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Understorey Bird Responses to the Edge-Interior Gradient in an Isolated Tropical Rainforest of Malaysia

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Abstract

The fact that the world is losing its biodiversity due to human activities, particularly around the tropical forest region, has been widely known. One of the biggest threats to biodiversity is the edge effects, especially in isolated and fragmented habitats. The change in understorey bird community composition and habitat variables were studied along an edge-to-interior gradient in a 1248 ha lowland rainforest patch in peninsular Malaysia. Birds and environmental variables such as vegetation structure and litter depth were detected within a 25 m radius of each of 93 sampling points distributed throughout the forest. Species composition differed along the edge-interior gradient at the guild and species level, although only a few species were entirely confined to either edge or interior habitat. Based on bird-habitat associations along the edge-interior gradient, two groups were distinguished. Abundance of the edge-specialist group, mainly foliage-gleaning insectivores and insectivore/ frugivores, was positively correlated with ground cover, light intensity, shrub cover, temperature, and percent of shrub cover between 0.5 and 2 m height. Some of these edge-preferring species also occurred in the matrix surrounding the patch and were extremely abundant, which may create problems for forest species. In contrast, the interior-specialist group, mainly terrestrial insectivores, avoided the forest edge and was positively associated with humidity, canopy cover, number of dead trees, percentage of litter cover, and depth of the litter layer. From a conservation perspective, forest remnants in the lowlands of Peninsular Malaysia that have a deep leaf litter layer, a dense canopy cover, high number of dead trees, and high relative humidity are able to support regionally significant understorey bird species that are sensitive to edge effects. As such these forests have important conservation value.

Keywords: Birds, Community analysis, Density, Diversity, Isolated forest, Population analysis

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1. Introduction

The rate of tropical forests depletion is fast and is brought about by deforestation and habitat fragmentation, which are the main causes of biodiversity loss (Laurance, 1999; Debinski and Holt, 2000; Leite *et al*., 2010). The focus on consequences of habitat destruction by conservation biologists have received very well in recent years (Bierregaard *et al*., 2001, Stratford and Robinson, 2005; Stouffer *et al*., 2006), where the stakes are high because of high species richness. This richness typically declines with decreasing forest patch size (Stratford and Stouffer, 1999; Stouffer *et al*., 2006; Ferraz *et al*., 2007; Butler *et al*., 2012) and increasing isolation (Ferraz *et al*., 2003; Ferraz *et al*., 2007). Forest fragmentation is linked to numerous negative processes, including the isolation of remaining forest patches and the creation of modified habitat at the edges (Laurance *et al*., 2002). Forest edges are seen in many areas around the world due to the loss of forest during human activity, including settlement, agriculture, resource extraction, and timber harvesting. As such, a large section of the landscape may face edge effects.

Species living in fragmented forests in the tropics are highly affected by the edges (Murcia, 1995; Laurance, 1999). These effects are a concern in biodiversity conservation as sensitivity to edges and extinction threat level of a species can be closely correlated (Lehtinen *et al*., 2003). The edge and area effects can also interact, such that the magnitude of edge to interior differences on bird community composition can decline highly with patch size (Leite *et al*., 2010). The change in bird species composition between forest interiors and edges was similar to the change in community composition between large and small patches (Cox *et al*., 2012). Only a few studies have defined forest edge versus interior bird species by specifically examining edge avoidance (Whitcomb *et al*., 1981; King *et al*., 1997; Germaine *et al*., 1997). Species that require forest interior may avoid edges due to altered microclimate, vegetation structure, or a high density of predators or brood parasites near edges (Murcia, 1995). Forest clearing usually increases the ratio of forest edge habitat to forest interior habitat (Collinge and Forman, 1998), so that the effective amount of habitat suitable for such birds is decreased (Burke and Nol, 1998; Drolet *et al*., 1999). Therefore, there may be changes in the avifauna from the edge to the deep interior of forests (Luck *et al*., 1999). To make informed management decisions, there is an urgent need for data on the patterns of association between landscape variables, local measures of habitat structure and heterogeneity, and the fauna present along edge-to-interior gradients. Indeed, some studies on bird assemblages have indicated that local environmental variables may be of greater importance than landscape-scale variables. For example Schmiegelow *et al*. (1997) found impacts of landscape-scale fragmentation were small on Canadian boreal bird communities, whereas in Spain local habitat factors had a more significant impact on understorey bird species than landscape factors

(Herrando and Brotons, 2002). Even in highly fragmented forest patches in agricultural landscapes, local variables often outweigh landscape variables in determining abundances and nesting success of forest birds (Chapa-Vargas and Robinson, 2006, 2007).

Disturbance in tropical forests can very well be indicated by understorey birds as these respond to changes in local vegetation structure (Barlow *et al*., 2002; Barlow and Peres, 2004), landscape-scale processes (Robinson, 1999; Pearman, 2002), and floristic composition and the availability of food resources (Barlow and Peres, 2004). Foraging guilds may also be useful tools for examining changes in species-rich communities because their functional organization can be investigated even if the communities being compared do not share any species (Terborgh and Robinson, 1986). For example, insectivores of understorey or terrestrial microhabitats are rarely resilient to the more severe forms of disturbance (Johns, 1991), and large canopy frugivores, understorey insectivores, and forest raptors are particularly vulnerable to fragmentation and edge effects (Renjifo, 2001; Newmark, 2006). Many rainforest understorey insectivores are specialists in their foraging techniques, use specific habitats and microhabitats, are sedentary, and have large territories (Terborgh *et al*., 1990; Stouffer and Bieregaard, 1995). Thus, examining responses of feeding guilds may provide new insights into how and why bird communities change from forest edges to the interior.

The goal of this study was to invesigate how understory bird communities change along an edge-to-interior gradient in a species-rich bird community in peninsular Malaysia where habitat loss and fragmentation have been extensive. We compared abundances of each species and of guilds of species along this gradient and compared these patterns with data on vegetation structure and other environmental variables that have been shown to change with distance from edges. Specifically, the following questions were asked. (1) How do species richness, density, and abundance differ along a gradient of increasing distance from edge to the interior? (2) are there any distinct guilds associated with certain habitat types and, if so, which environmental factors may explain such distributions? And (3) which understorey birds are forest dependent and how are they affected by forest edge? This aim was also to provide the managers, planners and policy makers with information on how to improve forest management for species that depend upon the forest interior and therefore are in the greatest danger of extinction from forest fragmentation.

2. Methods

Study site

The study area was located in the tropical lowland rainforest of the Ayer Hitam Forest Reserve, Puchong, Selangor and peninsular Malaysia. Research was conducted in this 1248-ha, isolated rain forest tract. The area is located at about

3˚ 00.00'N to 3˚ 02.20'N and 101˚ 37.90'E to 101˚ 40.00'E, approximately 20 km southwest of Kuala Lumpur. The Ayer Hitam Forest Reserve is surrounded by development, making it an isolated patch of forest in the middle of modern infrastructure and society of Puchong, Kinrara, Seri Kembangan, Serdang and the Multimedia Super Corridor (MSC) (Fig.1). This forest is surrounded by highways and housing developments. It was originally about 3500 ha in area. In 1997, however, the forest on the eastern side of Puchong was developed for housing projects and highways, and the forest area was decreased to 1248 ha. The Ayer Hitam Forest is the only lowland patch of natural habitat left in the densely populated Klang Valley for now and for generations to come (Varasteh Moradi *et al*., 2008).

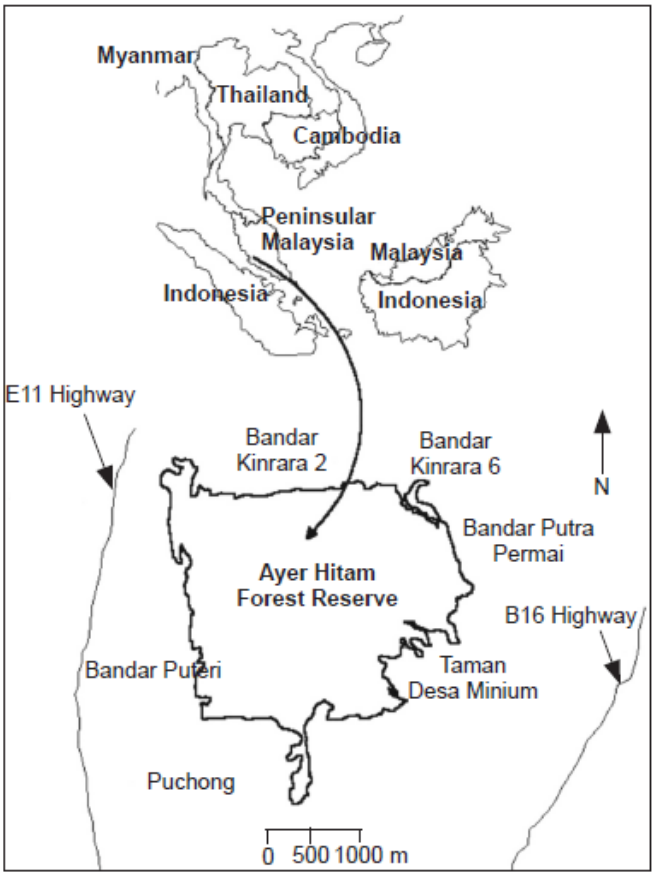


Figure 1. Map showing the position of Ayer Hitam Forest Reserve

Bird sampling

The distance sampling point-count method (Buckland *et al*., 2001) was used to survey the understorey bird individuals and species during the surveys at each of 93 survey points on ten visits between December 2006 and July 2008. The 14 parallel transects were systematically placed across the gradient of distance from the forest edge at 200 m intervals (to minimize the risk of counting the same individual twice) (Antongiovanni *et al*., 2005) beginning approximately 25 m from the forest edge. Data were collected at each of the 93 sampling points along 14 transects (Fig. 2); "Distance 1" refers to the 14 points closest to the edge (25 m from the forest edge), "Distances 2, 3, and 4 the next three sets of 14 sampling points 200 m, 400 m, and 600 m farther from the forest edge, "Distance 5" refers to 13 sampling points 800 m farther from the forest edge, "Distance 6" refers to 11 sampling points 1000 m farther from the forest edge, and "Distance 7" refers to 13 sampling points farthest (about 1200 m) from the forest edge. All sampling points were chosen randomly along each transect. To avoid time-of-day biases, the points were visited in reverse order on different visits. Birds were counted at each census station point for a period of 10 min (Marsden *et al*., 2001). Birds occurring within 25 m fixed radius of each station were recorded because it was often not possible to identify species past this distance (Watson *et al*., 2004). Only species sighted within the point count area were recorded as present. Vocalizations were used to locate birds and to aid identification. Bird surveys were carried out between 0730 h and 1030 h and only in the absence of rain or heavy mist. All point counts were conducted by one observer (H. Varasteh) to minimize observer effects.

