Persistence of lowland rainforest birds in a recently logged area in central Java

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Summary

In 2001 and 2002, we assessed avian richness in Linggoasri (central Java) where almost all lowland rainforest had been cleared 3 years previously. Bird surveys were carried out in a selectively-logged forest, two regenerating forests and one pine *Pinus merkusii* plantation. A comparison with a bird list complied at least 3 years prior to logging in Linggoasri showed that 10 lowland bird species may have been extirpated from this area following logging. However, further surveys will be needed to validate these extirpations. A comparison with a list of lowland forest birds of Java shows that only 37% of these occurred in Linggoasri. From the lowland avifauna of Java, sole frugivores and insectivores were less likely to be present in Linggoasri. Smaller, generalist-feeding lowland species, endemic to Java, were more likely to be present in this area. Persisting lowland bird species, however, did not appear to be seriously affected physiologically by habitat degradation, showing no significant loss of body condition or reduction in survival and reproduction. There is an urgent need to preserve the few remaining lowland forest patches of Java and, given the alarming rate of deforestation throughout Southeast Asia, it is critical to conserve adequately large primary lowland forests (e.g. >5,000 ha) if we are to preserve existing lowland avifauna.

Introduction

Human actions are degrading and destroying tropical rainforests at an unprecedented rate (Laurance 1999). Given the plethora of biodiversity harboured in these threatened biomes (Myers *et al.* 2000), they represent obvious foci for conservation biology research. Rainforest loss is rampant in Southeast Asia, with deforestation rates more than double those in other major tropical areas (Achard *et al.* 2002, Sodhi *et al.* 2004a). Only a few areas within Southeast Asia (e.g. Borneo and Sulawesi) retain large tracts of intact primary forests (Laurance 1999). Lowland rainforests of Southeast Asia in particular are gravely imperilled due to continuing anthropogenic actions that convert them into logging concessions, agricultural land and urban areas. Studies have shown that lowland forest isolation and loss can cause avifaunal extirpations in certain areas of Southeast Asia (e.g. Diamond *et al.* 1987, Castelletta *et al.* 2000, Brook *et al.* 2003).

Poor resilience to disturbance is generally assumed to be the characteristic of tropical birds, although certain degraded habitats or areas can continue to sustain a proportion of the primary forest avifauna (e.g. Mitra and Sheldon 1993, Warkentin *et al.* 1995, Marsden 1998, Hughes *et al.* 2002, Sodhi *et al.* 2005). The proportion of the local avifauna using degraded areas may depend on factors such as disturbance

history in addition to the quality and quantity of the remaining forest. Further, long-term viability of apparently resilient forest birds remains uncertain, as it is unclear whether they are able to maintain reproductively viable populations in degraded areas. With devastating deforestation now unfolding in most tropical regions, it is becoming increasingly important to understand what proportion of forest biotas are retained in different deforested areas, and how these species adapt to disturbance and fragmentation.

Lowland rainforest destruction in Indonesia is widespread, but with almost total loss in some areas (Jepson *et al.* 2001). For example, on the Indonesian island of Java, deforestation has reached the point where lowland forest has been completely obliterated in many areas (Van Balen 1999). We studied the avifauna in an area of central Java (Linggoasri) where almost all lowland forest was clear-felled 3 years prior to our study. To determine the lowland rainforest avifauna of the area, we sampled regenerating forest in logged areas, exotic plantation and selectively (illegally) logged submontane/lowland forest. We sampled the last two because such forests can potentially serve as refuges for lowland forest birds.

Previously, Van Balen (1999) sampled the lowland birds of 19 sites in Java including Linggoasri at least 3 years prior to logging. To determine the possible bird extirpations following logging, we compared our species list with that obtained by Van Balen (1999) from Linggoasri. Since Van Balen's bird list for our area seemed incomplete (see Results), we also compared our bird list with two checklists of lowland birds of Java (Wells 1985, Van Balen 1999). We were also interested in determining the ecological characteristics of lowland birds persisting in the study area. Therefore, using a more complete list of lowland forest birds of Java (Wells 1985), we compared the characteristics (body size, feeding guild membership and geographic range) of species present at our site with those that were absent. Body size, feeding guild membership and geographic distribution are considered individually or collectively as important predictors of bird extirpations (e.g. Gaston and Blackburn 1995, Kattan *et al.* 1994, Manne *et al.* 1999, Sodhi *et al.* 2004b). It may take over a century for a tropical forest bird species to be finally lost from an area following habitat degradation (Brooks *et al.* 1999), meaning the occurrence of a species in deforested or degraded areas may not be indicative of long-term viability. Because tropical birds are generally long-lived (Martin 1996), a convincing demonstration of resilience would require monitoring of marked individuals over many years. Even if such long-term studies could be conducted, time to implement conservation actions may be limited in light of the alarming rate of deforestation in Southeast Asia.

The major objective of our study was to determine the persistence (resiliency), at least over a short term, of an extremely badly affected lowland rainforest avifauna. We collected and compared data from different forest types on the body condition, proportion of individuals reproducing, age structure, sex ratio and recaptures, assuming that these represent adequate surrogates of avian reproductive success and survival (see Sodhi 2002). We demonstrate a low lowland avifaunal richness following massive forest loss, but nevertheless hope of some tangible conservation measures to protect remnant lowland rainforests of Java as well as of Southeast Asia.

