BIODIVERSITY RESEARCH

Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia

Kelvin S.-H. Peh[1,2]*, Navjot S. Sodhi[2], Johnny de Jong[1], Cagan H. Sekercioglu[3], Charlotte A.-M. Yap[2] and Susan L.-H. Lim[4]

[1]*The Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, Box 7007, 750 07 Uppsala, Sweden,* [2]*Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore,* [3]*Department of Biological Sciences, Stanford University, 371 Serra Mall, Stanford, California 94305-5020, USA and* [4]*Institute of Biological Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia*

ABSTRACT

Clearance of tropical forest for agricultural purposes is generally assumed to seriously threaten the survival of forest species. In this study, we quantified the conservation value, for forest bird species, of three degraded habitat types in Peninsular Malaysia, namely rubber tree plantations, oil palm plantations, and open areas. We surveyed these degraded habitats using point counts to estimate their forest bird species richness and abundance. We assessed whether richness, abundance, and activities of different avian dietary groups (i.e. insectivores and frugivores) varied among the habitats. We identified the critical habitat elements that accounted for the distribution of forest avifauna in these degraded habitats. Our results showed that these habitats harboured a moderate fraction of forest avifauna (approximately 46–76 species) and their functions were complementary (i.e. rubber tree plantations for moving; open habitats for perching; shrubs in oil palm plantations for foraging). In terms of species richness and abundance, rubber tree plantations were more important than oil palm plantations and open habitats. The relatively high species richness of this agricultural landscape was partly due to the contiguity of our study areas with extensive forest areas. Forecasts of forest-species presence under various canopy cover scenarios suggest that leaving isolated trees among non-arboreal crops could greatly attract relatively tolerant species that require tree canopy. The conservation value of degraded habitats in agricultural landscapes seems to depend on factors such as the type of crops planted and distance to primary forest remnants.

Keywords

Agriculture, deforestation, mixed-rural habitats, South-East Asia, tropical rainforest.

*Correspondence: Kelvin S.-H. Peh, School of Geography, University of Leeds, Leeds LS2 9JT, UK. E-mail: geokp@leeds.ac.uk

INTRODUCTION

Global land use is dominated by agricultural systems (Ormerod & Watkinson, 2000; Defries *et al.*, 2004), and the proportion of the global land area covered by cultivated lands is expected to increase further in conjunction with human population growth (Tilman *et al.*, 2001). Pressures from growing human populations and resource consumption are taking their toll on tropical landscapes, resulting in their rapid transformation into agricultural lands. Although native habitat loss is the leading cause of the loss of world's biodiversity (Myers *et al.*, 2000), some agroecosystems can harbour a substantial portion of the biodiversity of the original land cover (Vandermeer & Perfecto, 1997) and can also buffer and complement protected areas (Curran *et al.*, 2004; Schroth *et al.*, 2004). Yet the role of agricultural lands in the conservation of forest species is little known in the tropics (Luck & Daily, 2003). Current global changes in land use have aroused

considerable interest in the diversity patterns and conservation strategies for native species in agricultural lands and other rural human-dominated landscapes. Recent studies have examined a variety of taxa including plants (Fujisaka *et al.*, 1998; Harvey *et al.*, 2005; Mayfield & Daily, 2005), beetles (Estrada *et al.*, 1999, 1998), butterflies (Horner-Devine *et al.*, 2003), moths (Ricketts *et al.*, 2001), birds (Daily *et al.*, 2001), and primates (Estrada *et al.*, 1999). However, to our knowledge, such studies were carried out mostly in the New World tropics and there were only a few studies of species diversity patterns in South-East Asian agricultural landscapes (e.g. Mitra & Sheldon, 1993; Sodhi *et al.*, 2005).

In this paper, we describe the resident forest bird communities found in various agricultural habitats in Johor, southern Peninsular Malaysia. Previous research in the same region (Peh *et al.*, 2005) had recorded a moderate proportion of forest bird species occurring in the human-dominated landscape outside native forests (28–32%). These rural habitats play a potentially prominent

role in the survival of these forest species. However, the occurrence of forest birds within a mixed-rural habitat may be influenced by landscape composition (Peh *et al.*, 2005). We compared species richness and abundance of the resident forest avifauna between three different types of land use within mixed-rural habitats (i.e. rubber tree plantations, oil palm plantations, and open habitats) to assess their conservation value. There are few data on the utilization of agricultural landscapes by forest birds in this region and on the effects of vegetational structure on their distribution. We identified the main habitat elements that explained the distribution of forest avifauna in these degraded areas by using non-metric multidimensional scaling. In these habitats, we assessed whether diversity, abundance, and the activities of avian groups with different dietary requirements (e.g. insectivores and frugivores) varied among habitats. We hope that our study will highlight approaches needed to make the agricultural landscapes of South-East Asia more hospitable to native forest avifauna.