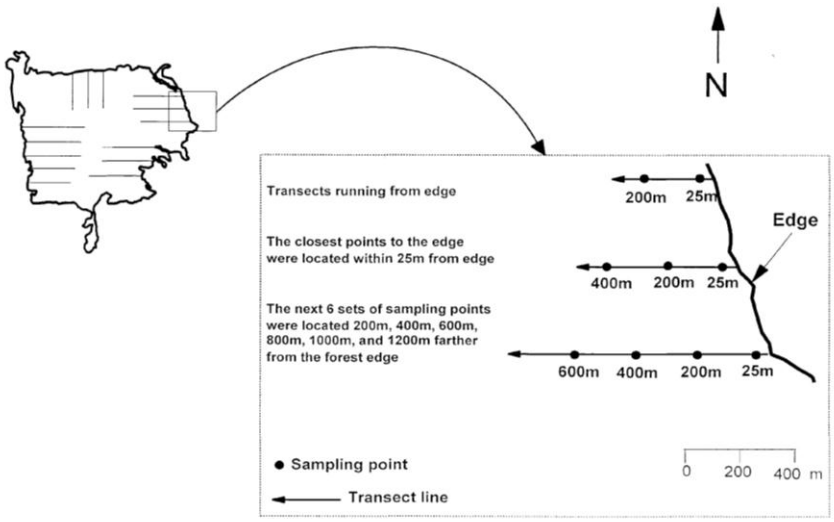


Figure 2. Map showing the position of sampling points

Habitat sampling

At each point, 31 microhabitat and microclimate variables were recorded within a 25-m radius (Castelletta *et al*., 2005). The variables recorded were: (DIS) the distance from the forest edge, (SLO) the slope, (TEM) the temperature, (HUM) the humidity, (LUX) the light intensity, (NFT) the number of fruiting trees, (NDT) the number of dead trees, (DDT) the dbh of dead trees, (NPT) the number of palm trees, (LDP) the leaf litter depth, (LPC) the leaf litter cover, (BSL) the basal area, (CCV) the canopy cover, (GCV) the ground cover, (SHC) the understorey shrub cover, (PSH2) the percent of shrub cover between 0.5 and 2 m height, (PSH6) the percentage of shrub cover between 2 and 6 m height, (NT<6) the number of trees less than 6 m height, (NT6) the number of trees 6-10 m height, (NT>10) the number of trees higher than 10 m height, (NT<2) the number of tree saplings with dbh less than 2 cm, (NT2) the number of trees with dbh 2-5 cm, (NT5) the number of trees with dbh of 5-10 cm, (NTS) the number of tree species, (NTI) the number of tree individuals, (NT10) the number of tree with dbh of 10-20 cm, (NT20) the number of tree with dbh of 20-30 cm, (NT30) the number of tree with dbh of 30-50 cm, (NT50) the number of tree with dbh of more than 50 cm, (MM) the number of *Melastoma malabathricum* shrubs, and (AL) the number of *Agrostistachys longifolia* trees. These latter two species were chosen because they are among the most abundant trees and shrubs in Ayer Hitam Forest Reserve.

Data analyses

Prior to conducting statistical analyses, each variable was tested for deviations from the normal distribution using Kolmogorov-Smirnov test for equality of variances. Differences in total number of individuals, species and diversity per plot between the seven different distances from the forest edge were tested with General Linear Models (*GLM*), to compensate for differences in sample sizes. A *post-hoc* Tukey's test was used to determine which forest edge-interior gradient types differed significantly in environmental variables. When the data were not normally distributed, or standard deviations between factors differed too much to apply *GLM*, non-parametrical Kruskal-Wallis (*K-W*) and Mann-Whitney *U*-tests were used. These tests were also applied to determine differences in habitat variables between different distances from the forest edge.

Hill's diversity measures (Hill, 1973) were used to examine the relationship between distance gradient and species diversity. These included Simpson diversity index, Simpson evenness index, N_0 (which examines the total number of species but is sensitive to rare species), and N_2 (which is the reciprocal of Simpson's index and emphasizes dominance). We also used the feeding guild classification of understorey birds. Birds were assigned to guilds following the methods of Wong (1986), who classified birds according to foraging substrate and diet. An analysis of similarity (ANOSIM), Using CAP 4.0 (Seaby *et al*., 2007), was performed to

test the patterns of species composition among the seven different distances from edge. ANOSIM procedure is a non-parametric permutations test that is analogous to an ANOVA for similarity matrices (Clarke and Warwick, 2001) to test whether predefined classes differ in mean similarities/dissimilarities. A Similarity Percentage (SIMPER) analysis was also used to examine the contribution of each bird species towards differentiating the seven distances from forest edge.

Using CANOCO 4.5 (Ter Braak and Smilauer, 2002) the relationship between understorey bird species abundances, understorey bird species diversity and habitat variables was explored. The canonical correspondence analysis (CCA) was performed to detect understorey bird species response to gradients in environmental variables. CCA is a method of "direct" gradient analysis, in which the relationship between sites and species is constrained by a set of external "environmental" variables (Legendre and Legendre, 1998). The default 'by species' scaling method was employed because the main interest was in the ordination of individual species with respect to one another and the environmental variables. The significance of the CCA was calculated using the Monte Carlo permutation test with 499 permutations. To reduce the influence that the most abundant species might have in the ordination analysis, the abundance of each species was log-transformed (Jongman *et al*., 1995). To determine which explanatory variables are more important, CCA analysis using a forward selection procedure was applied. Besides, to address the question how much variation in the understorey species data was purely related to distance gradient, variance partitioning was performed. The default 'attribute plots' based on sample scores was used to display the variability in the species composition (diversity index values) related to explanatory variables.

All statistical tests were performed using Minitab 15 except for ordination analysis performed with Canoco for windows 4.5., diversity index values using 'SDR4' software (Seaby and Henderson, 2006), and density estimates using the DISTANCE 5.0 program (Thomas *et al*., 2006). In text and tables, values are means $\pm$ SD. Statistical significance for all analyses was set at $\alpha = 0.05$.

3. Results

Diversity and abundance

During the study, a total of 2263 observations from 72 species, representing 48 genera and 19 families were recorded (Appendix. 1). Understorey bird species diversity differed substantially among different distances from the forest edge (Tab. 1). Distance 1 possessed the highest value of N_0 (*GLM*, $F_{6, 69}$=6.17, *P*=0.000), which represents the total number of species but is sensitive to rare species. This distance category also had a significantly lower value of Simpson evenness index, Simpson diversity index, and a higher number of dominant species than other distances (*K-W*, $H_{6,69}$=25.27, *P*=0.000, $H_{6, 69}$=13.14, *P*=0.041, and *GLM*, $F_{6,69}$=2.84,

P=0.018, respectively). In contrast, the interior sites (distances 6 and 7) had significantly higher values of evenness and diversity (*K-W*, $H_{6,\ 69}$=25.27, *P*=0.000 and $H_{\ 6,\ 69}$=13.14, *P*=0.041, respectively).

Table 1. Comparison of diversity indices for understorey avian species in relation to edge-interior gradient. Different means with different letters are significantly different. (*) Significant at $\alpha = 0.05$.

Variables	Observations in different distances from the forest edge (m)							*H* , *F*	*P*
	25	200	400	600	800	1000	1200		
Simpson evenness index	0.47± 0.08^{b}	0.76± 0.13^{a}	0.66± 0.07^{a}	0.68± 0.13^{a}	0.73± 0.15^{a}	0.77± 0.12^{a}	0.70± 0.13^{a}	25.27* K-W	0.000
Simpson diversity index	0.85± 0.05^{b}	0.93± 0.02^{a}	0.90± 0.02^{a}	0.89± 0.04^{ab}	0.88± 0.12^{ab}	0.92± 0.02^{a}	0.90± 0.05^{a}	13.14* K-W	0.041
Number of understorey species (N_0)	15± 5.81^{a}	12.8± 6.61^{ab}	13.1± 3.73^{ab}	12.1± 5.04^{ab}	10.7± 5.12^{b}	9.7± 4.03^{b}	11.5± 5.87^{b}	6.17* GLM	0.000
Number of dominant species (N_2)	6.87± 2.75^{b}	8.97± 3.4^{a}	8.57± 2.22^{ab}	7.81± 3.09^{ab}	7.27± 2.69^{ab}	7.16± 2.44^{ab}	7.54± 3.22^{ab}	2.84* GLM	0.018

There was a significant effect of distance gradient on the understorey bird species abundance (Tab. 2: *K-W*, $H_{6,92}$=19.67, *P*=0.003). Among the seven understorey guilds and sub-guilds, three showed a significant difference in the numbers observed. Terrestrial insectivores had significantly higher abundances in distances 6 and 7 (*K-W*, $H_{6,92}$=14.44, *P*=0.025). Two sub-guilds for which abundance was significantly high closer to the edge (distance 1) were arboreal foliage-gleaning insectivores (*K-W*, $H_{6,92}$=19.92, *P*=0.006) and arboreal foliage-gleaning insectivore/frugivores (*K-W*, $H_{6,92}$=24.66, *P*=0.000). Moreover, the species inhabiting the matrix (*K-W*, $H_{6,92}$=56.33, *P*=0.000) and brood parasitic species (*K-W*, $H_{6,\ 92}$=28.52, *P*= 0.000) were detected significantly more often close to the edges (Distance 1), whereas the Sunda sub-region endemic species had a significantly higher abundances in distances 5, 6, and 7 (*K-W*, $H_{6,92}$=13.42, *P*=0.040). Migratory species, which are of potential conservation concern, and uncommon species did not show any detectable changes along edge-interior gradient.