Methods

We conducted research between 8 April 2001 and 10 June 2002 at Linggoasri (109°30′E, 7°00′S), located in the Dieng Mountains of central Java, Indonesia (Fig. 1).
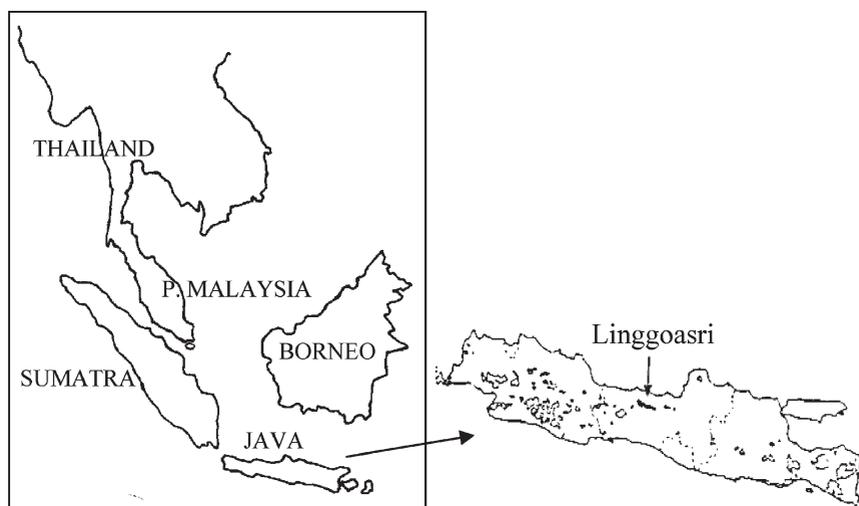
Figure 1. A map of Southeast Asia showing the location of the study area (Linggoasri, on the island of Java).

The total contiguous forested area of the Dieng Mountains is 25,500 ha, containing the last remaining large tracts of sub-montane and montane forests in central Java. Prior to logging in 1998, Linggoasri contained both undisturbed and disturbed lowland and montane forests (see Nijman and Van Balen 1998). Overall, Java has experienced massive deforestation, with only 2.3% of native lowland forest currently remaining (Van Balen 1999).

Research was conducted in selectively-logged submontane/lowland forest (at least 80 years old; 30–50% of the canopy illegally logged; elevation 1,200 m; hereafter selectively logged forest); two young secondary lowland forests (clear cut in 1998; Thomas Oni pers. comm.), one next to the selectively-logged forest (secondary forest 1; elevation 900 m) and the other (secondary forest 2; elevation 600 m) about 3 km away from the selectively-logged forest; and pine (*Pinus merkusii*; planted in 1952; elevation 700 m) plantation. All forests were contiguous with each other. Selectively-logged forest and secondary forests 1 and 2 collectively occupied about 520 ha. The pine plantation was approximately 120 ha in area. The non-forested areas surrounding the forests consisted of paddy fields (*c.* 132 ha) and small villages (*c.* 36 ha).

We sampled the bird community by two methods: point-counts and mist-netting. Continuing logging operations limited our point-count stations to 10 in the selectively-logged forest. Twenty five point-count stations were used in each of the other forest sites sampled. During each survey period (8–12 April, 9–13 June, 9–12 July 2001, 7–10 June and 7–10 July 2002), point-counts were made in all sites between 07h00 and 11h00 during fair weather (not during heavy rain or strong wind). At each point-count station, one observer recorded birds for 10 min (seen or heard; except those flying over the canopy, e.g. swifts and raptors) within 25 m radius. The same observer (M. C. K. S.) conducted all point-counts. Point-count stations during a survey period were 200 m apart and started from the edge of the forest. Due to safety concerns, all point-count stations were placed along the existing trails. We are aware that this might have caused underestimation of the existence and abundance of bird species that avoid forest trails.

Mist-netting was conducted at all sites, using 10–12 mist-nets (2.5 × 12.0 m, 36 mm mesh) placed along trails. During each of five sampling periods, 1.5 days of mist-netting were conducted at a site. Nets were usually opened at 06h00 and closed at 17h30. When it rained, nets were closed earlier to prevent bird mortality. Total net-hours were 825, 820, 941 and 770 in selectively-logged forest, secondary forest 1, secondary forest 2 and pine plantation, respectively. All captured individuals were identified, measured, banded and released.

Captured individuals were sexed (based e.g. on plumage coloration), aged (<1 or >1 year old, based on skull pneumatization) and weighed. Breeding status was assigned based on the presence or absence of a brood patch. A bird was considered recaptured if it was caught again at the same location during any of the subsequent mist-netting sessions (excluding days of the same survey period). Each individual was used only once for recapture calculations. We determined the presence of ectoparasites (chewing lice, suborder Mallophaga) by carefully examining the right wing against sunlight. Parasitic prevalence has been predicted to be high in lower-quality habitats (Sodhi 1995). We determined ectoparasite intensity by counting the number of lice present on the same right wing. The presence and number of fault bars was determined by carefully examining the tail against sunlight. Fault bars are suspected to be caused by nutritional stress during feather growth and are considered as indicators of body condition (e.g. Steeger and Ydenberg 1993). A rare species, at least in the undergrowth, was considered as one with less than two individuals caught per 1,000 net-hours (Sodhi 2002). Migratory birds were excluded from comparisons of body condition and demographic variables.

Comparisons were usually made at the community/population level (e.g. sex ratio). However, when sample sizes permitted, certain variables were compared in two species – Little Spiderhunter *Acrachnothera longirostra* and White-breasted Babbler *Stachyris grammiceps* – to determine whether community-level patterns were observed in species-level comparisons. White-breasted Babbler is endemic to Java (and Bali) and is a forest-dependent species, largely restricted to the understorey of primary forests and is globally Near Threatened (MacKinnon and Phillipps 1997, BirdLife International 2001), whereas Little Spiderhunter is also found commonly in secondary forests, plantations and gardens (MacKinnon and Phillipps 1997). We felt that these two species with differing habitat requirements would be ideal to test and compare species-level resilience in degraded forests.

To determine the vegetation/habitat characteristics, vegetation sampling was conducted at each study site. Within a 5 m radius of each point-count station, we recorded the diameter at breast height (DBH) of all trees, fruiting and flowering tree abundance, canopy cover using a densiometer, leaf litter depth (for each station, an average of 12 readings by inserting a metal ruler into the leaf litter) and shrub cover via visual estimation. To estimate an index of arthropod abundance at the sites, we performed 20 sweeps of shrubs at each point-count station using an insect net (30 cm × 60 cm). All arthropods sampled were counted and classified to the family level and were grouped as small (<1 cm in body length) or large (≥1 cm).

In the absence of comprehensive pre-disturbance data for the area, we used a list of lowland bird species occurring in Java made by Wells (1985). We inspected this list and removed some inappropriate species (e.g. montane species) such as Mountain Imperial Pigeon *Ducula badia*. To make this list comparable to our data, we also excluded nocturnal species, those that fly over the canopy (e.g. swifts and raptors) and

waterbirds. We classified species according to feeding guilds using Smythies (1981) and McKinnon and Phillipps (1997). Body lengths were obtained from McKinnon and Phillipps (1997). To determine how endemism is affecting resilience, we classified all lowland species as either endemic to Java or widespread (non-endemics).