METHODS

Study area

We collected data from the agricultural lands north-west of Johor, Peninsular Malaysia, situated between 2°20.84′ N, 103°09.41′ E and 2°03.90′ N, 103°31.57′ E. The mean monthly rainfall of the study region ranged from 138 mm in February to 247 mm in December. The months with the least rainfall were January, February, and June. The average daily minimum and maximum temperatures were 22.5 °C and 31.7 °C, respectively (Malaysian Meteorological Service, http://www.kjc.gov.my). The elevation of our study sites ranged from 80 m to 160 m a. s. l. Our study region comprised a mixed array of crop agricultural plots and open areas. The two major arboreal crops were the oil palm (*Elaeis guineensis*) and the rubber tree (*Hevea brasiliensis*). The oil palms and rubber trees in our study area were mature (at least 15 years old). The open habitats consisted of small orchards, unshaded coffee (*Coffea* spp.) plantations, and traditional garden plots close to homesteads. In Peninsular Malaysia, the major components of orchards and home gardens are fruit trees (e.g. *Durio* spp., *Musa* spp., *Artocarpus heterophyllus*, *Mangifera* spp.), non-native ornamental shrubs (e.g. *Hibiscus* spp.), and exotic forestry trees (e.g. *Acacia mangium*). Although we do not have detailed information on the land cover of all the vegetation types in our study area, the oil palm and rubber tree plantations covered 623,000 ha and 213,000 ha in Johor, respectively. They made up about 44% of total land use (Department of Agriculture, 1995). All the sites had small patches of recolonizing pioneer plant species, such as *Macaranga* spp., *Mallotus paniculatus*, *Melastoma malabathricum*, *Ficus* spp., *Trema orientalis*, and *Musa* spp. (wild bananas). Non-native forestry trees (e.g. *A. mangium*) and ornamental shrubs (e.g. *Lantana camara*, *Clidemia* sp.) were also common throughout the landscape. Prior to intensive clearing 30–35 years ago for agricultural development, the vegetation in our study sites consisted of large, contiguous primary forest.

Bird sampling

From 14 January to 3 June 2003, we used point counts (Bibby *et al.*, 2000) to sample the year-round resident bird communities in rubber tree plantations, oil palm plantations, and open habitats. We chose 240 point counts arbitrarily from a map, and aimed to sample habitats in proportion to their occurrence in the human-dominated landscape. The sampling points were < 10 km from primary forest and were at least 200 m from other sampling points. Admittedly, the distance of 200 m between the nearest sampling points may not always be sufficient to ensure independence. Therefore, we only recorded birds within 25 m of each sampling point and made sure not to double-count birds that were identifiably moving between two points. The primary forests were extensive hill dipterocarp forests of more than 80,000 ha. We surveyed a total of 48, 127, and 65 sites in the rubber tree plantations, oil palm plantations, and open habitats, respectively.

All bird surveys were conducted from 07:00 hours to 10:30 hours, only when the weather was fine (i.e. no precipitation or strong wind). All bird sampling was conducted by K.S.-H.P., who used 8×40 binoculars for observation. During each survey, the recorded birds were detected visually or aurally during a 10-min period within a 25-m radius of each sampling point. The observer recorded the call using a voice recorder and a parabolic microphone if a bird was heard and could not be identified, and then compared it to local bird vocalizations from a CD-ROM of the bird calls of tropical Asia (Scharringa, 2001). Bird location was noted to avoid counting the same individual twice. Nocturnal species, migrants, and raptors were not counted. The observer also did not count birds that were flying over or through the count areas. The bird nomenclature followed Inskipp *et al.* (1996).

To determine the bird species richness and abundance values associated with different rural habitats, we classified our surveys as 'rubber', 'palm', or 'open'. Birds may be attracted to different vertical vegetation strata within different habitats (Hughes *et al.*, 2002; Walther, 2002), so it is essential to determine the most important strata that are used by the forest bird community of each vegetation type. Therefore, we recorded the strata in which the birds were seen. We defined as canopy, the crown of the trees > 10 m tall; as middle, the understory layer between 2 m and 10 m; as shrub, any woody vegetation < 2 m tall; and as ground, the leaf litter. We also recorded the first observed activity (foraging, nesting, moving, or perching) of every individual to determine the activities associated with a particular habitat. Foraging refers to feeding or movement performed to obtain food. Nesting behaviour includes courtship display, collection of nesting materials, or flights to and from nests. Moving includes the locomotion of birds unrelated to foraging or nesting. Perching comprises all activities observed while perching, such as preening. We admit that visibility difference among the habitats can bias our data, but we attempted to minimize such bias by using a small sampling area (25-m radius) for each point count, by scanning dense vegetation extensively, and by identifying calling birds. Moreover, the openness of all habitat types enabled us to clearly

see the boundary of all sampling areas. The use of this fixed-area survey method can make cross-habitat comparisons possible and reduces the biases that result from unequal visibility (Thiollay, 1997; Sekercioglu, 2002).

Vegetation sampling

Birds may respond to variation in vegetational structure (Sekercioglu, 2002; Sodhi *et al.*, 2005). Therefore, we measured vegetational structure within a 5-m radius circular area around the bird count points to determine if forest bird communities were associated with certain structural characteristics within each habitat type (Sodhi *et al.*, 2005). Although our vegetation sampling plots were of 5 m radius, we assumed that they were representative of vegetational structure within the bird count plots of 25 m radius. We estimated the percentage of overhead canopy cover (> 10 m in height) using a spherical densiometer at a randomly selected position (Lemmon, 1957). At the sampling points, we recorded the percentage of foliage covering the grid area of the densiometer in the four cardinal directions (i.e. north, south, east, west); these readings were averaged for each sampling point. We assessed tall tree abundance by counting the number of trees > 10 m in height. We estimated the total vegetation volume (TVV) of shrubs and understory trees with an 8-m aluminium pole. The TVV of shrubs was estimated from 0 m to 2 m, and that of understory trees, from 0 m to 8 m. The pole was divided into eight equal sections of 1-m length. Each section was further divided into five equal subsections. We checked for vegetation presence and a leaf was considered a 'hit' if it was within a 5-cm radius of the pole at each subsection. Each subsection was allowed only one 'hit' in each cardinal direction. We calculated the average proportion of hits for each strata from the readings obtained in four cardinal directions.