Table 2. Comparison of guilds in relation to edge-interior gradient. Different means with different letters are significantly different. (*) Significant at $\alpha = 0.05$. USB=understorey birds, TIN=terrestrial insectivore, AFI=arboreal foliage gleaning insectivore, BGI=bark gleaning insectivore, SYI=sallying insectivore, AFF=arboreal foliage gleaning insectivore-frugivore, TIF=terrestrial insectivore-frugivore, NIF=nectarivoe-insectivore-frugivore, MAT=species inhabit in matrix, BPS=brood parasite species, PCC= species of potential conservation concern, MGT=migratory species, UCN=uncommon species, SES=sunda sub-region endemic species.

Guild	Observations in different distances from the forest edge (m)							*H*	*P*
	25	200	400	600	800	1000	1200		
USB	1.85± 0.18^{a}	1.68± 0.12^{b}	1.72± 0.17^{ab}	1.62± 0.21^{b}	1.54± 0.21^{b}	1.56± 0.19^{b}	1.61± 0.19^{b}	19.67*	0.003
AFI	1.42± 0.21^{a}	1.26± 0.22^{b}	1.27± 0.30^{ab}	1.17± 0.28^{b}	1.11± 0.18^{b}	1.04± 0.29^{b}	1.11± 0.20^{b}	19.92*	0.006
BGI	0.64± 0.33	0.87± 0.23	0.83± 0.2	0.63± 0.26	0.67± 0.29	0.72± 0.27	0.77± 0.25	9.05	0.171
TIN	0.68± 0.37^{ab}	0.63± 0.27^{b}	0.81± 0.27^{ab}	0.66± 0.27^{b}	0.73± 0.31^{ab}	0.93± 0.19^{a}	0.96± 0.21^{a}	14.44*	0.025
SYI	0.62± 0.30	0.72± 0.35	0.85± 0.27	0.86± 0.31	0.77± 0.31	0.71± 0.19	0.72± 0.23	6.37	0.383
AFF	1.46± 0.28^{a}	0.98± 0.2^{b}	0.96± 0.31^{b}	1.07± 0.21^{b}	0.83± 0.31^{b}	1.03± 0.24^{b}	0.91± 0.38^{b}	24.66*	0.000
TIF	0.47± 0.25	0.48± 0.22	0.43± 0.19	0.39± 0.14	0.43± 0.17	0.35± 0.12	0.36± 0.15	4.57	0.600
NIF	0.59± 0.31	0.57± 0.24	0.68± 0.28	0.57± 0.20	0.62± 0.24	0.42± 0.18	0.56± 0.23	7.02	0.319
MAT	1.12± 0.35^{a}	0.41± 0.14^{b}	0.34± 0.07^{b}	0.35± 0.09^{b}	0.30± 0.00^{b}	0.32± 0.05^{b}	0.32± 0.08^{b}	56.33	0.00*
BPS	0.48± 0.16^{a}	0.47± 0.10^{a}	0.35± 0.09^{b}	0.35± 0.08^{b}	0.31± 0.00^{b}	0.33± 0.07^{b}	0.35± 0.08^{b}	28.52	0.00*
PCC	0.63± 0.24	0.74± 0.17	0.81± 0.20	0.75± 0.25	0.71± 0.22	0.79± 0.20	0.77± 0.18	5.05	0.53
MGT	0.33± 0.09	0.33± 0.06	0.33± 0.06	0.37± 0.13	0.36± 0.10	0.33± 0.07	0.38± 0.10	4.54	0.60
UCN	0.38± 0.13	0.35± 0.09	0.46± 0.16	0.37± 0.13	0.37± 0.12	0.40± 0.12	0.48± 0.16	9.48	0.14
SES	0.68± 0.23^{b}	0.77± 0.12^{b}	0.78± 0.15^{b}	0.79± 0.27^{b}	0.86± 0.19^{a}	0.90± 0.24^{a}	0.91± 0.19^{a}	13.42	0.04*

Among the 72 understorey bird species in Ayer Hitam, seven showed a significant difference in the numbers observed in relation to distance from the edge (Tab. 3). Five understorey bird species for which abundance was significantly higher close to the edge were Striped Tit-babbler *Macronous gularis* with the highest number of observations at distance 1 (*K-W*, $H_{6,92}$=19.18, *P*=0.004), Fluffy-backed Tit-babbler *Macronous ptilosus* with the higher number of observations at distance 2 (*K-W*, $H_{6,92}$=17.10, *P*=0.009), Plaintive Cuckoo *Cacomantis merulinus* with the highest number of observations at distance 1 (*K-W*, $H_{6,92}$=13.52, *P*=0.041, Cream-vented Bulbul *Pycnonotus simplex* with the highest number of observation at distance 1 (*K-W*, $H_{6,92}$=48.17, *P*=0.000), and Yellow-vented Bulbul *Pycnonotus*

goiavier with the highest number of observations at distance 1 (*K-W*, $H_{6,\ 92}$=61.87, *P*=0.000). Two understorey species for which abundance increased significantly with increasing distance from the forest edge were Short-tailed Babbler *Malacocincla malaccensis* with the higher number of observations at distances 6 and 7 (*K-W*, $H_{6,92}$=15.11, *P*=0.019) and White-rumped Shama *Copsychus malabaricus* with the highest number of observations at distance 3 (*K-W*, $H_{6,92}$=15.69, *P*=0.016).

Table 3. Comparison of understorey bird species abundance in relation to edge-interior gradient. Different means with different letters are significantly different. (*) Significant at $\alpha = 0.05$.

Species	Observations in different distances from the edge (m)							*H*	*P*
	25	200	400	600	800	1000	1200		
Black-caped Babbler *Pellorneum capistratum*	0.32± 0.08	0.32± 0.08	0.37± 0.17	0.32± 0.08	0.32± 0.08	0.35± 0.12	0.42± 0.19	5.90	0.435
Chestnut-winged Babbler *Stachyris erythroptera*	0.44± 0.24	0.54± 0.26	0.51± 0.23	0.56± 0.27	0.52± 0.23	0.49± 0.24	0.41± 0.17	4.30	0.636
Common Tailorbird *Orthotomus sutorius*	0.64± 0.30	0.62± 0.30	0.67± 0.31	0.59± 0.23	0.58± 0.18	0.68± 0.23	0.54± 0.29	2.54	0.864
Cream-vented Bulbul *Pycnonotus simplex*	0.87± 0.41^{a}	0.32± 0.08^{b}	0.32± 0.08^{b}	0.34± 0.11^{b}	0.30± 0.00^{b}	0.30± 0.00^{b}	0.34± 0.13^{b}	48.17*	0.000
Fluffy-backed Tit-babbler *Macronous ptilosus*	0.41± 0.26^{ab}	0.58± 0.32^{a}	0.46± 0.28^{ab}	0.51± 0.31^{ab}	0.30± 0.00^{b}	0.30± 0.00^{b}	0.34± 0.13^{b}	17.10*	0.009
Red-eyed bulbul *Pycnonotus brunneus*	0.38± 0.15	0.30± 0.00	0.36± 0.17	0.38± 0.19	0.32± 0.08	0.30± 0.00	0.37± 0.26	5.43	0.491
Greater Racket-tailed Drongo *Dicrurus paradiseus*	0.55± 0.30	0.68± 0.31	0.76± 0.26	0.73± 0.28	0.70± 0.29	0.69± 0.18	0.60± 0.24	5.91	0.433
Olive-winged Bulbul *Pycnonotus plumosus*	0.42± 0.21	0.61± 0.31	0.55± 0.22	0.49± 0.26	0.39± 0.14	0.51± 0.25	0.56± 0.31	7.63	0.226
Short-tailed Babbler *Malacocincla malaccensis*	0.49± 0.30^{b}	0.59± 0.27^{b}	0.74± 0.30^{ab}	0.64± 0.26^{ab}	0.71± 0.30^{ab}	0.85± 0.26^{a}	0.85± 0.25^{a}	15.11*	0.019
Spectacled Bulbul *Pycnonotus erythropthalmos*	0.34± 0.11	0.38± 0.15	0.39± 0.16	0.44± 0.17	0.37± 0.18	0.53± 0.20	0.40± 0.21	10.45	0.107
Striped Tit-babbler *Macronous gularis*	1.21± 0.24^{a}	0.78± 0.27^{b}	0.90± 0.36^{b}	0.84± 0.37^{b}	0.82± 0.28^{b}	0.72± 0.83^{b}	0.83± 0.25^{b}	19.18*	0.004
White-rumped Shama *Copsychus malabaricus*	0.47± 0.15^{b}	0.55± 0.24^{ab}	0.65± 0.22^{a}	0.42± 0.17^{b}	0.49± 0.19^{ab}	0.40± 0.17^{b}	0.39± 0.19^{b}	15.69*	0.016
Yellow-breasted Flowerpecker *Prionochilus maculatus*	0.61± 0.21	0.50± 0.21	0.59± 0.29	0.68± 0.27	0.56± 0.19	0.63± 0.26	0.58± 0.22	4.52	0.607
Orange-bellied Flowerpecker *Dicaeum trigonostigma*	0.39± 0.14	0.39± 0.14	0.36± 0.14	0.44± 0.17	0.37± 0.13	0.35± 0.12	0.37± 0.18	4.00	0.676
Yellow-vented Bulbul *Pycnonotus goiavier*	1.16± 0.36^{a}	0.40± 0.11^{b}	0.30± 0.00^{b}	0.34± 0.11^{b}	0.30± 0.00^{b}	0.33± 0.09^{b}	0.30± 0.00^{b}	61.87*	0.000
Finsch's Bulbul *Alophoixus finschii*	0.38± 0.21	0.43± 0.19	0.55± 0.28	0.46± 0.24	0.52± 0.24	0.61± 0.27	0.42± 0.15	9.26	0.159
Banded Woodpecker *Picus mineaceus*	0.51± 0.23	0.61± 0.27	0.69± 0.19	0.49± 0.25	0.51± 0.25	0.56± 0.24	0.50± 0.26	7.59	0.202
Checker-throated Woodpecker *Picus mentalis*	0.36± 0.14	0.34± 0.10	0.38± 0.15	0.30± 0.00	0.35± 0.11	0.40± 0.17	0.38± 0.16	4.59	0.597
Maroon Woodpecker *Blythipicus rubiginosus*	0.34± 0.11	0.45± 0.22	0.34± 0.11	0.36± 0.14	0.38± 0.16	0.41± 0.15	0.51± 0.22	10.17	0.118