Analyses

Species accumulation curves were computed using EstimateS version 5.0 (Colwell 1997). We assessed sampling completeness using smoothed species accumulation curves (average of 100 random reorderings of the sample data). In addition to assessing sampling efficiency, we used these accumulation curves as rarefaction curves (Gotelli and Colwell 2001). We did not calculate any species richness estimators as there is no consensus on these and research on them is still evolving (see Walther and Martin 2001, Gotelli and Colwell 2001, Herzog *et al.* 2002).

  We used generalized linear modelling (GLM; logistic regression) to compare three characteristics of lowland species (i.e. body size, geographical distribution and feeding guild) that were either present or absent from our "disturbed" study areas. Species were classed as "resilient" to disturbance if present (code = 1), and "sensitive" if absent (code = 0). Body size (length, B) was represented as a log-transformed continuous predictor variable, whilst geographical range (R) and feeding guild (F) were specified as categorical predictors (R = Javan endemic or widespread; F = carnivore–insectivore, frugivore, frugivore–insectivore, insectivore or insectivore–nectivore). Taxonomic order was entered as a cofactor, to control for phylogenetically related statistical non-independence (see Koh *et al.* 2004), because our use of logistic regression, and the inclusion of categorical predictor variables, precluded the use of the more traditional nested analysis of variance (Harvey and Pagel 1991) and independent contrast analysis (Felsenstein 1985). The Akaike Information Criterion, corrected for small sample size (AIC_c) was used as an objective means of regression model selection, based on considerations of both predictive power and parsimony (see Burnham and Anderson 1998).

  All statistical analyses were performed using Minitab Statistical Software version 13.2 (Minitab 2000) and the Statistical Analysis System (SAS) package (SAS Institute 1990).

Results

Species richness

Species accumulation curves, for both point-counts and mist-netting, appeared to approach saturation for some but not all sites (Fig. 2). For example, in the pine plantation, where we caught only five individuals during 770 net-hours, sampling saturation could not be achieved (Fig. 2). Accumulation curves show that species richness was the highest in the secondary forest 2 and lowest in the pine plantation (Fig. 2). However, slightly higher species richness was found in secondary forest 1 than selectively logged forest through point-counts; a reverse trend was found using mist-netting data (Fig. 2).

  We did not record 10 lowland species recorded by Van Balen (40 species in total) from Linggoasri before it was logged in 1998 (Blue Whistling Thrush *Myiophonus caeruleus*, Crested Jay *Platylophus galericulatus*, Greater Racket-tailed Drongo
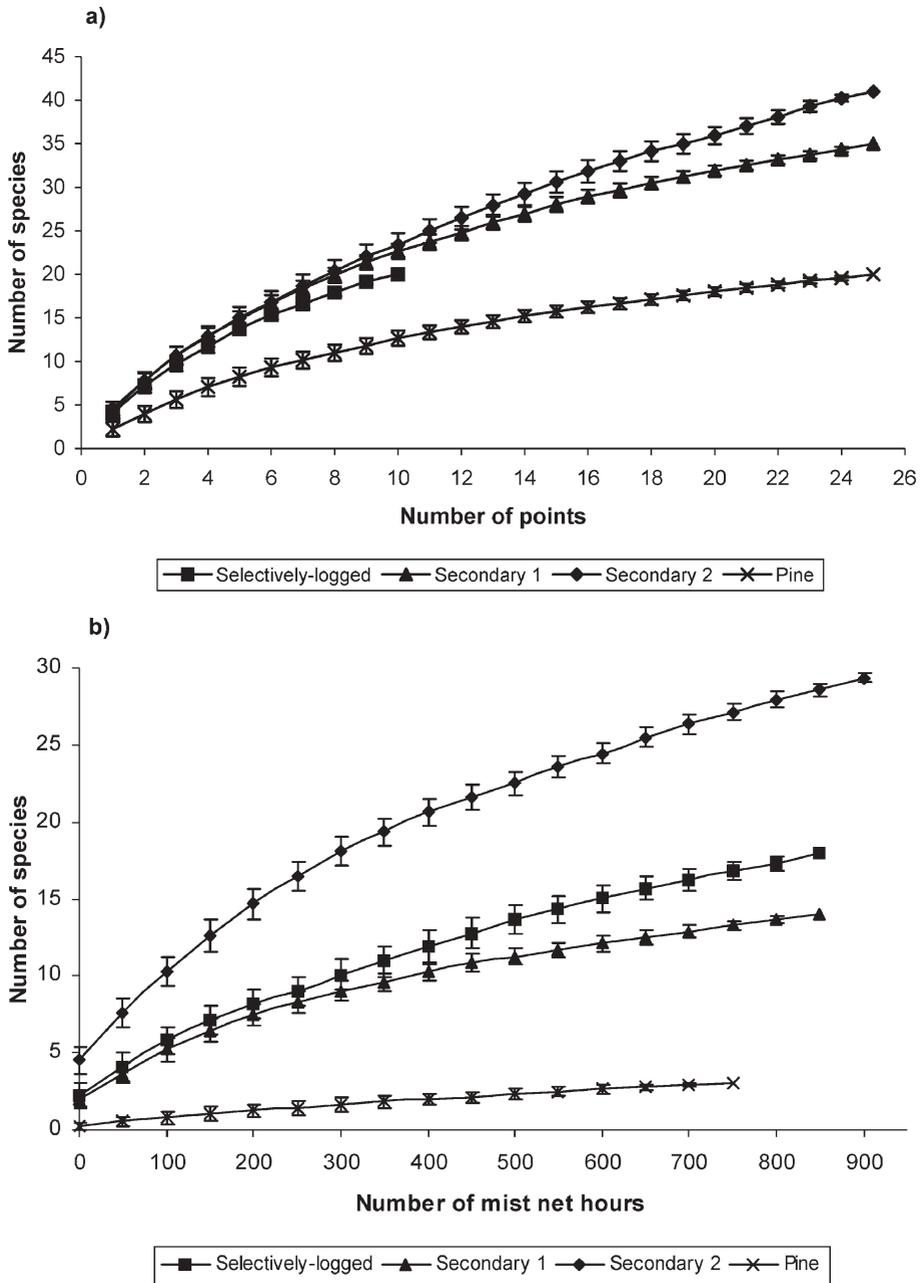
Figure 2. Smoothed species accumulation curves (± 95% confidence interval) for species recorded through point-counts (a) and mist-netting (b) in four forest sites in central Java.