Previous work in the same study area by Peh *et al.* (2005) revealed that variation in food abundance influenced the distribution of forest birds, so we quantified the differences in food abundance within different land uses. At each bird sampling point, we estimated the fruiting intensity of plants bearing bird-dispersed fruits to determine if food abundance affected avian frugivore distribution. Bird-dispersed fruits were defined as fleshy, black or red coloured, and small or medium sized (Hamann & Curio, 1999). A fruiting index was used to estimate fruiting intensity. Each sampling plot was given a score based on the number of bird-dispersed fruits observed: plots with one to 50 fruits = 1, 51–500 fruits = 2, and > 500 fruits = 3. We also recorded flowering intensity based on the same protocol and scores as the fruiting index. The summation of flowering and fruiting intensity indices produced the plant resource abundance index. Although insect abundance was not included in the computation of the resource index, it was partially accounted for by the abundance of flowers, which likely attracted insect pollinators. Therefore, this resource index gives equal weight to the value of flowers and fruits for frugivorous, nectarivorous, and insectivorous forest birds. The sampling cycles for the fruiting and flowering indices at each habitat followed those of the bird surveys (from January to June 2003), which comprised both wet and dry seasons.

Statistical analyses

We defined forest birds as species that were dependent primarily (not always exclusively) on lowland forests according to Wells (1985). We used the Kruskal–Wallis test (Zar, 1999) to test if the abundance of each forest species differed significantly among various habitats. We adjusted the sampling efforts for rubber tree plantations (by multiplying with a factor of 2.65) and open habitats (by multiplying with a factor of 1.95) to match that for oil palm plantations (1270 min of observation time). We used χ^2 analysis of contingency tables to compare, among different habitats, the occurrence of forest birds in different vegetational strata.

We classified all the observed forest species according to their dietary groups (e.g. insectivore, frugivore) based on their primary food choices. Information on diet was compiled from various authoritative sources (e.g. Gibbs *et al.*, 2001). We standardized the sampling effort at 1270 min of observation and used the 'goodness of fit' χ^2 test to compare the species number and abundance of two dietary groups, i.e. insectivores and frugivores, among habitat types. We performed the statistical tests using MINITAB version 13.2 (Minitab Inc., 2000).

To estimate the bird species richness for each habitat, we used nine different nonparametric species estimators from EstimateS (Colwell, 2000): ACE (abundance-based coverage estimator), ICE (incidence-based coverage estimator), Chao1, Chao2, Jackknife1, Jackknife2, Michaelis–Menten, and bootstrap methods. We graphed sample-based rarefaction curves rescaled to the number of samples (i.e. point counts) to compare forest-species density among different habitats. Sample-based rarefaction curves were also rescaled to the number of individuals to compare forest-species richness among these habitats. We plotted curves of the number of individuals against the number of samples to compare forest bird population density. We used taxon sampling curves because they accounted for both the differences in sampling efforts among different habitats and for the natural levels of sample heterogeneity (i.e. patchiness) (Gotelli & Colewell, 2001). Similarly, the species number and abundance of resident forest birds from the two nearest primary forests (Peh *et al.*, 2005) were also subjected to all nonparametric species estimators and taxon sampling curves.

To determine the relationship between the forest birds and the different degraded habitats with respect to their vegetational structure, we used non-metric multidimensional scaling (NMS) in PC-ORD version 4.14 (McCune & Mefford, 1999) to construct a graphical representation of sample units (i.e. point counts) in species space. We chose NMS because it is considered to be the most effective ordination method of ecological community data, whereby sample units are positioned according to the association among species and are not constrained by the a *priori* selection of environmental variables (McCune & Grace, 2002). We performed outlier analysis with the cut-off set at 2.0 standard deviations. We used 'autopilot (slow and thorough)' mode with random starting configurations and Sørensen (Bray–Curtis) as the distance measure. The number of runs with real data and maximum number of iterations were set at 10 and 100, respectively. Also, we examined the relationship of the vegetation variables with two ordination

axes representing the highest proportion of variance in the species data of the final optimum ordination space. The distance between two point count stations in the ordination of sample scores reflects the relative dissimilarity in their species compositions. We then plotted the vegetation variables as vectors on a joint plot to show their relationships with the species scores. We used PC-ORD version 4.14 (McCune & Mefford, 1999) to perform multiresponse permutation procedures (MRPP) to compare the forest avian communities of different habitats. As our dissimilarity measure, we chose Sørensen distance as recommended for community data by McCune and Mefford (1999). The test statistic, *T*, indicates the separation of the groups, and the chance-corrected within-group agreement, *A*, shows homogeneity within groups.

To forecast how an increase in the proportion of overhead canopy cover would affect the proportion of persistent forest species in the degraded habitats, we first performed binary logistic regression analyses on each of the species using canopy cover as a predictor and the presence–absence of each forest species as a response in 240 samples, which included all the different habitat types. The forest species that significantly responded to the proportion of main canopy cover ($P < 0.05$) were entered in a simulation, whereby the proportion of these forest species occurring was calculated for an increasing proportion of main canopy cover (i.e. 0%, 5%, … , 100%). A detailed description of the simulation method is in Soh *et al.* (2006).