Plaintive cuckoo *Cacomantis merulinus*	0.51± 0.23[a]	0.41± 0.19[b]	0.34± 0.11[b]	0.36± 0.12[b]	0.30± 0.00[b]	0.35± 0.12[b]	0.39± 0.14[b]	13.52*	0.041
Emerald Dove *Chalcophaps indica*	0.32± 0.08	0.47± 0.20	0.39± 0.18	0.36± 0.12	0.39± 0.14	0.32± 0.09	0.32± 0.08	9.58	0.144
Greater Yellownape *Picus flavinucha*	0.34± 0.10	0.42± 0.22	0.30± 0.00	0.32± 0.08	0.32± 0.08	0.36± 0.12	0.32± 0.08	7.02	0.319
Purple-naped sunbird *Hypogramma hypogrammicum*	0.52± 0.27	0.49± 0.25	0.59± 0.25	0.51± 0.20	0.57± 0.21	0.43± 0.18	0.51± 0.22	4.27	0.641
Buff-necked Woodpecker *Meiglyptes tukki*	0.41± 0.22	0.36± 0.12	0.43± 0.19	0.36± 0.17	0.43± 0.17	0.35± 0.12	0.34± 0.13	5.03	0.540
Little Spiderhunter *Arachnothera longirostra*	0.36± 0.13	0.41± 0.18	0.44± 0.21	0.39± 0.14	0.38± 0.16	0.30± 0.00	0.32± 0.08	7.31	0.293
Magpie Robin *Copsychus saularis*	0.49± 0.32	0.30± 0.00	0.34± 0.11	0.30± 0.00	0.30± 0.00	0.30± 0.00	0.30± 0.00	3.15	0.790

Density estimates

Density analyses were presented based on the understorey bird community as a whole, the seven understorey guilds and sub-guilds, and only for the 26 understorey avian species, the only groups for which we had enough data to use the program DISTANCE (Tab. 4). Understorey birds had their highest density at distance 1 (22.31±5.52 individuals/ha). The seven understorey guilds showed different responses to distance from edge (Tab. 4). The highest density of arboreal foliage-gleaning insectivores was at distance 1 (17.47±3.89individuals/ha) and the lowest abundance was at distance 6 (7.29±1.35 individuals/ha). Sallying insectivores occurred at highest densities at distance 4 (4.58±0.99 individuals/ha) and the lowest densities at distance 1 (2.24±0.84 individuals/ha), whereas bark-gleaning insectivores had the highest density at distance 2 (2.61±0.89 individuals/ha) and the lowest density at distance 4 (1.28±0.51 individuals/ha). As for terrestrial insectivores, the highest density occurred at distance 7 (3.13±0.54 individuals/ha) and lowest density at distance 2 (1.28±0.36 individuals/ha). Total abundances of arboreal foliage-gleaning insectivore-frugivores was highest at distances 1 (26.80±4.79 individuals/ha) and lowest at distance 5 (5.13±1.05 individuals/ha) whereas distances 3 (4.94±1.45 individuals/ha) and 6 (1.16±0.56 individuals/ha) were the highest and lowest respectively for nectarivore/ insectivore/frugivores.

At the species level, the understorey bird species exhibited different patterns of density across the distance gradient. Notably, variable in density were Red-eyed Bulbuls *Pycnonotus brunneus* (10.21±10.93 individuals/ha at distance 7 and 0.00 individuals/ha at distances 2 and 6), Yellow-vented Bulbuls (9.44±2.59 individuals/ha at distance 1 and 2.54±0.87 individuals/ha at distance 6), Striped Tit-babblers (9.62±3.23 individuals/ha at distance 1 and 2.54±0.87 individuals/ha at distance 6), Cream-vented Bulbuls (12.93±5.47 individuals/ha at distance1 and 0.00 individuals/ha at distances 5 and 6), Fluffy-backed Tit-babblers (4.56±2.07 individuals/ha at distance 2 and 0.00 individuals/ha at distances 5 and 6), Short-

tailed Babblers (2.70±0.58 individuals/ha at distance 7 and 0.87±0.44 individuals/ha at distance 1), Plaintive Cuckoos (0.40±0.13 individuals/ha at distance 1 and 0.00 individuals/ha at distance 5), and Maroon Woodpeckers *Blythipicus rubiginosus* with 0.73±0.25 individuals/ha at distance 7 and 0.12±0.08 individuals/ha at distance 1.

Table 4. Density estimates (individuals per ha) ± %se and 95% confidence intervals for understorey bird species in relation to different distances from the forest edge

Groups or species	Density in different distances from the forest edge(m)						
	25	200	400	600	800	1000	1200
understorey birds	22.31 ±5.52	20.29 ±3.99	23.48 ±4.96	18.03 ±4.36	15.62 ±3.54	15.05 ±3.21	16.89 ±3.35
Arboreal foliage gleaning insectivores	17.47 ±3.89	13.27 ±2.72	14.80 ±3.40	11.45 ±2.71	8.12 ±1.46	7.29 ±1.35	8.33 ±1.41
Bark gleaning insectivores	1.57 ±0.71	2.61 ±0.90	2.27 ±0.80	1.28 ±0.51	1.63 ±0.76	1.70 ±0.61	1.88 ±0.64
Sallying insectivores	2.24 ±0.84	3.36 ±1.01	4.39 ±1.09	4.58 ±0.99	3.52 ±0.95	2.38 ±0.44	2.62 ±0.52
Terrestrial insectivores	1.86 ±0.58	1.28 ±0.36	2.26 ±0.45	1.39 ±0.34	2.06 ±0.65	2.81 ±0.63	3.13 ±0.54
Arboreal foliage gleaning insectivore/frugivores	26.80 ±4.79	7.15 ±1.26	7.74 ±1.77	9.29 ±1.61	5.13 ±1.05	8.49 ±1.79	8.21 ±3.14
Terrestrial insectivore/frugivores	0.56 ±0.30	0.63 ±0.26	0.35± 0.21	0.28± 0.14	0.45 ±0.21	0.89 ±0.91	0.23 ±0.17
Nectarivore/insectivore/frugivores	3.84 ±1.31	2.93 ±1.04	4.94 ±1.45	2.70 ±0.77	3.50 ±1.02	1.16 ±0.56	2.76 ±0.91
Cream-vented Bulbul *Pycnonotus simplex*	12.93 ±5.47	0.20 ±0.21	0.20 ±0.21	0.20 ±0.21	0.00	0.00	0.44 ±0.46
Emerald Dove *Chalcophaps indica*	0.06 ±0.06	0.54 ±0.25	0.30 ±0.19	0.18 ±0.11	0.26 ±0.13	0.08 ±0.08	0.06 ±0.07
Finsch's Bulbul *Alophoixus finschii*	0.86 ±0.73	1.01 ±0.43	2.30 ±0.91	1.44 ±0.67	1.86 ±0.74	2.93 ±0.94	0.77 ±0.30
Little Spiderhunter *Arachnothera longirostra*	0.82 ±0.46	1.09 ±0.65	2.18 ±1.34	1.09 ±0.52	1.17 ±0.70	0.00	0.29 ±0.30
Olive-winged Bulbul *Pycnonotus plumosus*	0.42 ±0.21	1.43 ±0.51	0.84 ±0.25	0.78 ±0.38	0.26 ±0.11	0.76 ±0.31	0.90 ±0.38
Orange-bellied Flowerpecker *Dicaeum trigonostigma*	0.95 ±0.45	0.95 ±0.45	0.71 ±0.53	1.67 ±0.66	0.77 ±0.43	0.30 ±0.31	1.28 ±0.84
Purple-naped Sunbird *Hypogramma hypogrammicum*	2.44 ±0.91	2.09 ±0.96	3.32 ±0.95	1.92 ±0.58	2.63 ±0.74	1.11 ±0.53	2.26 ±0.71
Red-eyed Bulul *Pycnonotus brunneus*	3.55 ±2.91	0.00	4.74 ±4.09	5.92 ±4.71	5.92 ±4.71	0.00	10.21 ±10.93
Spectacled Bulbul *Pycnonotus erythropthalmos*	0.19 ±0.13	0.28 ±0.20	0.47 ±0.22	0.66 ±0.30	0.40 ±0.31	1.20 ±0.37	0.61 ±0.41
Yellow-breasted Flowerpecker *Prionochilus maculatus*	0.94 ±0.25	0.61 ±0.19	1.11 ±0.36	1.39 ±0.33	0.78 ±0.18	1.20 ±0.42	0.90 ±0.25
Yellow-vented Bulbul *Pycnonotus goiavier*	9.44 ±2.59	0.40 ±0.21	0.00	0.08 ±0.08	0.00	0.10 ±0.10	0.00