Dicrurus paradiseus, Grey-cheeked Green Pigeon *Treron griseicauda*, Hill Blue Flycatcher *Cyornis banyumas*, Large Wood-shrike *Tephrodornis gularis*, Large Wren-babbler *Napothera macrodactyla*, Pale Blue Flycatcher *Cyornis unicolor*, Slender-billed Crow *Corvus enca* and Velvet-fronted Nuthatch *Sitta frontalis*). Most

likely these species have gone extinct from Linggoasri following logging. However, we could not do further analyses as we found that we recorded nine more lowland species (e.g. Banded Pitta *Pitta guajana* and Banded Woodpecker *Picus miniaceus*) by point-counts alone that Van Balen did not record from Linggoasri. Therefore Van Balen's bird inventory was probably incomplete.

When we pooled the point-count and mist-netting data, the number of lowland birds was highest in the secondary forest 2 (31 species), followed by the secondary forest 1 (26), selectively-logged forest (20) and pine forest (11). Using a list of 105 lowland bird species occurring in Java (Wells 1985), 29.5%, 24.8%, 19.0% and 10.5% of species were found in the secondary forest 2, secondary forest 1, selectively-logged forest and pine plantation, respectively. However, if we use 83 lowland bird species recently found occurring in Java by Van Balen (1999), 37.3%, 31.3%, 24.1% and 13.3% species were recorded in the secondary forest 2, secondary forest 1, selectively-logged forest and pine plantation, respectively. Based on point-count data, the mean number of lowland species was 4.6 ± 0.42 (standard error), 4.4 ± 0.98, 4.1 ± 0.57 and 2.4 ± 0.34 in secondary forest 2, secondary forest 1, selectively-logged forest and pine plantation, respectively (repeated ANOVA, $F_{1,2} = 50.44$, $P = 0.02$). Similarly, mist-netting data also showed that on average the highest (4.58 ± 0.26 species/100 net-hours) and lowest (0.36 ± 0.19) lowland species richness was in secondary forest 2 and pine plantation, respectively ($F_{1,2} = 30.90$, $P = 0.03$).

GLM using information-theoretic model selection showed that body length, endemism and feeding guild were all important predictors of the presence of lowland birds at the disturbed sites, after correcting for phylogenetic non-independence (Table 1). Without a phylogenetic correction, body length was not included in the most parsimonious model (Table 1). The logistic regression equation for the best model was as follows:

Table 1. Model selection results, relating "resilience" of lowland birds to disturbance (i.e. presence in or absence from degraded sites) in central Java to log-transformed body length [B], geographical range [R] and feeding guild [F], with (i) a cofactor included to control for phylogenetically related statistical non-independence (taxonomic order [O]), and (ii) no phylogenetic control. Model selection criteria are the maximized log-likelihood [log(L)], number of parameters (K; includes regression intercept and coefficients), information criterion (AIC$_c$), difference from best model (Δ_i) and Akaike weight (w_i).

Model	log(L)	K	AIC$_c$	Δ_i	w_i
Taxonomic order as phylogenetic control factor					
O+B+R+F	54.55	12	136.5	0.0	0.34
O+B+F	56.14	11	137.1	0.6	0.25
O+R+F	56.26	11	137.4	0.9	0.22
O+F	58.19	10	138.7	2.2	0.11
O+B+R	61.60	8	140.7	4.2	0.04
O+B	63.37	7	141.9	5.4	0.02
O+R	64.14	7	143.4	6.9	0.01
No phylogenetic control factor					
R+F	59.65	6	132.2	0.0	0.46
B+R+F	58.99	7	133.1	1.0	0.28
F	62.00	5	134.6	2.4	0.14
B+F	61.24	6	135.3	3.2	0.09
B+R	66.27	3	138.8	6.6	0.02
R	67.93	2	140.0	7.8	0.01
B	68.44	2	141.0	8.8	0.01

$$\text{Logit(Resilience)} = 6.26 - 1.19 * \ln(B) + 1.70 * (R) - \alpha_1 F - \alpha_2 O$$

$G = 31.38$, df = 11, $P < 0.001$, Concordance = 77.2%, where B is body length, R is geographical range (1 = Javan endemic), F is feeding guild, O is taxonomic order, α_1 = [carnivore–insectivore = 0, frugivore = −1.26, frugivore–insectivore = −0.45, insectivore = −1.21 and insectivore–nectivore = 21] and α_2 = [Columbiformes = −1.55, Coraciiformes = −4.10, Cuculiformes = −4.24, Passeriformes = −2.88 and Piciformes = 1.83] (Table 1). A goodness of fit test revealed no significant deviation from the assumptions of a logistic generalized linear model ($\chi^2 = 73.6$, df = 70, $P = 0.361$), and no over-dispersion of variance ($\hat{c} = 1.05$). From the lowland avifauna of Java, sole frugivores and insectivores were less likely to be present in our disturbed forests. Smaller, generalist-feeding species, endemic to Java, were more likely to be present in our disturbed forests (see Appendixes 1 and 2). The mean body length (in cm) of the bird species was 14.14 ± 1.01 (SE), 14.61 ± 0.91, 15.85 ± 0.85 and 13.00 ± 1.31 in selectively-logged forest, secondary forest 1, secondary forest 2 and pine plantation, respectively. The body lengths did not differ across the sites (Kruskal Wallis ANOVA, $KW = 2.72$, df = 3, $P = 0.77$). The number of frugivores and insectivores also did not differ across the sites (χ^2 tests, $P > 0.33$).

Demographics and body condition of the lowland avifauna

Because very few individuals were captured from the pine plantation, this site is excluded from the following analyses. Across all lowland species, proportionately more females were found in the selectively-logged forest than either secondary forests (Table 2). The number of individuals with brood patches did not differ among the sites (Table 2).