RESULTS

In our point counts, we sighted 498 individuals representing 62 forest species. All degraded habitats had lower estimated species richness values than those of the primary forests (Fig. 1). Of the 188 forest species recorded in the local primary forest sites (Peh *et al.*, 2005), approximately 24% were recorded in rubber tree plantations, 20% in oil palm plantations, and 16% in open habitats. Since the sampling efforts were unequal in different habitats, the mean forest species richness estimates (± 95% confidence interval) for the different habitats were 76.0 ± 9.0 for rubber tree plantations, 46.3 ± 3.1 for oil palm plantations, and 53.1 ± 7.2 for open habitats (Fig. 1). In contrast, the two nearby primary forests had higher mean forest species richness values of 208.4 ± 13.4 and 180.0 ± 8.2, respectively (Peh *et al.*, 2005). The mean number of forest species recorded per sample (i.e. species density) among the habitats were 2.58 ± 0.48, 1.64 ± 0.22, and 1.17 ± 0.34 for rubber tree plantations, oil palm plantations, and open habitats, respectively. The two primary forests had higher species densities of 6.06 ± 0.46 species per sample and 5.61 ± 0.42 species per sample (Peh *et al.*, 2005). The rarefaction curves suggested that all degraded habitats had lower forest-species richness, forest-species density, and population density than primary forests (Fig. 2a–c). Among degraded habitats, rubber tree plantations had the highest forest-species richness, forest-species density, and population density, whereas open habitats and oil palm plantations had similar values. At the specific level, eight species showed significant differences in individual abundance between different habitats (Table 1). All these species were significantly more abundant in the rubber tree plantations than the other habitats. The most common forest species in the rubber tree plantations was *Dicaeum trigonostigma*.

The presence of the different dietary groups of forest birds did not vary with habitat type because the richness and abundance of frugivores and insectivores were not significantly different across habitat types. However, the use of the different vertical vegetational strata by the birds varied with habitat type ($\chi^2 = 28.88$, d.f. = 6, $P < 0.01$), with more forest bird individuals seen in the shrubs in oil palm plantations and fewer in the understory stratum in rubber tree plantations than expected. The observed activity of each dietary group of forest birds also varied with habitat type. More frugivores were seen moving in rubber tree plantations and fewer were seen perching in open habitats than expected ($\chi^2 = 13.30$, d.f. = 4, $P < 0.01$). More insectivorous individuals were seen perching in open habitats and fewer were doing so in rubber tree plantations ($\chi^2 = 18.09$, d.f. = 4, $P < 0.01$). Overall, more forest birds were seen moving in rubber tree plantations and perching in open habitats ($\chi^2 = 20.29$, d.f. = 4, $P < 0.01$).

When we applied NMS to the matrix of species abundance for 97 forest and non-forest bird species, seven species were identified as outliers and were therefore excluded from the analysis. A final optimal three-dimensional ordination space explained 65.5% of the variance in the data (Table 2). We plotted joint plots of sample scores and species scores using the second and third
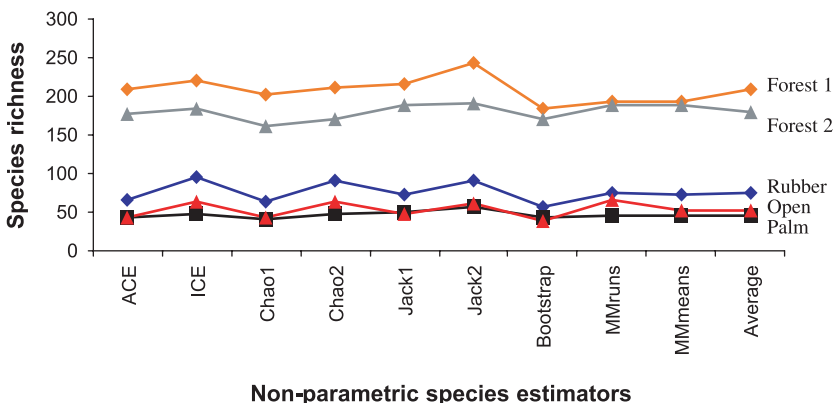
Figure 1 Nonparametric species richness estimations of different habitats. MMruns and MMmeans refer to Michaelis – Menten runs and Michaelis – Menten means, respectively.

NMS axes, which explained 23.9% and 21.0% variance of the data, respectively (Table 2). A graphical overlay of habitat on the ordination of sample scores distinguished open habitat point count stations from those found in the oil palm plantations (Fig. 3a). However, the rubber tree plantation point counts were scattered among those of the oil palm plantations and open habitats. This suggests that the dissimilarity in species composition between rubber tree plantations and both oil palm plantations and open habitats was lower than that between the latter two habitats. Furthermore, our MRPP analysis showed that although all the pairs of habitats were significantly different from each other, the difference between open habitat and oil palm point counts was greater ($T = -54.86$, $A = 0.19$, $P = 0.01$) than the difference between rubber tree and oil palm plantations ($T = -23.47$, $A = 0.08$, $P = 0.01$), and that between rubber tree plantations and open habitats ($T = -26.75$, $A = 0.14$, $P = 0.01$). The ordination of

species scores identified the bird species separating the point count stations of different habitats (Fig. 3b). For example, *Dryocopus javensis* (Sp2) and *Megalaima australis* (Sp9) were forest species that were associated more with open habitats than with the plantations, whereas *Chalcophaps indica* (Sp28) and *Pycnonotus simplex* (Sp44) were associated with oil palm plantations. Three distinct clusters of forest bird species were broadly formed in relation to the vegetation variables (Fig. 3a,b). Vector plots of vegetation variables showed that bird species dominating open habitat point counts and species in group 1 (e.g. *Pycnonotus zeylanicus*), both of which clustered in the upper left quadrant of the ordinations, were associated with vegetation < 8 m and with shrub volume and food resource abundance. On the other hand, birds dominating oil palm plantation point counts and species in group 2 (e.g. *Cacomantis variolosus*) clustered in the upper and the lower right quadrants of the ordinations and were associated with canopy cover. Finally, group 3 comprised the species that were not sensitive to the number of tall trees (e.g. *Orthotomus atrogularis*).

Binary logistic regression showed that 11 of the 62 forest species found in degraded habitats responded significantly to canopy cover. Our simulations revealed that all these species, except one, would not be found at point count stations without canopy cover (Fig. 4). However, they should be present in point count stations with at least 5% canopy cover.