Banded Woodpecker *Picus mineaceus*	0.71 ±0.27	1.18 ±0.38	1.35 ±0.31	0.65 ±0.28	0.82 ±0.45	0.90 ±0.35	0.76 ±0.35
Buff-necked Woodpecker *Meiglyptes tukki*	0.62 ±0.40	0.27 ±0.15	0.62 ±0.27	0.36 ±0.28	0.57 ±0.24	0.23 ±0.16	0.19 ±0.19
Checker-throated Woodpecker *Picus mentalis*	0.34 ±0.25	0.23 ±0.15	0.45 ±0.26	0.00	0.24 ±0.17	0.58 ±0.32	0.49 ±0.28
Common Tailorbird *Orthotomus sutorius*	3.43 ±1.03	3.29 ±1.11	4.00 ±1.28	2.57 ±0.78	2.15 ±0.47	3.46 ±0.88	2.31 ±0.90
Greater racket-tailed Drongo *Dicrurus paradiseus*	1.26 ±0.65	1.86 ±0.64	2.26 ±0.70	1.10 ±0.61	1.93 ±0.64	1.52 ±0.42	1.22 ±0.40
Greater Yellownape *Picus flavinucha*	0.12 ±0.09	0.49 ±0.32	0.00	0.06 ±0.06	0.07 ±0.06	0.16 ±0.11	0.07 ±0.06
Magpie Robin *Copsychus saularis*	1.37 ±0.79	0.00	0.08 ±0.07	0.00	0.00	0.00	0.00
Maroon Woodpecker *Blythipicus rubiginosus*	0.12 ±0.08	0.55 ±0.24	0.12 ±0.08	0.18 ±0.13	0.26 ±0.15	0.23 ±0.12	0.73 ±0.25
Plaintive Cuckoo *Cacomantis merulinus*	0.40 ±0.13	0.20 ±0.09	0.07 ±0.05	0.07 ±0.05	0.00	0.09 ±0.06	0.16 ±0.07
White-rumped Shama *Copsychus malabaricus*	0.08 ±0.02	0.01 ±0.00	0.02 ±0.00	0.06 ±0.02	0.07 ±0.03	0.05 ±0.03	0.05 ±0.03
Black-caped Babbler *Pellorneum capistratum*	0.94 ±0.93	0.94 ±0.93	0.38 ±0.25	0.94 ±0.93	0.10 ±0.10	0.24 ±0.16	0.61 ±0.28
Chestnut-winged Babbler *Stachyris erythroptera*	0.50 ±0.25	0.84 ±0.28	0.67 ±0.24	0.95 ±0.33	0.72 ±0.25	0.64 ±0.28	0.30 ±0.14
Fluffy-backed Tit-babbler *Macronous ptilosus*	2.05 ±1.49	4.56 ±2.07	2.51 ±1.76	3.42 ±1.92	0.00	0.00	0.49 ±0.51
Short-tailed Babbler *Malacocincla malaccensis*	0.87 ±0.44	1.05 ±0.35	1.92 ±0.48	1.34 ±0.37	1.82 ±0.55	2.52 ±0.60	2.70 ±0.58
Striped Tit-babbler *Macronous gularis*	9.62 ±3.23	3.90 ±1.39	5.90 ±1.98	5.08 ±2.06	3.81 ±1.23	2.54 ±0.87	4.10 ±1.23

Species composition patterns

ANOSIM showed that for understorey birds there were some variations with different distances from edge. There was significant difference between distance 1 and distances 2, 3, 4, 5, 6, and 7 (P=0.00). Furthermore, distance 2 was significantly different from distance 7 (P=0.033). The forest edge (distance 1) was dominated by Yellow-vented Bulbuls, Striped Tit-babblers, and Cream-vented Bulbuls (SIMPER, percentage of contribution to similarity of 32.9, 27.4, and 12.7, respectively), some of which occurred at extremely high densities (see above). While at distances 2, 3, 4, and 5 the dominant species was Striped-tit Babbler (SIMPER, percentage of contribution to similarity of 18.8, 19.5, 21.2, and 22.6, respectively). The forest interior, distances 6 and 7, was dominated by the Short-tailed Babbler (SIMPER, percentage of contribution to similarity of 22.6 and 28.8, respectively), Striped Tit-Babbler (SIMPER, percentage of contribution to similarity of 13.8 and 24.6, respectively), and Greater Racket-tailed Drongo *Dicrurus paradiseus* (SIMPER, percentage of contribution to similarity of 13.8 and 7.8, respectively).

Ordination and community analysis

There was a strong relationship between environmental variables and understorey avian species abundance. The total ordination of species along environmental variable gradients was significant (P=0.002, Monte Carlo simulations at 499 permutations). The first two axes explained 39.6% of the variation in the species data that can be explained with the environmental explanatory variables. The first two axes explained 57.7% of this, which works out as 22.85% of the understorey bird species variables. Species-environment correlations for the first two axes were 0.91 and 0.72. These correlations measure how well environmental variables explain the extracted variation in community composition.

Environmental variables differed in their relation to the first and second axes of CCA ordination (Fig. 3). The first axis represented the vegetation and distance gradient. Environmental variables significantly related with this axis were: light intensity, shrub cover, ground cover, temperature, leaf litter cover, humidity, leaf litter depth, and distance from the forest edge. The second axis represented a vegetation and topographic gradient. The variables significantly correlated with second axis were: slope, the number of palm trees, the basal area, the number of tree with dbh 20-30 cm, the number of tree with dbh 30-50 cm, and the percent of shrub cover between 2 and 6 m height.

The first axis, describing vegetation and distance gradient, successfully separated two groups of understorey birds: Group A (including species such as Short-tailed Babbler, Black-capped Babbler *Pellorneum capistratum*, and few other species such as Banded Woodpecker *Picus mineaceus*, Moustached Babbler *Malacopteron magnirostre*, Bronzed Drongo *Dicrurus aeneus*, and White-rumped Shama) in the positive direction with distance from forest edge at the left side of ordination diagram and group B (including species such as Yellow-vented Bulbul, Cream-vented Bulbul, Striped Tit-babbler, Fluffy-backed Tit-babbler, Zebra Dove *Geopelia striata*, Magpie Robin *Copsychus saularis*, and Buff-vented Bulbul *Iole olivacea*) in the negative direction with distance from forest edge at the right side of the ordination diagram (Fig. 3). The CCA ordination biplot (Fig. 3) indicated that group A was positively correlated with humidity, leaf litter percent, leaf litter depth, number of dead trees, and canopy cover (hereafter interior-specialist group). At the other end, group B was positively correlated with ground cover, light intensity, shrub cover, temperature, and percent of shrub cover between 0.5 and 2 m height (hereafter the edge-specialist group). Some species such as Spectacled Spiderhunter *Arachnothera flavigaster*, Arctic Warbler *Phylloscopus borealis*, Puff-backed Bulbul *Pycnonotus eutilotus*, Olive-backed Woodpecker *Dinopium rafflesii*, and Red-eyed Bulbul showed no tendency to occur more in either group.