Two species were mist-netted at all four study sites. For White-breasted Babbler, none of the demographic and body condition variables differed across sites. Proportionately fewer Little Spiderhunter adults were found in secondary forest 1 than the other forests (Table 3) and those individuals were more likely to have fault bars in greater numbers than individuals of the same species found at the other study sites (Table 3).

Table 2. Characteristics of bird communities in Linggoasri, Java.

	Selectively logged	Secondary 1	Secondary 2
Rarity (%)	42.9 (14)	33.3 (9)	40.0 (20)[a]
Recapture rate (%)	19.7 (61)	24.3 (37)	15.8 (95)[b]
Proportion of adults (%)	80.3 (61)	75.7 (37)	81.1 (95)[c]
Proportion of males (%)	**33.3 (42)**	**73.1 (26)**	**62.4 (71)[d]**
Proportion of breeding adults (%)	49.0 (49)	37.0 (27)	31.0 (71)[e]
Proportion of individuals with parasites (%)	43.5 (62)	43.2 (37)	31.9 (94)[f]
Mean ectoparasitic intensity	10.08 ± 3.74	9.16 ± 3.17	5.44 ± 1.50[g]
Proportion of individuals with fault bars (%)	29.5 (61)	40.0 (35)	25.0 (92)[h]
Mean number of fault bars	1.10 ± 0.27	1.43 ± 0.49	0.76 ± 0.20[i]

Sample sizes are in parentheses. Significant ($P < 0.05$) results are in bold.
[a]$\chi^2 = 0.21$, $P = 0.9$; [b]$\chi^2 = 1.34$, $P = 0.51$; [c]$\chi^2 = 0.49$, $P = 0.78$; [d]$\chi^2 = \mathbf{13.41}$, $\mathbf{P = 0.001}$; [e]$\chi^2 = 4.00$, $P = 0.14$; [f]$\chi^2 = 2.72$, $P = 0.26$; [g]Kruskal Wallis test $KW = 3.05$, $P = 0.22$; [h]$\chi^2 = 1.34$, $P = 0.51$; and [i]Kruskal Wallis test $KW = 2.66$, $P = 0.26$. $\pm$ indicates the standard error.

Table 3. Population characteristics of two bird species mist-netted at all four study sites in Linggoasri, Java. The top and bottom figures refer to the White-breasted Babbler (*Stachyris grammiceps*) and Little Spiderhunter (*Arachnothera longirostra*), respectively.

	Selectively-logged	Secondary 1	Secondary 2	χ^2 or *KW*	*P*
Recapture rate (%)	20.7 (29)	25.0 (12)	46.1 (13)	2.96	0.23
	50.0 (8)	10.0 (10)	22.9 (35)	4.00	0.14
Proportion of adults (%)	65.5 (29)	91.7 (12)	92.3 (13)	5.45	0.07
	87.5 (8)	40.0 (10)	77.1 (35)	**6.45**	**0.04**
Proportion of males (%)	17.6 (17)	60.0 (10)	50.0 (12)	5.75	0.06
	42.9 (7)	75.0 (4)	51.7 (29)	1.08	0.58
Proportion of breeding adults (%)	88.9 (18)	90.9 (11)	52.8 (13)	5.32	0.07
	0.0 (7)	0.0 (4)	18.5 (27)	2.35	0.31
Proportion of individuals with ectoparasites (%)	75.9 (29)	58.3 (12)	38.4 (13)	5.53	0.06
	12.5 (8)	20.0 (10)	34.3 (35)	1.94	0.38
Mean ectoparasitic intensity	20.24 ± 7.59	3.67 ± 1.13	7.38 ± 4.67	5.20	0.07
	0.63 ± 0.63	8.00 ± 5.54	7.23 ± 3.09	1.69	0.43
Proportion of individuals with fault bars (%)	28.6 (28)	27.3 (11)	30.8 (13)	0.04	0.98
	50.0 (8)	70.0 (10)	21.2 (33)	**8.9**	**0.01**
Mean number of fault bars	1.21 ± 0.43	0.45 ± 0.28	0.62 ± 0.29	0.21	0.90
	1.25 ± 0.56	2.00 ± 1.03	0.59 ± 0.25	**7.79**	**0.02**[a]

Sample sizes are in parentheses. ± indicates the standard error.
[a]Results from Duncan's multiple range test show mean fault bar intensity is significantly higher in secondary 1 than in secondary 2.

Discussion

Lowland avifaunal persistence

Since we did not find 10 lowland bird species in Linggoasri that had been recorded prior to logging suggests there possibly were extirpations caused by logging. However, further surveys using playbacks will be needed to validate these extinctions. Our study also showed that only *c.* 37% of the Javan lowland avifauna was found in the degraded forests of Linggoasri, despite extensive surveys. It is likely that some of the lowland birds of Java did not occur at the site or were extirpated because of continuing disturbance at the site prior to logging. Our inventory also did not reach saturation at all sites. We attempted to minimize this bias by using two sampling methods (i.e. point-counts and mist-netting).

Nonetheless, a similar pattern of low occurrence of forest birds is reported from other degraded areas/sites in Southeast Asia. Only 33% of the original 91 forest bird species in Singapore survived following loss of more than 95% of the forest since the 1800s (Castelletta *et al.* 2000). In Java only 11 lowland bird species persisted in the Bogor Botanical Gardens (86 ha) after 50 years of isolation from nearby forests (Diamond *et al.* 1987). This number represents only about 10% of the lowland avifauna of Java (Wells 1985, Van Balen 1999). Some of our results were similar to those documented by Diamond *et al.* (1987). For example, Horsfield's Babbler *Malacocincla sepiarium* and Little Spiderhunter were present at both sites, while species such as Velvet-fronted Nuthatch were absent from the both sites. However, species such as Banded Pitta, Grey-cheeked Bulbul *Alophoixus bres*, Black-capped

Babbler *Pellorneum capistratum* and Crimson Sunbird *Aethopyga siparaja* were lost from the Bogor Botanical Garden but not from Linggoasri.