DISCUSSION

Approximately, a third of forest bird species were found in the agricultural countryside of southern Peninsular Malaysia. These species included some globally threatened forest birds such as *Psittinus cyanurus* and *P. zeylanicus*. Although this may imply that the clearance of forest for agricultural purposes may not spell immediate doom for some of these vulnerable species, we have to emphasize that the two extensive nearby fragments of primary forest in the study region undoubtedly contributed to the relatively high forest species richness observed in these degraded habitats. Furthermore, we do not have data on the long-term sustainability of the forest bird populations in degraded habitats and it is possible that nearby primary forests serve as a source habitat. The two major avian dietary groups, frugivores and insectivores, were represented in all land-use types, potentially providing important ecological services to these degraded habitats (Sekercioglu *et al.*, 2004).

Since sample-based rarefaction curves of rubber tree plantations did not reach an asymptote, our rapid assessment is likely to have underestimated the occurrence of forest birds and more forest species could have been detected with more point counts in rubber tree plantations. Based on the estimates of the actual species richness of this habitat, we failed to observe 19–51% of forest species found in rubber tree plantations. Also, 19–54% and 5–32% of forest species were missed in open habitats and oil palm plantations, respectively. We conducted our surveys over a relatively short time period (6 months) and undoubtedly overlooked some inconspicuous species. For example, *Rollulus rouloul* was regularly encountered by the indigenous people in
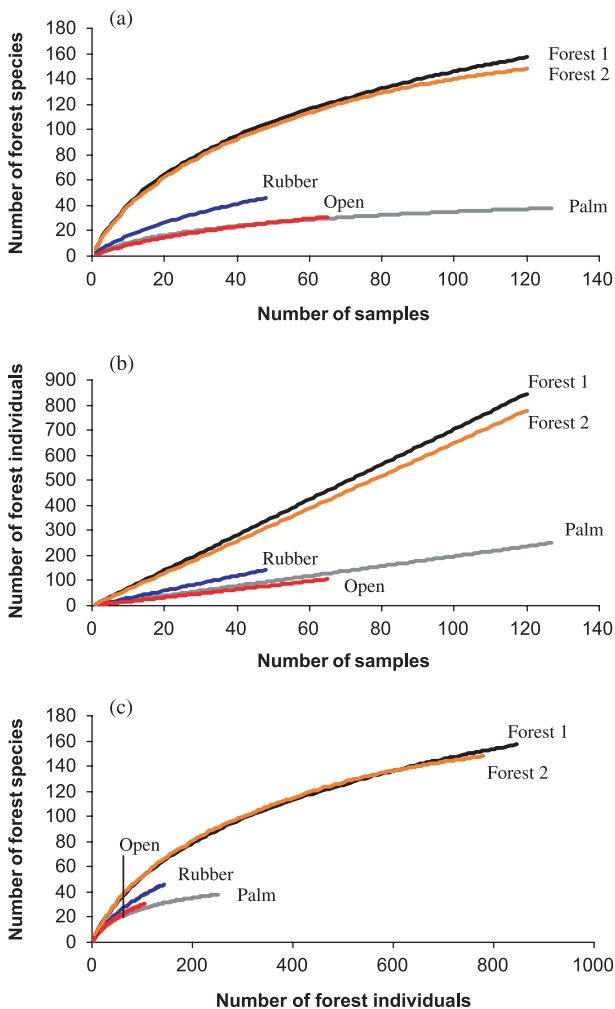
Figure 2 Sample-based rarefaction curves displaying estimated forest bird (a) species richness, (b) species density, and (c) population density in rubber tree plantations (rubber), oil palm plantations (palm), open habitats (open), primary forest in Sungei Bantang (forest 1) (Peh *et al.*, 2005), and primary forest in Gunung Belumut (forest 2) (Peh *et al.*, 2005).

Table 1 Mean numbers of individuals of bird species recorded per point count in rubber tree plantations, oil palm plantations and open habitats