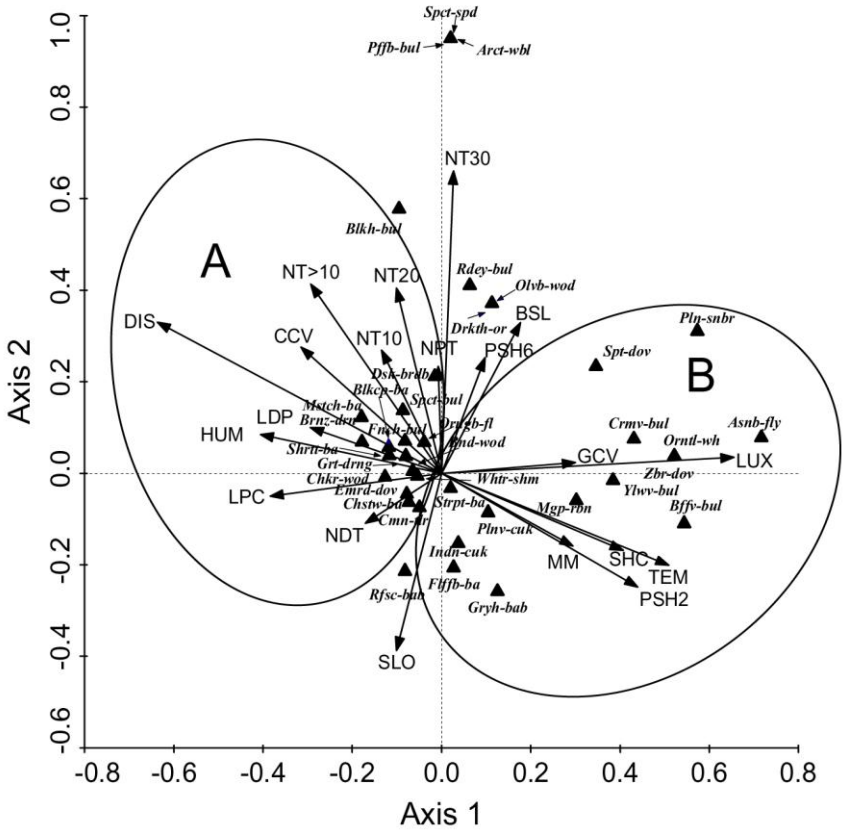


Figure 3. Ordination diagram of the first two axes of CCA for understorey bird species and all environmental variables in Ayer Hitam Forest Reserve. Axes 1 and 2 accounted for 16.33 and 6.52% of the variance in the species data. Arrows represent directions of greatest change of variables. Environmental variables: (LUX) the light intensity, (TEM) the temperature, (SHC) the shrub cover, (PSH2) the percent of shrub cover between 0.5 and 2 m height, (GCV) the ground cover, (HUM) the humidity, (DIS) the distance from the edge forest, (NPT) the number of palm trees, (CCV) the canopy cover, (SLO) the slop, (LPC) the leaf litter cover, (NT30) the number of tree with dbh 30-50 cm, (NDT) the number of dead trees, (BSL) the basal area, (PSH6) the percent of shrub cover between 2 and 6 m height, (NT10) the number of tree with dbh 10-20 cm, (NT20) the number of tree with dbh 20-30 cm, (NT>10) the number of trees higher than 10 m height, (LDP) the leaf litter depth, (MM) the number of *Melastoma malabathricum* shrubs. Understorey bird species: (Plnv-cuk) Plaintive Cuckoo, (Indn-cuk) Indian Cuckoo, (Mgp-rbn) Magpie Robin, (Flffb-ba) Fluffy-backed Tit-babbler, (Gryh-bab) Grey-headed Babbler, (Strpt-ba) Striped Tit-babbler, (Bnd-wod) Banded Woodpecker, (Chstw-ba) Chestnut-winged Babbler, (Shrtt-ba) Short-

tailed Babbler, (Dsk-brdb) Dusky Broadbill, (Grt-drng) Greater Racket-tailed Drongo, (Mstch-ba) Moustached Babbler, (Blkc-ba) Black-caped Babbler, (Whtr-shm) White-rumped Shama, (Pln-snbr) Plain Sunbird, (Spt-dov) Spotted Dove, (Crmv-bul) Cream-vented Bulbul, (Orntl-wh) Oriental White-eye, (Asnb-fly) Asian Brown Flycatcher, (Zbr-dov) Zebra Dove, (Ylwv-bul) Yellow-vented Bulbul, (Bffv-bul) Buff-vented Bulbul, (Rfsc-bab) Rufous-crowned Babbler, (Cmn-tlr) Common Tailorbird, (Emrd-dov) Emerald Dove, (Chkr-wod) Checker-throated Woodpecker, (Brnz-drn) Bronzed Drongo, (Fnch-bul) Finsch's Bulbul, (Spct-bul) Spectacled Bulbul, (Orngb-fl) Orange-bellied Flowerpecker, (Drkth-or) Dark-throated Oriole, (Olvb-wod) Olive-backed Woodpecker, (Rdey-bul) Red-eyed Bulbul, (Spct-spd) Spectacled spiderhunter, (Arct-wbl) Arctic Warbler, (Pffb-bul) Puff-backed Bulbul, (Blkh-bul) Black-headed Bulbul, (Rfs-tlr) Rufous-tailed Tailorbird.

A forward selection procedure (Fig. 4) indicated that shrub cover, light intensity, number of *Melastoma malabathricum* shrubs, distance from the forest edge, canopy cover, number of palm trees, number of trees with dbh of 10-20 cm, number of trees with dbh of 20-30 cm, number of trees with dbh of 30-50 cm, and the number of trees higher than 10 m are the most important explanatory variables describing understorey species composition. Also the variance partitioning results indicated that the variation in the species data purely related to distance gradient was 2.2%. The other explanatory variables explained 51.4%. There was also a certain degree of shared information (collinearity) between them: 4.1

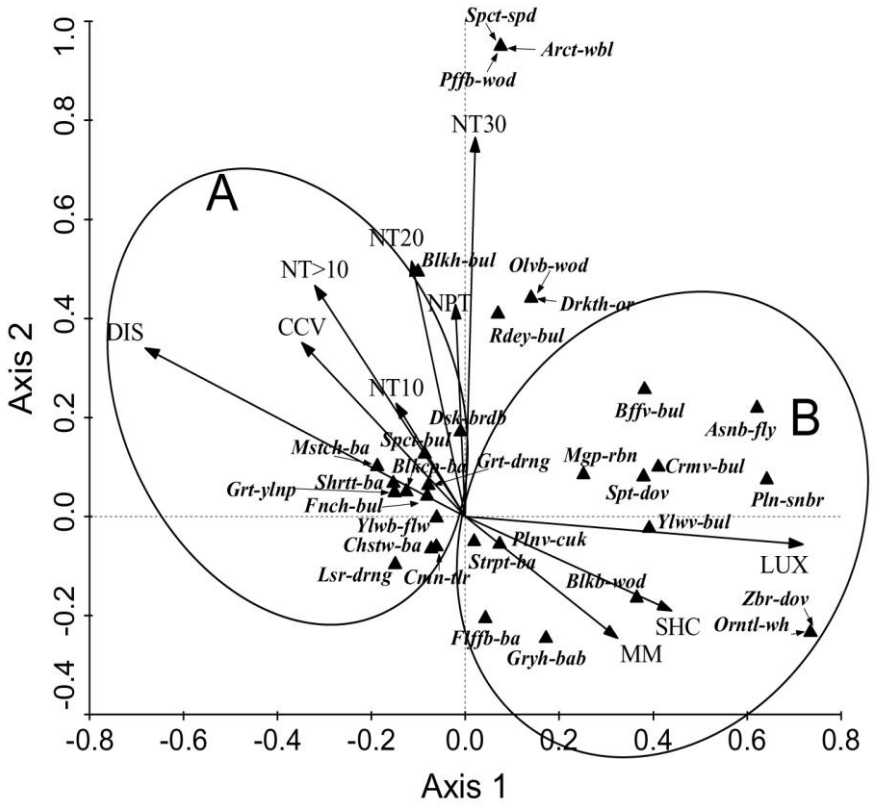


Figure 4. Ordination diagram of the first two axes of CCA for understorey bird species and important environmental variables in Ayer Hitam Forest Reserve. Axes 1 and 2 accounted for 8.7 and 2.7% of the variance in the species data. Arrows represent directions of greatest change of variables. Environmental variables: (LUX) the light intensity, (DIS) the distance from the edge forest (SHC) the shrub cover, (CCV) the canopy cover, (NT30) the number of tree with dbh 30-50 cm, (NT10) the number of tree with dbh 10-20 cm, (NT20) the number of tree with dbh 20-30 cm, (NT>10) the number of trees higher than 10 m height, (NPT) the number of palm trees, (MM) the number of *Melastoma malabathricum* shrubs. Understorey bird species: (Plnv-cuk) Plaintive Cuckoo, (Mgp-rbn) Magpie Robin, (Flffb-ba) Fluffy-backed Tit-babbler, (Gryh-bab) Grey-headed Babbler, (Strpt-ba) Striped Tit-babbler, (Chstw-ba) Chestnut-winged Babbler, (Shrtt-ba) Short-tailed Babbler, (Grt-drng) Greater Racket-tailed Drongo, (Mstch-ba) Moustached Babbler, (Blkc-ba) Black-caped Babbler, (Pln-snbr) Plain Sunbird, (Spt-dov) Spotted Dove, (Crmv-bul) Cream-vented Bulbul, (Orntl-wh) Oriental White-eye, (Asnb-fly) Asian Brown Flycatcher, (Zbr-dov) Zebra Dove, (Ylwv-bul) Yellow-vented Bulbul, (Bffv-bul) Buff-vented Bulbul, (Cmn-tlr) Common Tailorbird, (Fnch-bul) Finsch's Bulbul, (Spct-bul) Spectacled Bulbul, (Drkth-or)

Dark-throated Oriole, (Olvb-wod) Olive-backed Woodpecker, (Rdey-bul) Red-eyed Bulbul,(Spct-spd) Spectacled spiderhunter, (Arct-wbl) Arctic Warbler, (Pffb-bul) Puff-backed Bulbul, (Blkh-bul) Black-headed Bulbul, (Blkb-wod) Black and buff Woodpecker, (Dsk-brdb) Dusky Broadbill, (Grt-ylnp) Greater Yellownape, (Ylwb-flw) Yellow-breasted Flowerpecker, (Lsr-drng) Lesser Racket-tailed Drongo.

Fig. 5 plots the variability in understorey bird species composition (diversity index values) related to explanatory variables along edge-interior gradient, the biplot diagrams with the most important environmental variables and plots by using the default values for the loess method (isoline) corresponding to species diversity indices. The number of understorey bird species (N_0) was positively correlated with the number of palm trees, the number of trees with dbh of 30-50 cm, light intensity, and shrub cover and was negatively correlated with distance from the edge forest (Fig. 5a). The Simpson diversity index was positively correlated with the number of trees with dbh of 30-50 cm, the number of palm trees, and the distance gradient and was negatively correlated with light intensity and shrub cover (Fig. 5b). Moreover, the Simpson evenness index and the number of dominant species (N_2) were negatively correlated with distance from the forest edge and ground cover and were positively correlated with the number of trees with dbh 30-50 cm and the number of palm trees (Fig. 5c & d).