There may be a number of reasons for these differences. First, our use of mist-netting probably increased sampling efficiency. Second, the Bogor Botanical Garden is not a typical lowland forest site, since it includes other habitats such as a pond and a river. It is also possible that either the resilience in some species may be site-specific, stochastic, or the species present at our site may be there due to extinction lag time and will be extirpated in future.

Our study also shows that all our degraded forests had low conservation value for lowland forest birds of Java. It is unclear why secondary forest 2 had more lowland birds than other forest. This forest was not particularly high in the environmental variables that we measured (Appendix 3). Perhaps other factors such as differences in human disturbance may be responsible for this pattern. The fact that even a 50,000 ha site contained only 70 lowland bird species suggests that some, if not all, existing Javan lowland forests suffer from human disturbances such as illegal logging, poaching and/or agricultural encroachments (Van Balen 1999). Clearly, better protection of these forests is needed.

Faunal characteristics

Elsewhere in Southeast Asia, studies have shown that 59–97% of the primary forest avifauna is encountered in degraded forests (e.g. plantations or regenerating forests) (e.g. Wong 1986, Johns 1992, Mitra and Sheldon 1993, Thiollay 1995). However, these studies did not show whether birds were reproducing (and thereby maintaining viable populations) in degraded forests. Our study showed that between 31% and 49% of the persisting lowland birds were probably breeding in degraded forests (Table 2), and thus it is possible that moderately degraded forests can continue to provide resources for some lowland species to carry out their breeding activities (see also Wong 1985). It can be argued that a breeding bird might travel to a neighbouring forest to feed, thus giving an erroneous estimate of breeding activities at a forest. Given that breeding forest birds can be sedentary (e.g. Peh and Ong 2002), chances of this bias are minimal. Nest-searches and monitoring would have yielded more precise data but were beyond the scope of the present research.

Variables indicating body condition (the proportion of individuals with ectoparasites and those with fault bars) suggest that the avifaunal community of the degraded forests in Java does not fare worse, physiologically, than that in larger forests (> 2,000 ha) of Sarawak (see Sodhi 2002). As an example, although more than 21% of Little Spiderhunters had fault bars (except for secondary forest 2) – a minimum number reported for the larger Sarawakian forests (Sodhi 2002) – conversely only 18% had ectoparasites (again, except for secondary forest 2) – a minimum value for the larger lowland forests of Sarawak.

Comparative data on the demographics of the endemic White-breasted Babbler are not available, but all the recorded body condition and demographic variables were within the range of those reported for Chestnut-winged Babbler *Stachyris erythroptera* from two large forest fragments (> 450 ha) in Singapore (Sodhi 2002). This suggested that this species may be adapting to forest disturbance, which is a good sign, given its listing as Near Threatened (BirdLife International 2001).

Because of the high species diversity, a typical primary lowland forest contains numerous rare species (Pearson 1977), and is therefore considered a fragile ecosystem particularly vulnerable to environmental disturbance (Goerck 1997). Close to 70% of species are found to be rare in some Southeast Asian primary forests (Wong 1985, Sodhi 2002). Rarity observed by us in degraded Javan forests (33.3–42.9%) was similar to that in fragmented forests (23.1–33.3%; Sodhi 2002), indicating that degraded Javan forests may have failed to retain rare species found in the original primary forest.

Like rarity, recaptures can indicate the quality of a tropical forest. Due to relatively low environmental variability and high bird longevity, quality tropical forests should intuitively have high recaptures (Wong 1986, Karim-Dakong *et al.* 1997, Sodhi 2002). About 20% recaptures have been reported from primary forests (Nagata *et al.* 1996, Sodhi 2002), and all our degraded forests had recaptures close to this number (Table 2). It is therefore possible that remnant avifauna can indeed survive, at least over several months, in degraded forests.

Proportionately more females were found in the selectively-logged forest, possibly indicating high-quality forest, as has been shown for temperate forest (e.g. Gibbs and Faaborg 1990). This forest had the highest canopy cover, larger trees and greater small-sized arthropod abundance compared with other sites (Appendix 3). Further, artificial nests in this forest suffered lower predation than in secondary forest 1 (Sodhi *et al.* 2003). These variables suggest that this forest habitat was of higher quality than other sites and may have attracted more females. However, continued disturbance may have made this site inhospitable for some forest species, and therefore we did not observe the highest species richness at this site. Alternatively, this finding may be because data from different species were pooled.

The lower proportion of adult Little Spiderhunters and more individuals with fault bars indicated that secondary forest 1 habitat may have been lower quality and resources may be limited there, at least for this species. Although the number of flowering tress did not vary across the sites, secondary forest 1 had the lowest abundance of small-sized arthropods, a breeding season food of Little Spiderhunter.

Resilience

The resilient or persistent species in our degraded forests were smaller, generalist in their feeding habits, and endemic to Java. Larger-bodied animals are less able to persist in degraded areas compared with smaller ones (e.g. Gaston and Blackburn 1995). Extinction-proneness of large animals is enhanced because of factors such as low population size, low reproductive rates, large area requirements and/or high food intake (Terborgh 1974, Leck 1979, Pimm *et al.* 1988, Sieving and Karr 1997). Specialist frugivores may be vulnerable in degraded or reduced forests because such areas may not have year-round fruit availability (Leck 1979), and insectivores may not be able to persist because of impoverishment of insect fauna and/or their poor dispersal abilities (Sekercioglu *et al.* 2002). Our results show that certain endemic species were able to cope with forest disturbance. Previous studies have shown that common endemic forest species are able to exploit disturbed habitats (Jones *et al.* 2001). It is possible that certain endemic species may be able to adapt to human disturbance,

especially in historically disturbed areas such as Java. We agree that avian endemism should be high on the conservation agenda (Balmford and Long 1994), but suggest that it should not necessarily be the only variable in assigning conservation priorities.

Conservation implications

Of 10 million ha of original tropical lowland forest on Java, only 2.3% now remains (Van Balen 1999). This remnant forest is severely fragmented in most places, and although 50% of the remaining forest is protected, it is unclear whether this protection is adequate. Our study is based on one location on the island, but if we generalize results for Java, it indicates low conservation potential of degraded forests for the lowland rainforest avifauna. The species most vulnerable to deforestation and disturbance seem to be those with large body sizes, feeding exclusively on insects or fruits. Sites possessing a large number of species with these characteristics should be priority areas for protection. There is an urgent need to preserve existing lowland forest patches on Java, and throughout Southeast Asia, because the maintenance of these is critical to the long-term persistence of the region's surviving avifauna.