Scientific name	Common name	Code	Rubber	Oil palm	Open
Celeus brachyurus	Rufous woodpecker	Sp1	0	0.063	0.046
Dryocopus javensis	White-bellied woodpecker	Sp2	0	0	0.015
Picus miniaceus	Banded woodpecker	Sp3	0.042	0.031	0
Picus puniceus	Crimson-winged woodpecker	Sp4	0.042	0	0.015
Picus mentalis	Checker-throated woodpecker	Sp5	0.042	0.008	0
Meiglyptes tristis	Buff-rumped woodpecker	Sp6	0	0.039	0.031
Megalaima chrysopogon	Gold-whiskered barbet	Sp7	0.083	0.008	0.015
Megalaima henricii	**Yellow-crowned barbet**	**Sp8**	**0.021**	**0**	**0.031**
Megalaima australis	Blue-eared barbet	Sp9	0	0	0.015
Calorhamphus fuliginosus	Brown barbet	Sp10	0.021	0	0
Anthracoceros malayanus	**Black hornbill**	**Sp11**	**0**	**0**	**0.046**
Aceros comatus	**White-crowned hornbill**	**Sp12**	**0**	**0.016**	**0.046**
Alcedo meninting	Blue-eared kingfisher	Sp13	0.042	0.008	0
Ceyx erithacus	Oriental dwarf kingfisher	Sp14	0	0.016	0
Lacedo pulchella	Banded kingfisher	Sp15	0.021	0	0.015
Nyctyornis amictus	Red-bearded bee-eater	Sp16	0	0.008	0
Cuculus micropterus	Indian cuckoo	Sp17	0.021	0.031	0.015
*Cuculus saturatus**	Oriental cuckoo	Sp18	0.042	0	0
Cacomantis sonneratii	Banded bay cuckoo	Sp19	0	0.016	0
Cacomants variolosus	Brush cuckoo	Sp20	0.021	0	0
Surniculus lugubris	Drongo cuckoo	Sp21	0.021	0.008	0
Phaenicophaeus sumatranus	**Chestnut-bellied malkoha**	**Sp22**	**0**	**0**	**0.031**
Phaenicophaeus curvirostris	Chestnut-breasted malkoha	Sp23	0.021	0	0.015
Psittinus cyanurus	**Blue-rumped parrot**	**Sp24**	**0.083**	**0.039**	**0.077**
Loriculus galgulus	Blue-crowned hanging parrot	Sp25	0.146	0.354	0.415
Psittacula longicauda	**Long-tailed parakeet**	**Sp26**	**0.021**	**0.055**	**0.077**
Hemiprocne comata	Whiskered treeswift	Sp27	0.042	0	0
Chalcophaps indica	Emerald dove	Sp28	0.083	0.031	0.015
Treron olax	Little green pigeon	Sp29	0.021	0.039	0.077
Treron curvirostra	Thick-billed green pigeon	Sp30	0.021	0	0
Ducula aenea	Green imperial pigeon	Sp31	0	0.008	0
Cymbirhynchus macrorhynchos	Black-and-red Broadbill	Sp32	0.021	0	0
*Gerygone sulphurea**	Golden-bellied gerygone	Sp33	0.063	0	0.031
*Irena puella**	Asian fairy bluebird	Sp34	0.063	0	0
Chloropsis cyanopogon	Lesser green leafbird	Sp35	0	0	0.015
Chloropsis cochinchinensis	Blue-winged leafbird	Sp36	0.021	0.016	0
*Dicrurus paradiseus**	Greater racket-tailed drongo	Sp37	0.375	0.134	0.077
Hypothymis azurea	Black-naped monarch	Sp38	0	0.008	0
*Tephrodornis gularis**	Large woodshrike	Sp39	0.063	0	0
*Copsychus malabaricus**	White-rumped shama	Sp40	0.063	0.016	0
Gracula religiosa	Hill myna	Sp41	0.042	0.071	0.015
Pycnonotus zeylanicus	**Straw-headed bulbul**	**Sp42**	**0.021**	**0.039**	**0.015**
Pycnonotus cyaniventris	**Grey-bellied bulbul**	**Sp43**	**0.042**	**0**	**0**
Pycnonotus simplex	Cream-vented bulbul	Sp44	0	0.024	0
Pycnonotus brunneus	Red-eyed bulbul	Sp45	0.021	0.055	0.046
Pycnonotus erythropthalmos	Spectacled bulbul	Sp46	0.063	0.016	0.031
Ixos malaccensis	Streaked bulbul	Sp47	0	0.016	0
Hemixos flavala	Ashy bulbul	Sp48	0.042	0	0.031
Orthotomus atrogularis	Dark-necked tailorbird	Sp49	0.125	0.205	0.169
Malacocincla abbotti	Abbott's babbler	Sp50	0	0.024	0
Macronous gularis	Striped tit babbler	Sp51	0.063	0.157	0.077
Prionochilus maculatus	Yellow-breasted flowerpecker	Sp52	0.021	0	0
Prionochilus percussus	Crimson-breasted flowerpecker	Sp53	0.042	0.016	0
Dicaeum chrysorrheum	Yellow-vented flowerpecker	Sp54	0.021	0	0
*Dicaeum trigonostigma**	Orange-bellied flowerpecker	Sp55	0.646	0.228	0.077
*Dicaeum concolor**	Plain flowerpecker	Sp56	0.146	0.031	0

Table 1 Continued

Scientific name	Common name	Code	Rubber	Oil palm	Open
Dicaeum cruentatum	Scarlet-backed flowerpecker	Sp57	0.021	0.031	0
Anthreptes singalensis	Ruby-cheeked sunbird	Sp58	0.042	0.016	0.015
Hypogramma hypogrammicum	Purple-naped sunbird	Sp59	0.021	0	0
Arachnothera longirostra	Little spiderhunter	Sp60	0.021	0.071	0
Arachnothera chrysogenys	Yellow-eared spiderhunter	Sp61	0.021	0	0
Arachnothera affinis	Grey-breasted spiderhunter	Sp62	0.042	0.016	0.015

Species are broadly grouped based on non-metric multidimensional scaling (Fig. 3). Scientific and common names follow Inskipp *et al.* (1996). Species in bold are globally threatened or near threatened (BirdLife International, 2000). *denotes statistical significance ($P < 0.05$) of Kruskal–Wallis test for bird abundance across the habitats.

Table 2 Proportion of variance represented by the final three axes of the NMS ordination and the Pearson correlation coefficients of vegetation structural variables with axes

	NMS1	NMS2	NMS3
Variance represented (r^2)			
Increment	0.206	0.239	0.210
Cumulative	0.206	0.446	0.655
Correlation with NMS axis (r)			
Tall tree	0.363	0.067	0.180
Canopy cover	−0.064	0.474	−0.163
Food resources	0.094	−0.102	0.096
Shrub volume	0.039	−0.303	0.113
Understory volume	0.172	−0.188	0.109

their home gardens, but was not observed during our surveys. Furthermore, we missed some species that bred during the period of surveys. For instance, *Pycnonotus atriceps*, which frequents open habitats (K.S.-H.P., pers. obs.) was not seen in any of the surveys that coincided with their breeding period of January to September (Robson, 2000). During the breeding season, forest birds may be more sedentary (Peh & Ong, 2002) and confined to specific habitats (Yap, 2005). Lastly, we also failed to observe some species that undertook local migrations during their non-breeding season (e.g. *Ptilinopus jambu*; Robson, 2000), which coincided with our surveys.