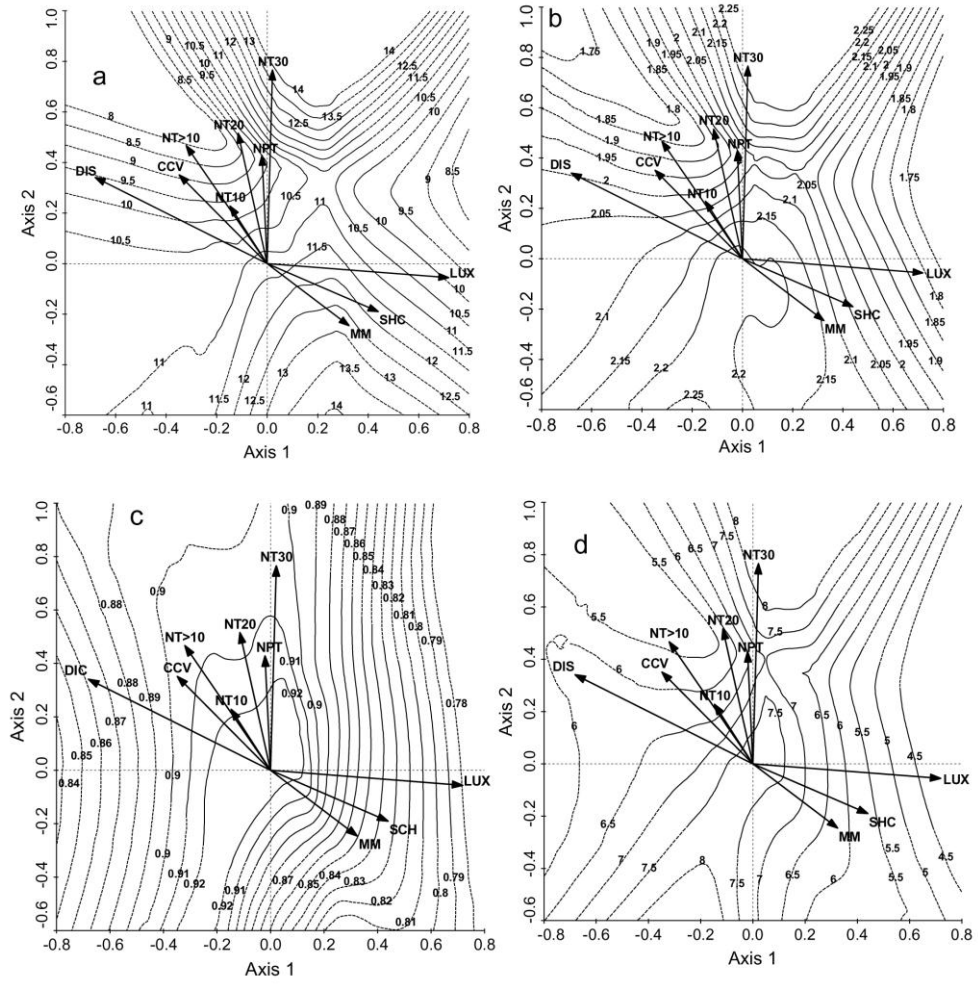


Figure 5. The isolines of understorey avian species diversity of samples with the most important environmental variables, plotted in the CCA ordination diagram. (a) The number of understorey bird species, (b) Simpson diversity index, (c) Simpson evenness index, (d) the number of dominant species (N_2). The numbers correspond to the value of species diversity indices on the isolines. (LUX) the light intensity, (DIS) the distance from the edge forest (SHC) the shrub cover, (CCV) the canopy cover, (NT30) the number of tree with dbh 30-50 cm, (NT10) the number of tree with dbh 10-20 cm, (NT20) the number of tree with dbh 20-30 cm, (NT>10) the number of trees higher than 10 m height, (NPT) the number of palm trees, (MM) the number of *Melastoma malabathricum* shrubs.

4. Discussion

Understorey birds inhabiting forest edge or forest interior in an isolated tropical forest patch responded to micro-environmental changes in a diverse and complex manner. Species diversity differed substantially with distance from the forest edge. Forest interior habitat exhibited higher species diversity indices than forest edge. The high values of Simpson diversity index, Simpson evenness index, and the number of dominant species in the interior habitat was mainly a result of co-variation of some habitat variables such as canopy cover, the number of tall trees with high dbh values, and the number of palm trees. Edge habitat had the highest total number of species (N_0), which was positively correlated with the shrub cover and light intensity. N_0 examines the total number of species but it is sensitive to rare species. Controlling for the effects of rare species on diversity index values, all diversity indices increased along edge to the interior gradient, which is consistent with previous studies, which showed that species diversity of understorey birds are highly sensitive to the forest edge and forest disturbance (Kattan *et al*. 1994, Stouffer and Bierregaard 1995, Sekercioglu *et al*. 2002, Zurita *et al*. 2012).

There was also a significant effect of distance gradient on understorey bird abundance. Among the seven understorey guilds in Ayer Hitam Forest Reserve, three showed a significant difference in the numbers observed with distance to edge. Terrestrial insectivores had a significantly higher number at distances 6 and 7. The two sub-guilds for which abundance was significantly high closer to the edge were arboreal foliage-gleaning insectivores and arboreal foliage-gleaning insectivore/frugivores. These differences were related to differences in species composition among different distances from the forest edge due to different abundance distribution patterns and hierarchical position of species (e.g. change in the species dominance at different distances from edge). There was also a significant difference between forest edge and forest interior in species composition. The forest edge was dominated by Yellow-vented Bulbul, Striped Tit-babbler, and Cream-vented Bulbul whereas the forest interior was dominated by Short-tailed Babbler, Striped Tit-Babbler, and Greater Racket-tailed Drongo.

In this study, habitat quality along the edge-interior gradient was defined as a complex function of the 31 environmental variables we measured, which influenced understorey species abundance and diversity as shown in our CCA ordination. Edge effects for understorey birds were an indirect response to a cascade of effects that involved microclimatic and microhabitat variables. CCA successfully separated two groups of understorey birds: Interior-specialists with a positive direction with distance from the forest edge and edge-specialists with a negative response to distance from the forest edge. The CCA ordination biplot indicated that the interior-specialist group was positively correlated with humidity, leaf litter percentage and depth, number of dead trees, and canopy cover. This group of birds included terrestrial insectivores such as Short-tailed Babbler, Black-

caped Babbler, and few other species such as Banded Woodpecker, Moustached Babbler, Bronzed Drongo, and White-rumped Shama. Several studies have reported declines in terrestrial insectivores at the forest edge, especially wren babblers (genera *Napothera, Kenopia, Ptilocicbla)* and pittas (Lambert 1992). Terrestrial insectivores have previously been shown to be adversely affected when their habitats are altered (Varasteh *et al*., 2008) and are thought to be intolerant of high temperatures and high light intensity (Zakaria *et al*., 2002). This shade-preferring group of insectivores (Varasteh *et al*., 2008) tends to occupy a special microhabitat with high humidity, deep leaf litter layer, and dense canopy cover. Furthermore, terrestrial insectivores may avoid edges because they tend to have specialized diets, narrow ranges of environmental tolerance, and use specialized microhabitats that are not available at the forest edge (Lindell *et al*., 2004). One reason for edge avoidance could be loss of a sheltered understorey in large sections of the forest edge, which could affect food supply for these birds. As an unwillingness to enter or even to cross open habitats is a well documented feature of many understorey insectivores (Borges & Stouffer, 1999; Develey & Stouffer, 2001), it seems likely that the increased canopy openness close to edge (Barlow *et al.,* 2002; Haugaasen *et al*., 2003) was sufficient to limit the movement and dispersal of most insectivorous understorey birds associated with forest interior, especially terrestrial insectivores. Food supply for insectivorous birds has been shown to vary with fragment size as a result of edge effects, because invertebrates, especially surface dwellers, are prone to desiccation and may not survive well in edge habitat, which is often warmer and drier than the forest interior (Zanette *et al*., 2000). In addition, various studies have also shown that terrestrial insectivores are especially sensitive to human impacts in neotropical forests (Johns, 1991; Thiollay, 1992).

On the contrary, edge-specialists were positively correlated with ground cover, light intensity, shrub cover, temperature, and percentage of shrub cover between 0.5 and 2 m height. This group of understorey birds consisted of bird species such as Cream-vented Bulbul, Yellow-vented Bulbul, Buff-vented Bulbul, Striped Tit-babbler, and Fluffy-backed Tit-babbler that could be classified under arboreal foliage gleaning insectivore/frugivores and arboreal foliage gleaning insectivores. In general, arboreal foliage-gleaning insectivores adapt to microclimatic changes associated with disturbance of the forest structure because they forage in the understorey of shrubs and trees (Johns 1991), both of which tend to occur more in disturbed areas. Arriaga-Weiss *et al*. (2008) reported that the arboreal insectivore-frugivore guild are usually associated with secondary vegetation and tolerate a wide range of microclimate conditions. Their abundance also generally reflects the amount of understorey vegetation and its associated insects as well as the microclimatic conditions (Johns, 1991). Arboreal foliage gleaning insectivore/ frugivores, especially bulbuls, are known as colonizer or secondary species and are

common in disturbed areas (Nordin and Zakaria, 1997; Sliwinski and Koper, 2012). This is an extremely important distinction; species that live primarily in the matrix may only use forest at the edge; they may even be creating problems for forest-interior species as they may compete for food resources and even to act as predators or parasites (Brush Cuckoo). The extremely high population densities of some of these species, which are among the highest ever documented for a tropical forest bird community (Terborgh *et al.*, 1990; Robinson *et al.*, 2000), may competitively overwhelm other species feeding in the same niches either through aggressive exclusion from some resources or through simple exploitative competition. These generalists can switch their diet between insects and fruit depending on the food types available (Varasteh *et al.*, 2008; Ries and Sisk, 2010). There were abundant secondary plant species such as *Macaranga* and *Trema* species that bear small fruits at the forest edge. These small fruits are preferred especially by the bulbuls (Zakaria and Nordin 1998). The bulbuls that were abundant at the edge are thought to tolerate high temperature and light intensity (Zakaria *et al.*, 2002) and often feed on fruits in the hot mid-afternoon period *(*Zakaria and Nordin, 1998). It should be noted, however, that some species of sallying insectivores, nectarivores and bark gleaning insectivores showed no evidence for an edge effect due to microhabitat variables, as these species did not have their variance explained by habitat variables at either edge or interior sites. One possible explanation for this is that they were mapping onto some unmeasured resources such as food.