Acknowledgements

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Appendix 1. Mean abundance of birds with standard error at four study sites in Linggosari, Java. These data were obtained through point-counts. Common and scientific names, and bird geographic distribution are from MacKinnon and Phillipps (1997). Species in bold represent birds that are dependent extensively or exclusively on lowland forests according to Wells (1985) and were used in our regression model.

Common name	Scientific name	Selectively-logged	Secondary 1	Secondary 2	Pine
Chesnut-bellied Patridge‡	*Arborophila javanica*			0.04 ± 0.04	
Small Buttonquail	*Turnix sylvatica*				0.04 ± 0.04
Pink-necked Green-Pigeon	*Treron vernans*			0.08 ± 0.06	0.12 ± 0.07
Dark-backed Imperial-Pigeon	*Ducula lacernulata*		0.04 ± 0.04		
Barred Cuckoo-Dove	*Macropygia unchall*		0.04 ± 0.04		
Spotted Dove	*Streptopelia chinensis*			0.04 ± 0.04	0.12 ± 0.07
Yellow-throated Hanging-Parrot+	**Loriculus pusillus**		0.04 ± 0.04	0.04 ± 0.04	
Oriental Cuckoo	*Cuculus saturatus*		0.04 ± 0.04	0.04 ± 0.04	
Plaintive Cuckoo	*Cacomantis merulinus*			0.08 ± 0.06	0.12 ± 0.07
Chesnut-breasted Malkoha	**Phaenicophaeus curvirostris**		0.04 ± 0.04		
Greater Coucal	*Centropus sinensis*			0.04 ± 0.04	0.04 ± 0.04
Orange-breasted Trogon	**Harpactes oreskios**		0.04 ± 0.04	0.04 ± 0.04	0.08 + 0.06
Collared Kingfisher	*Todirhamphus chloris*				
Wreathed Hornbill	**Aceros undulates**			0.08 ± 0.06	
Brown-throated Barbet‡	*Megalaima corvine*		0.12 ± 0.07		
Black-banded Barbet+	**Megalaima javensis**	0.2 ± 0.08	0.12 ± 0.07	0.12 ± 0.07	
Orange-fronted Barbet+	**Megalaima armillaris**	0.2 ± 0.08	0.04 ± 0.04	0.04 ± 0.04	
Blue-eared Barbet	*Megalaima australis*	0.4 ± 0.1	0.48 ± 0.1	0.68 ± 0.1	0.16 ± 0.07
Common Goldenback	*Dinopium javanense*			0.04 ± 0.04	
Crimson-winged Woodpecker	*Picus puniceus*	0.1 ± 0.06	0.08 ± 0.06		
Banded Woodpecker	**Picus miniaceus**			0.04 ± 0.04	
Banded Broadbill	*Eurylaimus javanicus*		0.16 ± 0.07	0.08 ± 0.06	
Banded Pitta	**Pitta guajana**		0.04 ± 0.04	0.08 ± 0.06	
Black-winged Flycatcher-shrike	**Hemipus hirundinaceus**		0.04 ± 0.04	0.04 ± 0.04	
Scarlet Minivet	**Pericrocotus flammeus**			0.08 ± 0.06	0.04 ± 0.04
Common Iora	*Aegithina tiphia*		0.08 ± 0.06	0.08 + 0.06	0.04 ± 0.04
Greater green Leafbird	**Chloropsis sonnerati**			0.04 ± 0.04	
Blue-winged Leafbird	**Chloropsis cochinchinensis**		0.04 ± 0.04		
Black-headed Bulbul	**Pycnonotus atriceps**			0.16 ± 0.07	

Appendix 1. Continued.

Common name	Scientific name	Selectively-logged	Secondary 1	Secondary 2	Pine
Black-crested Bulbul	**Pycnonotus melanicterus**		0.08 ± 0.06	0.24 ± 0.09	
Sooty-headed Bulbul	Pycnonotus aurigaster			0.04 ± 0.04	0.36 ± 0.1
Cream-vented Bulbul	Pycnonotus simplex			0.04 ± 0.04	
Grey-cheeked Bulbul	Alophoixus bres	0.2 ± 0.08	0.36 ± 0.1	0.28 ± 0.09	
Short-tailed Magpie	Cissa thalassina	0.3 ± 0.16	0.12 + 0.06		
Great Tit	Parus major			0.08 ± 0.06	
Lesser Shortwing	Brachypteryx leucophrys			0.04 ± 0.04	
Black-capped Babbler	**Pellorneum capistratum**			0.04 ± 0.04	
Horsfield's Babbler	Malacocincla sepiarium		0.16 ± 0.07	0.24 ± 0.09	0.16 ± 0.07
Crescent-chested Babbler†	Stachyris melanothorax			0.04 ± 0.04	
Lesser Forktail	**Enicurus velatus**	0.2 ± 0.08	0.2 ± 0.08		
Arctic Warbler*	Phylloscopus borealis			0.04 ± 0.04	0.08 ± 0.06
Common Tailorbird	Orthotomus sutorius	0.1 ± 0.06		0.04 ± 0.04	0.08 + 0.06
Ashy Tailorbird	Orthotomus ruficeps	0.2 ± 0.08	0.08 ± 0.06	0.16 ± 0.07	
Olive-backed Tailorbird†	Orthotomus sepium	0.7 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.28 ± 0.09
Mountain Tailorbird	Orthotomus cuculatus	0.1 ± 0.06	0.04 ± 0.04	0.04 ± 0.04	
Yellow-bellied Prinia	Prinia flaviventris	0.2 ± 0.08		0.04 ± 0.04	
Bar-winged Prinia	Prinia familiaris		0.04 ± 0.04	0.04 ± 0.04	0.04 ± 0.04
Little Pied Flycatcher	Ficedula westermanni		0.08 ± 0.06	0.04 ± 0.04	
Black-naped Monarch	Hypothymis azurea		0.04 ± 0.04		
Olive-backed Sunbird	Nectarinia jugularis		0.16 ± 0.07	0.04 ± 0.04	0.04 ± 0.04
Crimson Sunbird	Aethopyga siparaja	0.2 ± 0.08	0.04 ± 0.04	0.08 ± 0.06	0.04 ± 0.04
Javan Sunbird‡	**Aethopyga mystacalis**				0.12 ± 0.07
Little Spiderhunter	**Acrachnothera longirostra**	0.1 ± 0.06	0.2 ± 0.08	0.36 ± 0.1	0.04 ± 0.04
Crimson-breasted Flowerpecker	Prionochilus percussus		0.16 ± 0.07	0.04 ± 0.04	
Orange-bellied Flowerpecker	**Dicaeum trigonostigma**	0.1 ± 0.06	0.12 + 0.06		
Blood-breasted Flowerpecker	Dicaeum sanguinolentum	0.2 ± 0.08			
Scarlet-headed Flowerpecker	Dicaeum trochileum			0.04 ± 0.04	0.04 ± 0.04
Oriental White-eye	**Zosterops palpebrosus**	0.2 ± 0.08	0.2 ± 0.08		0.48 ± 0.1
Javan Munia	Lonchura leucogastroides		0.28 ± 0.09	0.04 ± 0.04	0.04 ± 0.04

