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HABITAT STRUCTURE AND ITS EFFECTS ON BIRD ASSEMBLAGES IN THE KALAKAD-MUNDANTHURAI TIGER RESERVE (KMTR), INDIA

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The majority of faunal studies focus on diversity and endemism on elevational gradients. It is claimed that a complex interplay of factors explains the variability of observed gradient patterns, including non-biological ones such as differences in sampling regime. Little is known of factors influencing bird community composition at local levels in tropical rainforest. Along successional gradients, habitat structure and tree species composition influence bird community structure, wherein structurally and floristically similar sites tend to have similar bird communities. In addition, canopy dwelling species have been often ignored or under sampled due to logistical problems. The present study explores variations in local bird community structure along a disturbance gradient in a tropical rainforest of the Western Ghats of India using traditional ground-based sampling in conjunction with canopy sampling.

Key words: Community structure, canopy, sampling, feeding guilds, secondary forests

INTRODUCTION

Tropical secondary forests make up one-sixth of all primary forests that were clear-felled during the 1990s (Wright 2005), and are most likely to be a dominant feature in tropical landscapes of the future (Wright and Muller-Landau 2006). This expansion of degraded and abandoned lands in deforested landscapes may have important implications for the long-term conservation of tropical forest wildlife (Daily 2001; Lindenmayer and Franklin 2002; Wright and Muller-Landau 2006). The values of areas of native regeneration and secondary growth are poorly understood, and our current knowledge base fails to predict whether these habitats will help conserve tropical forest species in the future (Brook *et al*. 2006; Gardner *et al*. 2007). Birds are one of the best known faunal groups in the tropics (Hill and Hamer 2004; Stotz *et al*. 1996) and the canopies are the most dominant feature of these landscapes. Yet canopy-based studies of birds are few and scattered, being mainly confined to the Neotropics.

Birds are an important component of the canopy habitat and many species depend on it for their survival. The analysis of patterns of vertical stratification and canopy utilisation by birds has been limited by difficulties associated with studying the top layers of the forests, and this has been the case for other groups of organisms too; e.g., ants (Tobin 1995), lizards (Reagan 1995), and bats (Kalko and Handley 2001). Limitations faced by canopy studies so far have been difficulty in access and problems of insufficient replication (Barker and Sutton 1997; Bongers 2001) and ground-based studies also lead to inaccurate generalisations and bias in the estimates of richness and abundance. Little work has been done on canopies in India, with most of the work restricted to the Western Ghats (Devy 1999; Devy and Davidar 2003; Ganesh and Devy 2000).

The vertical organisation of the avian community with respect to vegetation and habitat is essential to understanding terrestrial bird assemblages. Various factors combine to shape bird communities like resource availability, vegetation structure, and abiotic factors like temperature, light and precipitation (Cody 1985; Wiens 1989). The influence of forest height on vertical structuring of bird communities in temperate and tropical forests has been studied intensively (Anderson *et al*. 1979; Bell 1982; Cody 1974; Cody 1985; Greenberg 1981; Marra and Remesen 1997; Orians 1969; Pearson 1971; Smith 1973; Terborgh 1980; Terborgh and Weske 1969; Walther 2002a). The structure of vegetation and its density change with respect to the height of the forest (Pearson 1971; Richards 1996; Terborgh 1980). Densities of foliage are highest in the canopies and the understorey with the mid-storey having more open spaces (Bell 1982; Pearson 1971; Pearson 1975; Terborgh 1980; Terborgh and Weske 1969).

Forest height leads to change in such variables as evaporation, temperature and wind (Longman and Jenkins 1974; Richards 1996), ambient light (Endler 1993), foliage density and resources (see Pearson 1971). The above mentioned factors shape many forest communities, and species are specific to strata as they are adapted to environmental conditions of the strata they inhabit.

