). The pattern often found in Latin America, that is a high susceptibility of insectivorous birds to land-use change, does not hold for the conversion of submontane forest into (shaded) cacao in Sulawesi. This, together with evidence that herbivory on cacao is independent from distance to forest edge (Adams and Clough, unpublished results), suggests that top–down pressure exerted by the insectivorous bird community on arthropods in natural systems may be maintained in cacao agroforests. The decrease of frugivorous bird species richness with distance to forests implies a strong dispersal limitation of bird-dispersed plant species in cacao landscapes away from the forest edge. Currently, this has no visible effect as landscapes are intensively managed and seedling growth is suppressed by cacao farmers through weeding, but should parts of the agricultural landscape be abandoned, as has been the case elsewhere, this limitation might strongly affect regeneration (Gomes et al., 2008). Likewise, the decrease in nectarivore species richness may have severe impacts on the reproduction of trees and plants such as orchids at any distance from the forest edge, but data and published studies on landscape effects on plant–animal interactions in Southeast Asia are lacking.

4.2. Vegetation effects

Cacao landscapes are heterogeneous due to differences in management, especially shade management, between smallholders. There is a large range in shading practices with a large range of numbers of shade trees and shade tree species per plot. Indeed, shading and choice of shade trees are separate variables in the management choices of the smallholder, and consequently, these factors are correlated only to some extent. For example, cacao plots may have a large number of shade trees of a few species only, especially leguminous shade trees and candlenut *A. moluccana*. We found the variation in both shading variables to be clearly reflected in the richness and composition of the avifauna. A number of studies from Latin America, covering a variety of habitats including cacao agroforests, have reported shade tree cover and shade tree diversity to be a decisive factor for the bird species richness of migrant birds but with little or no effects on resident species (e.g. Greenberg et al., 2000). Migrants are virtually absent from the cacao landscapes, and indeed uncommon in Sulawesi as a whole (Coates et al., 1997), but we found strong effects of shade for resident bird species. This effect was independent of distance to forest, contrary to our expectation that shade trees would be most important near the forest edge, close to the largest species pool, while at a distance to the habitat generalist species would use cacao as a habitat indifferently of the extent or diversity of the shade tree cover. The results of the analyses showed that high values for number of tall trees and to a lesser extent shade tree species diversity in the plot were effective across the habitat specialisation and most of the avian functional groups, i.e. insectivores, frugivores and nectarivores could be shown to benefit. There is no data to be certain of how this will affect ecosystem functioning. However, the correlation of bird diversity and predation found in bird exclusion studies from other regions (Van Bael et al., 2008 and references therein), together with the fact that cacao trees in the plots used in this study support fewer herbivores and suffer less leaf damage when shaded (Adams and Clough, unpublished results) suggests significant positive effects in terms of biological control. Data from Ecuador (Lozada et al., 2007) shows that tree cover in agroecosystems results in increased seed deposition by seed-dispersing birds, resulting in high seedling regeneration of species not locally present before. Granivorous birds were the only group which did not respond to any vegetation characteristics. The absence of correlation with weed cover of granivorous birds shows that weeds may not significantly contribute to their diet, suggesting they may use cacao plantations to predate insects during breeding season, or to nest (black-faced and scaly-breasted munias *Lonchura molucca*, and *Lonchura punctulata*, respectively; DDP, pers. obs.). The extent and diversity of the herbaceous layer did not affect any of the groups analysed, which suggests that canopy structure rather than herbs are the key variable for most species in cacao-forest landscapes. Tree cover has been highlighted several times as being a surrogate for habitat suitability for birds in human-dominated landscapes in Southeast Asia (Abrahamczyk et al., 2008; Lee et al., 2005), but this is the first time these variables were addressed at the scale of a single landuse type. Given the trend towards removing shade in cacao plantations, we predict that species richness will decrease in the coming years, with uncertain ecological consequences, if nothing is done to promote shaded systems.

5. Conclusions

More studies are needed to predict how ecosystems will respond to decreases – or conservation – of the richness of the avifauna. The study of the ecological role of birds in agroforestry systems is still in its infancy and analyzing functional groups separately is a first step (Sekercioglu et al., 2002; Tscharntke et al., 2008). So far, species richness of frugivores and nectarivores, to a lesser extent insectivores, decreased with increasing distance to forest, whereas granivorous birds increased in richness, showing the need to include the landscape context in bird diversity studies (Anand et al., 2008). Only forest specialists, overwhelmingly endemic species, but not habitat generalists, responded to this landscape matrix effect. Our study has also shown that cacao plantations with a large number of shade trees and high shade tree species number support substantially higher diversity levels of birds across all relevant functional groups. Certainly, forest specialists are unlikely reap large benefits from measures to increase shade in cacao plantations further away from the forest, but shaded cacao may act as a buffer zone in the immediate proximity of the forest. But for habitat generalists, large increases in species diversity can be attained by countering the current trend of cacao intensification by providing incentives to conserve and replant a diverse shade cover (Bhagwat et al., 2008).

Acknowledgements

We would like to thank Daniele Cicuzza, Michael Kessler and the assistants in the cacao team for herb data, Stefan Erasmi for satellite maps, Dominik Seidel for shade data as well as Sigit Andhirahman, Alam Anshary, Damayanti Buchori, Wolfram Lorenz and Adam Malik for their support. Péter Batáry, Dagmar Clough, Lian Pin Koh, Cagan Sekercioglu and an anonymous reviewer provided valuable comments on earlier versions of the manuscript. The study was financed by the DFG in the framework of the SFB-552 "Stability of Rainforest Margins in Indonesia" (STORMA).