Conservation Implications

Our findings showed that understorey birds can be grouped into two categories: (1) forest interior-specialist species that used the interior habitats preferentially and tended to avoid the edge and (2) forest edge-specialist species that appeared to largely avoid the interior (except for the striped tit-babbler). These groups have to be treated as different conservation targets as they have different reactions to spatial and environmental changes, different levels of tolerance to microclimatic changes, and are influenced in different ways by the edge effects. Edge specialists are mostly species that also occur in the medium around the patch; conserving them may not be necessary and, if some of these species are declining or endangered, they can perhaps be managed better in the medium around the forest patches. Interior-specialists, on the other hand, and especially terrestrial insectivores, should be treated especially as they reflect the habitat quality of the forest interior and their disappearance may be an indication of habitat degradation in an isolated forest. These species should be monitored more closely, because they are highly sensitive to perturbation and are often the most vulnerable to edge effect. From a conservation perspective, forest remnants in the lowlands of Peninsular Malaysia that have a deep leaf litter layer, a dense canopy cover, high number of

dead trees, and high relative humidity are able to support understorey bird species that are sensitive to edge effects. Based on our findings, we recommend that larger lowland forest remnants, with less edge be conserved in Peninsular Malaysia. In this way, there is a higher chance that these species (and other biodiversity) can persist in the area. We also further caution against more development plans in the studied area as through such development cut down might happen in the forest. Roads and recreational facilities within the forest preserve can have a large bearing on this trend and such should be conducted with utmost care.

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Appendix 1. The number of independent understorey bird observations based on visual cues in different distances from the forest edge in Ayer Hitam Forest Reserve. NT=nearly threatened, VU=vulnerable, MATRIX=species that may live mainly in the matrix and only invade the forest at the edge, PARASITE=brood parasite, SS=Sunda sub-region, OR=Oriental region, M=Migrant, SE=Southeast Asia, CE=Central and East Asia, TIN=terrestrial insectivore, AFI=arboreal foliage gleaning insectivore, BGI=bark gleaning insectivore, SYI=sallying insectivore, AFF=arboreal foliage gleaning insectivore-frugivore, TIF=terrestrial insectivore-frugivore, NIF=nectarivoe-insectivore-frugivore.

Species	Conservation concern	Habitat	Parasitic	Distribution	Feeding guild	No. obsv.
Black-caped Babbler *Pellorneum capistratum*	-	Forest	-	SS	TIN	18
Black-throated Babbler *Napothera atrigularis*	NT	Forest	-	SS	TIN	2
Short-tailed Babbler *Malacocincla malaccensis*	NT	Forest	-	SS	TIN	196
Magpie Robin *Copsychus saularis*	-	Matrix	-	OR	TIN	18
Siberian Blue Robin *Luscinia cyane*	-	Forest	-	M	TIN	5
Hooded Pitta *Pitta sordida*	NT	Forest	-	M	TIN	1
Arctic Warbler *Phylloscopus borealis*	-	Forest	-	M	AFI	1
Chestnut-winged Babbler *Stachyris erythroptera*	-	Forest	-	SS	AFI	80
Eyebrowed Wren-babbler *Napothera epilepidota*	-	Forest	-	OR	AFI	10
Fluffy-backed Tit-babbler *Macronous ptilosus*	NT	Forest	-	SS	AFI	60
Gray-headed Babbler *Stachyris poliocephala*	-	Forest	-	SS	AFI	6
Moustached Babbler *Malacopteron magnirostre*	-	Forest	-	SS	AFI	4
Rufous-crowned Babbler *Malacopteron magnum*	NT	Forest	-	SS	AFI	12
Scaly-crowned Babbler *Malacopteron cinereum*	-	Forest	-	SE	AFI	2
Striped Tit-babbler *Macronous gularis*	-	Forest	-	OR	AFI	374
White-bellied Yuhina *Yuhina zantholeuca*	-	Forest	-	OR	AFI	2
Banded Bay Cuckoo *Cacomantis sonneratii*	-	Forest	Parasite on Sunbirds	OR	AFI	2

Drongo Cuckoo *Surniculus lugubris*	-	Forest	Parasite on Babblers	OR	AFI	4
Indian Cuckoo *Cuculus micropterus*	-	Forest	Parasite on Drongos	OR	AFI	10
Plaintive Cuckoo *Cacomantis merulinus*	-	Matrix	Parasite on Tailorbirds and Warblers	OR	AFI	28
Common Tailorbird *Orthotomus sutorius*	-	Forest	-	OR	AFI	142
Dark-necked Tailorbird *Orthotomus atrogularis*	-	Forest	-	OR	AFI	13
Rufous-tailed Tailorbird *Orthotomus sericeus*	-	Forest	-	SS	AFI	1
Oriental White-eye *Zosterops palpebrosus*	-	Matrix	-	OR	AFI	2
White-rumped Shama *Copsychus malabaricus*	-	Forest	-	OR	AFI	66
Banded Woodpecker *Picus mineaceus*	-	Forest	-	SS	BGI	104
Black and buff Woodpecker *Meialyptes iugularis*	-	Forest	-	OR	BGI	1
Buff-necked Woodpecker *Meiglyptes tukki*	-	Forest	-	SS	BGI	32
Checker-throated Woodpecker *Picus mentalis*	-	Forest	-	SS	BGI	19
Common Flameback *Dinopium javanense*	NT	Forest	-	OR	BGI	1
Crimson-winged Woodpecker *Picus puniceus*	-	Forest	-	SS	BGI	2
Greater Flameback *Chrysocolaptes lucidus*	NT	Forest	-	OR	BGI	3
Greater Yellownape *Picus flavinucha*	-	Forest	-	OR	BGI	16
Maroon Woodpecker *Blythipicus rubiginosus*	-	Forest	-	SS	BGI	35
Olive-backed Woodpecker *Dinopium rafflesii*	NT	Forest	-	SS	BGI	1
Asian Brown Flycatcher *Muscicapa dauurica*	-	Forest	-	M	SYI	1
Asian Paradise Flycatcher *Terpsiphone paradisi*	-	Forest	-	CE	SYI	5
Black-naped Monarch *Hypothymis azurea*	-	Forest	-	OR	SYI	2
Chestnut-winged Flycatcher *Philentoma pyrhopterum*	-	Forest	-	SS	SYI	12
Dark-sided Flycatcher *Muscicapa sibirica*	-	Forest	-	M	SYI	9

Golden-bellied Gerygone *Gerygone sulphurea*	-	Forest	-	SE	SYI	1
Green-backed Flycatcher *Ficedula elisae*	-	Forest	-	M	SYI	3
Grey-headed Canary Flycatcher *Culicicapa ceylonensis*	-	Forest	-	OR	SYI	3
Bronzed Drongo *Dicrurus aeneus*	-	Forest	-	OR	SYI	4
Crow-billed Drongo *Dicrurus annectans*	-	Forest	-	M	SYI	8
Greater Racket-tailed Drongo *Dicrurus paradiseus*	-	Forest	-	OR	SYI	173
Lesser Racket-tailed Drongo *Dicrurus remifer*	-	Forest	-	OR	SYI	8
Dusky Broadbill *Corydon sumatranus*	NT	Forest	-	SE	SYI	9
Pied Fantail *Rhipidura javanica*	-	Forest	-	SE	SYI	4
Black-headed Bulbul *Pycnonotus atriceps*	-	Forest	-	OR	AFF	3
Buff-vented Bulbul *Iole olivacea*	NT	Forest	-	SS	AFF	4
Cream-vented Bulbul *Pycnonotus simplex*	-	Matrix	-	SS	AFF	72
Finsch's Bulbul *Alophoixus finschii*	NT	Forest	-	SS	AFF	76
Hairy-backed Bulbul *Tricholestes criniger*	NT	Forest	-	SS	AFF	8
Olive-winged Bulbul *Pycnonotus plumosus*	-	Forest	-	SS	AFF	89
Puff-backed Bulbul *Pycnonotus eutilotus*	NT	Forest	-	SS	AFF	2
Red-eyed Bulbul *Pycnonotus brunneus*	-	Forest	-	SS	AFF	21
Spectacled Bulbul *Pycnonotus erythropthalmos*	-	Forest	-	SS	AFF	37
Yellow-vented Bulbul *Pycnonotus goiavier*	-	Matrix	-	SE	AFF	125
Black-naped Oriole *Oriolus chinensis*	-	Matrix	-	OR	AFF	5
Dark-throated Oriole *Oriolus xanthonotus*	NT	Forest	-	SS	AFF	2
Brown Fulvetta *Alcippe brunneicauda*	NT	Forest	-	SS	AFF	5
Orange-bellied Flowerpecker *Dicaeum trigonostigma*	-	Forest	-	OR	AFF	26

Yellow-breasted Flowerpecker *Prionochilus maculates*	-	Forest	-	SS	AFF	119
Emerald Dove *Chalcophaps indica*	-	Forest	-	OR	TIF	24
Spotted Dove *Streptopelia chinensis*	-	Matrix	-	OR	TIF	5
Zebra Dove *Geopelia striata*	-	Matrix	-	SE	TIF	2
Red Junglefowl *Gallus gallus*	VU	Forest	-	SE	TIF	5
Plain Sunbird *Anthreptes simplex*	-	Matrix	-	SE	NIF	4
Purple-naped Sunbird *Hypogramma hypogrammicum*	-	Forest	-	SE	NIF	89
Little Spiderhunter *Arachnothera longirostra*	-	Forest	-	OR	NIF	24
Spectacled Spiderhunter *Arachnothera flavigaster*	-	Forest	-	SS	NIF	1