Species being adapted to particular foraging techniques have consequently led to varying breadths in foraging strata. The vertical distribution of foraging substrates may also cause species to have different stratum breadths (Walther 2002b). The distribution of resources can also lead to specialisation and narrow foraging strata according to resource abundance (Marra and Remsen 1997).

Forest disturbance, such as selection-felling and shade tree plantations, can generally result in decrease in stature of stands. Hence, the available habitat for birds is also reduced and may result in restructuring and even possible expatriation of habitat specialists. Keeping this in mind, this paper focuses on understanding the differences in bird community structure between habitats in relation to habitat structure, including vertical strata, by canopy sampling in conjunction with terrestrial sampling.

METHODOLOGY AND STUDY AREA

The study was carried out in the mid-elevation evergreen forests around Kakachi and Upper Kodayar in the Kalakad-Mundanthurai Tiger Reserve (KMTR) (77° 15' – 77° 30' N; 8° 16' – 8° 40' E) in the Agasthyamalai range of southern Western Ghats, India. The area is home to several endemic, rare and threatened species of plants and animals (Ramesh *et al.* 1997). The study site at Kakachi-Kodayar area is located on the saddle of a hill range running north-south. It forms a gentle undulating plateau with stands of undisturbed wet evergreen forest. Part of this area is under tea and eucalyptus plantation. The average altitude of the plateau is 1,200 m. Annual total rainfall averages about 3,500 mm and is well distributed throughout the year, with a great proportion falling during the northeast monsoon between October and December.

During 1972, the forests of the Kakachi were opened for plantation activity and timber extraction. Parts of the forests were selectively felled to raise cardamom and to supply timber for the match industry. The canopy was opened up by removing large trees such as *Cullenia exarillata*, *Palaquium ellipticum*, *Myristica dactyloides*, and *Calophyllum austroindicum*. In addition, valuable mid-canopy species were also illegally logged. Some parts of the forests were clear-felled to raise tea, coffee and eucalyptus plantations, but were abandoned without being planted. Also, the areas around upper Kodayar were clear-felled for the construction of a dam across the Kodayar river (Ganesan 2001). Hence, the Kakachi-Kodayar plateau is a complex habitat matrix of primary forests with an average canopy height of *c*. 30 m interspersed with areas of selectively-felled and clear-felled regenerating areas and is ideal for the study.

Avifaunal sampling

Six semi-permanent canopy sampling platforms were established in each of the three habitat types (primary, selectively-felled and clear-felled). To maintain spatial independence, no two stations were closer than 500 m. Point counts were carried out from these platforms and from five stations on the ground, one directly below the platform and one in each of the four cardinal directions from the platform with 100 m between each point. Timed point counts were carried out from 06:30 hrs to 18:00 hrs at each station (platform and five ground points) for two days in a season. This data was collected for seven seasons from March 2006 to February 2009. All bird registrations (sighting and calls) were recorded during point counts. Number of individuals, distance from the observer, height, behaviour, foraging tactics, light habitat, and position were also noted. All over-flying birds and uncertain identifications were removed from the analysis. To maintain independence between points (and to avoid any potential double counting) all detections >50 m from the observer were excluded from the analysis. For vertical stratification absolute height was used as it could be accurately ascertained as the platform height and tree heights in the sample locations were known.

Habitat structure

We measured all standing trees $\geq$10 cm DBH and enumerated $\leq$10 cm DBH saplings in 10 plots measuring 10 x 10 m, established at each of the 18 canopy platform locations. We only recorded trees having more than half of their stem within each plot. The canopy cover was calculated using digital photographs taken at waist height, avoiding obstruction of understorey vegetation. Results are analysed using Gap Light Analyzer v. 2.0 (Frazer *et al*. 1999).

We obtained data on the vertical distribution of vegetation density at the study site. Using SRT and descending on a rope and we passed a one-metre stick in a horizontal circle at one-metre intervals from the top of the canopy to the ground. At each height, the number of leaves touching the stick was counted. A total of 90 descents were made, with 30 in each habitat and data from all descents within a habitat was averaged (Fig. 3).