Appendix A

Multi-model-inference summary statistics for the best-model subset explaining total, forest specialist and habitat generalist bird species richness; R: region, A: altitude, FD: forest distance, NTT: number of tall trees, TSR: tree species richness, WC: weed cover, ":" denotes two-way interaction.

R	A	FD	NTT	TSR	WC	FD:NTT	FD:TSR	FD:WC	K	NLL	AICc	Delta AICc	AICc.w	*R* square
All species														
0	0	0	1	0	0	0	0	0	3	93.91	194.60	0.00	0.44	0.31
0	0	0	1	1	0	0	0	0	4	92.81	194.96	0.36	0.37	0.35
0	1	0	1	0	0	0	0	0	4	93.46	196.25	1.66	0.19	0.32
Endemic species														
0	1	0	1	0	0	0	0	0	4	62.50	134.33	0.00	0.27	0.34
0	1	1	1	0	0	0	0	0	5	61.57	135.21	0.87	0.17	0.37
1	1	1	1	0	0	0	0	0	6	60.19	135.38	1.05	0.16	0.42
0	1	0	1	1	0	0	0	0	5	61.73	135.53	1.20	0.15	0.37
1	1	0	1	0	0	0	0	0	5	61.82	135.70	1.37	0.14	0.36
1	0	1	1	0	0	0	0	0	5	61.97	136.00	1.67	0.12	0.36
Non-endemic resident species														
0	0	0	1	0	0	0	0	0	3	81.90	170.57	0.00	0.40	0.32
0	0	0	1	1	0	0	0	0	4	81.05	171.43	0.87	0.26	0.35
1	0	0	1	0	0	0	0	0	4	81.40	172.14	1.58	0.18	0.34
0	1	0	1	0	0	0	0	0	4	81.54	172.41	1.84	0.16	0.33
Forest specialists														
1	0	1	1	0	0	0	0	0	5	45.69	103.45	0.00	0.73	0.31
0	0	1	1	0	0	0	0	0	4	48.04	105.41	1.96	0.27	0.22
Habitat generalists														
0	0	0	1	0	0	0	0	0	3	85.97	178.70	0.00	0.63	0.33
0	0	0	1	1	0	0	0	0	4	85.22	179.78	1.07	0.37	0.36

Appendix B

Multi-model-inference summary statistics for the best-model subset explaining species richness of birds classified into four diet groups; R: region, A: altitude, FD: forest distance, NTT: number of tall trees, TSR: tree species richness, WC: weed cover, ":" denotes two-way interaction.

R	A	FD	NTT	TSR	WC	FD:NTT	FD:TSR	FD:WC	K	NLL	AICc	Delta AICc	AICc.w	*R* square
Insectivores														
0	0	0	1	0	0	0	0	0	3	74.65	156.07	0.00	0.62	0.28
0	1	0	1	0	0	0	0	0	4	73.86	157.05	0.98	0.38	0.31
Frugivores														
1	1	0	1	0	0	0	0	0	5	66.00	144.07	0.00	0.12	0.29
0	1	0	1	0	0	0	0	0	4	67.38	144.10	0.03	0.12	0.21
0	1	0	0	0	0	0	0	0	3	68.71	144.19	0.12	0.11	0.13
1	0	1	1	0	0	0	0	0	5	66.18	144.42	0.35	0.10	0.28
0	1	0	0	0	1	0	0	0	4	67.70	144.73	0.66	0.09	0.19
0	1	0	0	1	0	0	0	0	4	67.74	144.82	0.75	0.08	0.19
0	1	0	0	1	1	0	0	0	5	66.49	145.05	0.98	0.07	0.26
1	0	0	1	0	0	0	0	0	4	67.91	145.15	1.08	0.07	0.18
0	1	0	1	0	1	0	0	0	5	66.71	145.49	1.42	0.06	0.25
1	0	0	0	1	0	0	0	0	4	68.23	145.79	1.72	0.05	0.16
1	1	0	1	0	1	0	0	0	6	65.43	145.85	1.78	0.05	0.32
1	1	0	0	0	0	0	0	0	4	68.31	145.95	1.88	0.05	0.15
1	1	1	1	0	0	0	0	0	6	65.50	146.00	1.93	0.05	0.32
Nectarivores														
1	0	0	1	1	0	0	0	0	5	36.77	85.61	0.00	0.16	0.52
0	1	1	1	1	0	0	0	0	6	35.34	85.69	0.07	0.15	0.56
0	1	1	1	0	0	0	0	0	5	37.02	86.10	0.49	0.12	0.51
1	1	1	1	1	0	0	0	0	7	34.08	86.31	0.70	0.11	0.59
1	0	1	1	0	1	0	0	1	7	34.19	86.53	0.92	0.10	0.58
1	1	1	1	0	0	0	0	0	6	35.83	86.65	1.04	0.09	0.54
0	1	1	1	0	0	1	0	0	6	36.03	87.06	1.44	0.08	0.54
1	1	0	1	1	0	0	0	0	6	36.14	87.27	1.66	0.07	0.53
1	0	1	1	1	0	0	0	0	6	36.16	87.33	1.71	0.07	0.53
0	1	1	1	1	0	1	0	0	7	34.61	87.37	1.76	0.06	0.57
Granivores														
0	1	1	0	0	0	0	0	0	4	33.35	76.03	0.00	0.55	0.50
0	1	0	0	0	0	0	0	0	3	34.83	76.43	0.40	0.45	0.41

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