Our surveys broadly distinguished two major species groups: species associated with dense canopy cover in oil palm plantations and species connected with high food resource abundance and dense vegetation < 8 m in open habitats. Generally, due to its closed canopy, the interior of an oil palm plantation is darker and supports fewer shrubs than the interior of other rural habitats. However, oil palm plantations may still function as habitat for some forest species (e.g. *O. atrogularis*) that feed in the dense canopy layer. On the other hand, the lush shrub layers and fruiting plants attracted some species (e.g. *Treron olax*) to open habitats.

Rubber tree plantations are clearly more attractive to forest birds than are other types of agricultural land. Rubber tree plantations harboured a higher species richness and abundance of forest birds than other degraded habitat types for several possible reasons. First, this artificial habitat had stands of tall trees

> 10 m, providing a main canopy stratum that was possibly used by various arboreal species, such as *Irena puella* and *Tephrodornis gularis*, which were found only in rubber trees. Second, the thin canopy and the straight, tall trunks of mature rubber trees provide light and space for the development of understory and shrub layers (Appendix). These attract a variety of bird species that utilize the different vegetational strata and could explain why rubber tree plantations shared a higher similarity in forest species composition with both oil palm plantations and open habitats. Third, we observed that rubber tree trunks provided a microhabitat that fulfilled the requirements of some bark-gleaning species. For instance, more *Picus mentalis* individuals were encountered in these plantations, feeding on the trunks of rubber trees. However, there was also a small group of species that were not at all sensitive to the density of tall trees and were more common in oil palm plantations and open habitats (e.g. *Meiglyptes tristis*).

The occurrence of a moderate fraction of the forest avifauna in agricultural habitats does not necessarily imply that these degraded habitats are suitable for forest species over longer periods. First, we have no evidence that even the more abundant species are able to sustain their populations in these agricultural habitats in the long term. We believe that the majority of the forest species do not breed in any of our study habitats. Nesting behaviour was observed in only one forest species — *Anthreptes singalensis* — during our surveys in the agricultural landscape. Also, we know little about the availability of food and nesting resources in these degraded areas. More research is needed to monitor the long-term population viability and to understand the phenology and reproductive success of forest species found in these degraded habitats.

Second, the nearby primary forest may act as a source habitat and result in a steady influx of forest birds to our study habitats. Therefore, the bird community we have observed may not be representative of the forest avifauna in agricultural lands that have no primary forests nearby. Fewer forest bird species and individuals tend to utilize food resources that are located further away from their forest habitats (Luck & Daily, 2003).

Finally, the forest avifauna in rural habitats faces competition from both non-forest species (e.g. Oriental magpie robin, *Copsychus saularis*) and invasive species (e.g. white-vented myna and common myna, *Acridotheres* spp.). In rubber tree plantations, oil palm plantations and open habitats, forest species constituted

(a)

(b)
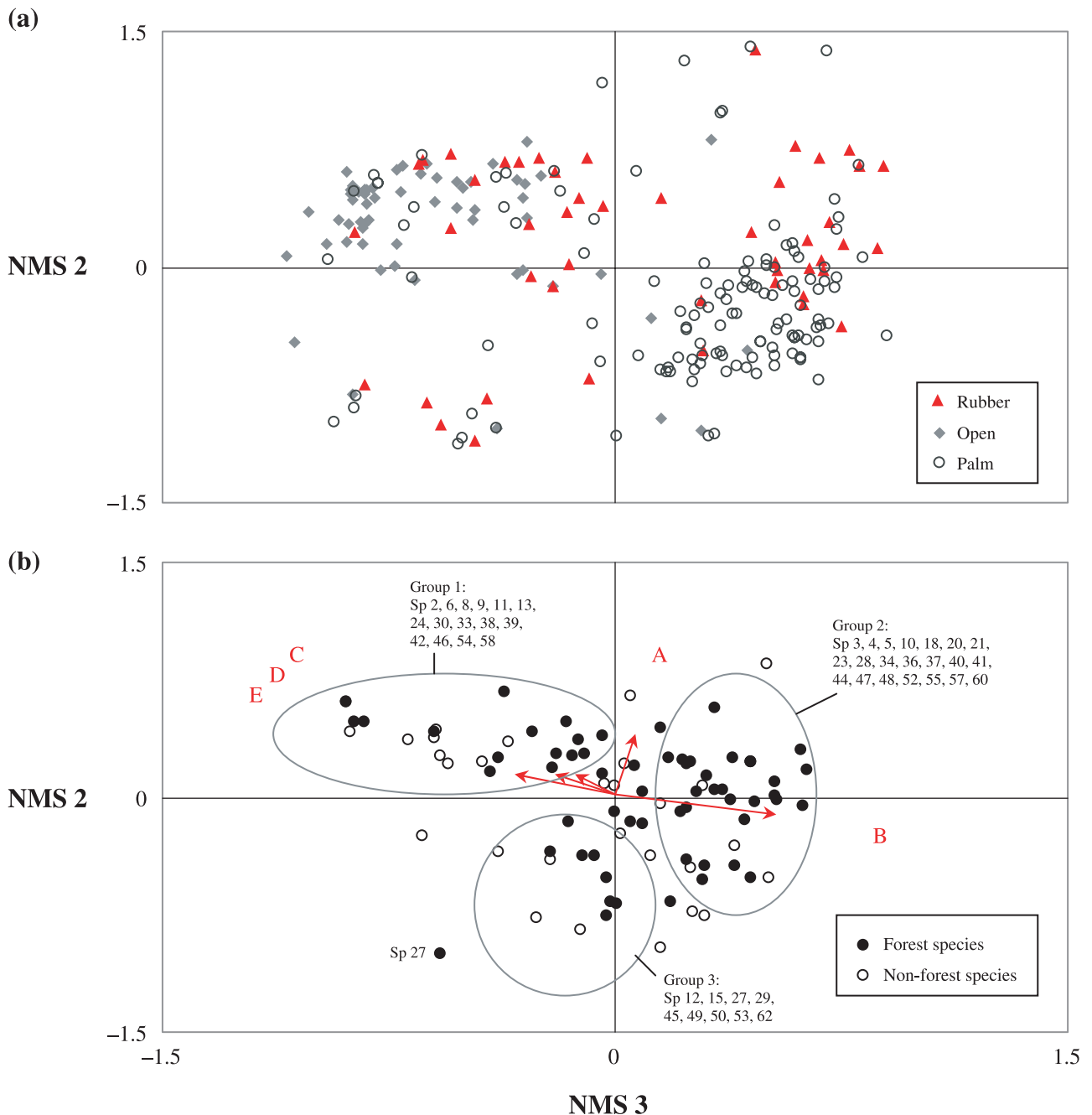
Figure 3 Non-metric multidimensional scaling (NMS) ordination joint plot of sample scores (a) and species scores (b) with vegetation variables: A, number of tall trees > 10 m; B, overhead canopy cover; C, resource(fruit and flower) abundance; D, understory volume; and E, shrub volume. See Table 1 for definitions of species codes and Table 2 for summary statistics of the NMS ordination.