Analysis

Most census techniques do not sample animal populations perfectly, and all references to abundance in this paper refer to relative abundance derived from our sampling techniques instead of the ‘true’ abundance, which is unknown. Point counts in tropical forests are more effective for sampling avifauna in mature forest (Blake and Loiselle 2001). For indications of bird-sampling completeness and estimated species richness, Coleman curves were compared with estimators Chao2, ICE, and MMMean (Chao 1987; Lee and Chao 1994; Raaijmakers 1987), which are considered optimal estimators for tropical birds (Herzog *et al*. 2002; Matlock *et*

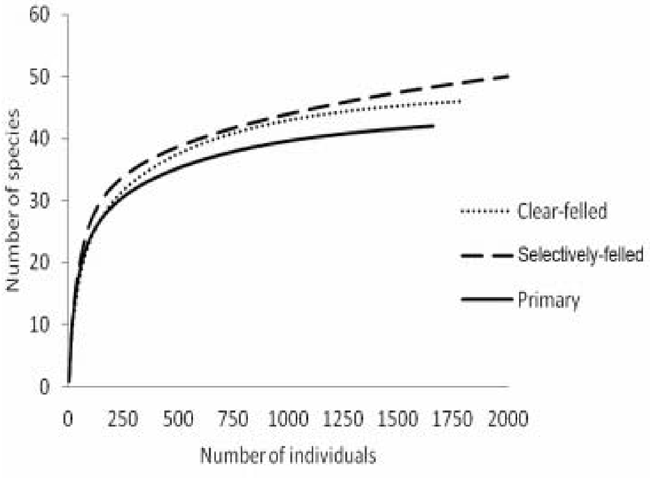

Fig. 1: Coleman curves for bird sampling in the three habitat types

al. 2002; Walther and Martin 2001). Patterns of species richness between different forest types were compared using sample-based rarefaction curves constructed using the analytical formulae implemented in estimateR (Oksanen *et al*. 2011).

Location and dispersion of frequency distributions can be calculated in a number of ways (Sokal and Rohlf 1995; Zar 1996), but the most widely used statistics are the mean and standard deviation (Fowler and Cohen 1986). We used those statistics because they were also used in a previous analysis of the relationship between the mean and the standard deviation of foraging height (Terborgh 1980; Walther 2002b). A weighted least-squares regression was used to fit a parabolic model ($y = b_2 x^2 + b_1 x^1 + b_0$) to the data, using the program R (R Development Core Team 2011) which allows a direct graphical depiction of the relationship, and it may have ecological relevance.

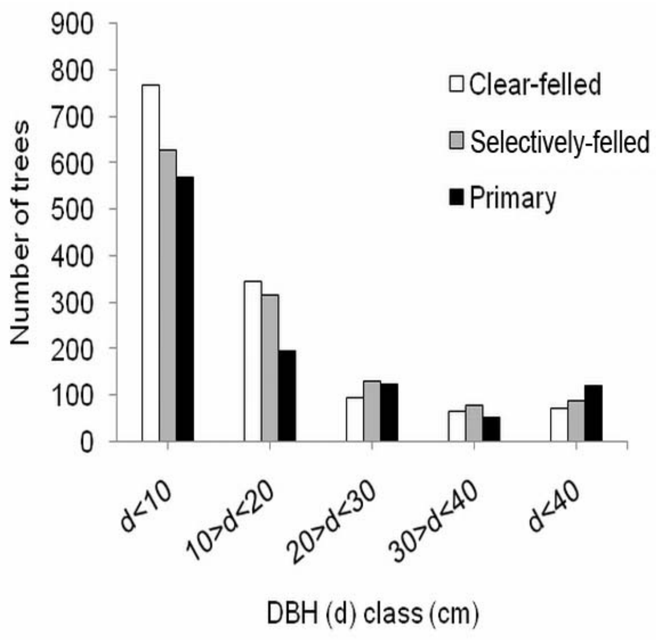

Fig. 2: Distribution of tree diameter at breast height (DBH) of clear-felled, selectively-felled and primary forests in Kakachi and Kodayar (n=174)