*Migratory
†Endemic to Java and Bali
‡Endemic to Java

Appendix 2. Birds species mist-netted at four different forests in Linggosari, Java. The numbers of individuals recaptured (if any) are in parentheses. Common and scientific names, and bird geographic distribution are from MacKinnon and Phillipps (1997). Species in bold represent birds that are dependent extensively or exclusively on lowland forests according to Wells (1985) and were used in our regression model.

Common name	Scientific name	Selectively-logged	Secondary 1	Secondary 2	Pine
Red-legged Crake	*Rallina fasciata*			1	
Ruddy Cuckoo-Dove	***Macropygia emiliana***	1			
Emerald Dove	*Chalcophaps indica*	1		6 (1)	
Rufous-backed Kingfisher	*Ceyx rufidorsa*	1	2	2	
Banded Kingfisher	Lacedo pulchella			1	
Black-banded Barbet†	*Megalaima javensis*	1			
Rufous Piculet	***Sasia abnormis***		4 (1)	4	
Grey-and-buff Woodpecker	Hemicircus concretus			1	
Banded Broadbill	Eurylaimus javanicus			2	
Banded Pitta	*Pitta guajana*	2	1	1	
Scarlet Minivet	*Pericrocotus flammeus*			1	
Common Iora	*Aegithina tiphia*			1	
Black-crested Bulbul	*Pycnonotus melanicterus*			1	
Cream-vented Bulbul	*Pycnonotus simplex*			7	
Grey-cheeked Bulbul	*Alophoixus bres*	5	3	8 (1)	
Great Tit	Parus major			1	
Black-capped Babbler	*Pellorneum capistratum*	3	3 (1)	1	
Temminck's Babbler	*Pellorneum pyrrogenys*	7	3	5	
Horsfield's Babbler	*Malacocincla sepiarium*	2 (1)		3	2
Scaly-crowned Babbler	***Malacopteron cinereum***	5	1	1	
White-breasted Babbler‡	*Stachyris grammiceps*	29 (5)	12 (2)	13 (4)	2
Siberian Thrush*	*Zoothera sibirica*	1			
Yellow-bellied Warbler	***Abroscopus superciliaris***		2		
Olive-backed Tailorbird‡	*Orthotomus sepium*		1	12	
Black-naped Monarch	***Hypothymis azurea***	1			
Ruby-cheeked Sunbird	***Anthreptes singalensis***			3	
Purple-throated Sunbird	Nectarinia sperata	1			
White-flanked Sunbird‡	*Aethopyga eximia*		1	1	
Crimson Sunbird	*Aethopyga siparaja*			2	
Javan Sunbird‡	*Aethopyga mystacalis*	1			
Little Spiderhunter	*Acrachnothera longirostra*	8 (3)	10	35 (7)	
Long-billed Spiderhunter	***Acrachnothera robusta***			1	
Grey-breasted Spiderhunter	***Acrachnothera affinis***	1		3	
Scarlet-breasted Flowerpecker**	*Prionochilus thoracicus*			1	
Yellow-breasted Flowerpecker**	*Prionochilus maculatus*			1	
Crimson-breasted Flowerpecker	*Prionochilus percussus*	4	1	7	
Orange-bellied Flowerpecker	*Dicaeum trigonostigma*	3	3 (2)	5	1
Javan Munia	*Lonchura leucogastroides*			2	

*Migratory.
**Possible new record for Java.
†Endemic to Java and Bali.
‡Endemic to Java.

Appendix 3. Habitat variable means with standard error at four study sites in Linggoasri, Java.

Habitat variable	Selectively logged ($n = 10$)[a]	Secondary 1 ($n = 25$)	Secondary 2 ($n = 25$)	Pine ($n = 25$)	KW	P
Canopy cover (%)	87.96 ± 1.55	65.13 ± 4.55	65.30 ± 5.73	84.49 ± 2.58	23.270	<<0.001
Shrub cover (%)	82.50 ± 2.50	91.33 ± 0.94	82.95 ± 2.71	58.75 ± 5.19	32.378	<<0.001
Leaf litter (cm)	2.81 ± 0.25	2.78 ± 0.12	2.53 ± 0.16	2.35 ± 0.14	8.079	0.044
No. of fruiting trees	0.50 ± 0.27	0.25 ± 0.10	0.35 ± 0.18	0	7.067	0.069
No. of flowering trees	0.25 ± 0.16	0.35 ± 0.17	0.20 ± 0.11	0	5.641	0.130
DBH (cm)	15.00 ± 1.77	11.91 ± 0.97	10.37 ± 1.77	26.28 ± 1.73	31.871	<<0.001
No. of small arthropods (≤1 cm)	3.52 ± 2.75	2.83 ± 0.99	2.94 ± 1.47	3.20 ± 1.84	7.862	0.049
No. of large arthropods (>1 cm)	1.62 ± 1.05	1.44 ± 0.60	1.40 ± 0.47	1.45 ± 0.49	1.577	0.665

[a]*n*, number of sampling stations.