only 39%, 26%, and 17% of the total individuals observed (excluding invasive birds), respectively (K.S.-H.P, unpublished data). Non-forest species clearly outnumber forest species in these agricultural landscapes and compete with them for important resources. In addition, ubiquitous invasive species such as *Acridotheres javanicus* add to the competition for food and nesting holes (Yap & Sodhi, 2004).

Our analysis of avian activity showed that movement was the predominant behaviour of forest species in rubber tree planta-

tions. Together with open habitats, which were used more frequently for perching, both habitat types can act as corridors that increased the connectivity between forest remnants for forest species persisting in agricultural landscapes (Graham, 2001). Our canopy cover simulation suggests that isolated trees found among non-arboreal crops (e.g. banana and coffee) in open habitats may attract many species tolerant of agricultural habitats but sensitive to the absence of canopy cover. In South-East Asia, the oil palm has gained popularity as a profitable crop, and oil
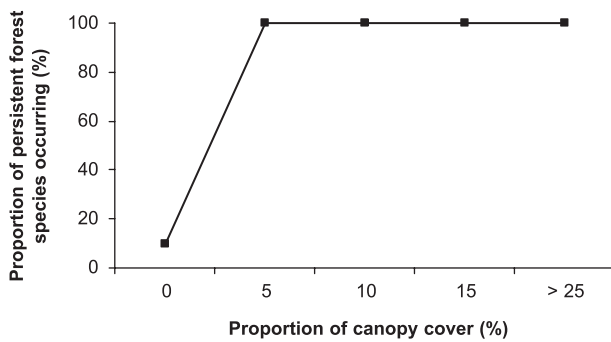
Figure 4 Proportion of persistent forest species occurring in simulated samples with an increasing proportion of main canopy cover.

palm plantations are rapidly replacing other agricultural land uses (Johor Department of Agriculture, http://agrolink.moa.my). Although the dense canopy cover in our oil palm plantations attracts some arboreal species, the simplification of the vertical vegetational structure of this habitat has led to a substantial reduction in the richness of the forest avifauna. The use of shrubs as a preferred stratum by forest birds in oil palm plantations underlines the importance of preserving recolonizing native flora in degraded habitats (Harvey & Haber, 1999).

The practice of agroforestry, in which plantations consisting of arboreal and non-arboreal crops simulate the complex vertical vegetational structure of a forest (i.e. denser canopy cover, higher understory and shrub volume, more food resources), might maximize the occurrence of forest birds in agricultural land-scapes (Schroth *et al.*, 2004). For instance, Thiollay (1995) reported a substantially higher proportion of forest birds (58%) than our study (24%) in Sumatran rubber tree plantations mixed with at least 12 other species of forest and fruit trees. The conservation value of degraded habitats in agricultural landscapes is likely to depend on factors such as the type of crops planted, distance to nearest primary forest, intensity of farming, hunting pressure, amount of remaining native vegetation, and landscape disturbance history. Although preserving large tracts of pristine forest is the only way to protect most forest species, conservation value of agro-ecosystems can be increased by enhancing wildlife habitats between forest remnants.

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Appendix Vegetational structural parameters of rubber tree plantations (rubber), oil palm plantations (palm), open habitats (open), primary forest in Sungei Bantang (forest 1) (Peh *et al.*, 2005), and primary forest in Gunung Belumut (forest 2) (Peh *et al.*, 2005) with 95% confidence intervals.

Parameter	Rubber	Palm	Open	Forest 1	Forest 2
Average number of tall trees > 10 m	3.27 ± 0.27	0.00	0.06 ± 0.06	5.42 ± 0.41	5.60 ± 0.47
Average overhead canopy cover (%)	90.22 ± 1.94	78.30 ± 2.51	23.21 ± 7.64	97.05 ± 0.47	95.40 ± 0.92
Average food resource index	2.23 ± 0.61	1.37 ± 0.20	2.32 ± 0.41	0.82 ± 0.24	0.73 ± 0.22
Average understory volume index	5.20 ± 1.04	6.07 ± 0.76	7.63 ± 1.22	8.89 ± 0.61	10.16 ± 0.59
Average shrub volume index	2.45 ± 0.51	2.17 ± 0.20	4.21 ± 0.61	3.73 ± 0.27	5.36 ± 0.31