All community structure analyses were undertaken using square-root transformed abundance data to reduce the influence of the most dominant species, and site-standardised to account for differences in total abundance. Ordination analyses were implemented in R (Oksanen *et al*. 2011) using De-trended Correspondence Analysis on individual sites to see if there was any distinct grouping. Species were assigned to foraging and dietary guilds following Ali and Ripley (1981), supplemented by field observations.

RESULTS

Bird sampling completeness and comparative bird species richness

A total of 2,578 detections of 59 species were made over 1,464 hours point count observations from the canopy and understorey samples combined. Sampling completeness was estimated at 85-91% Clear-felled (CF), 82-88% Selectively-felled (SF), and 72-76% Primary Forest (PF) (Table 1). Overall species richness in selectively-felled areas (50) was higher than in clear-felled (46) and primary (40) forest areas, but the difference was not significant (÷^{2}=5.39, df=2, P=0.07) (Fig. 1).

The estimated species-richness values were taken as relative bird species-richness between sites, rather than absolute values, because the protocols were standardised across sites.

Habitat Structure

Vegetation: The tree DBH distribution differed between forest types (÷^{2}=69.29, df =8, P<0.001) (Fig. 2).

The height class distribution of trees <10 m and >10 m differed significantly among the forest types (÷^{2}=196.21, df =2, P< 0.001) with the primary and the selectively-felled areas having higher density per hectare of tall trees and clear-felled areas having greater density of shorter trees (Table 2). Percentage canopy cover was also significantly different across the habitat.

Table 1: Estimated bird species richness for the three forest types

Forest Type	Coleman rarefaction	Chao 2	ICE	MM means
Clear-felled	51.9 ±1.8	54.2 ±1.3	59.2 ±1.3	61.3
Selectively-felled	59.0 ±1.6	62.7 ±3.1	67.3 ±1.9	68.3
Primary forest	56.6 ±1.2	57.1 ±1.9	71.1 ±2.9	67.3

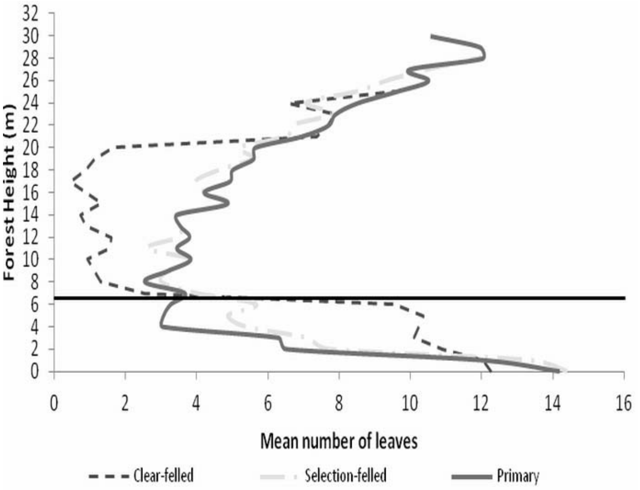

Fig. 3: Forest height versus vegetation density, i.e., the mean number of leaves (data points were smoothed by averaging over a symmetrical 3 m interval). The thin line indicates mean density in primary forest which was 6.51±3.35 [mean ±SD]

Vertical stratification

We restricted the analysis to species that were observed in all habitats and with at least five detections in each (a total of 1,122 observations of 31 species). These species, with the exception of cryptic and nocturnal species, can be considered the most abundant species in our study area. For the measure of foraging height, the standard deviation is a parabolic function of the mean, with the maximum point close to the middle of the range of absolute height for all the habitats (Figs 4a-c).

In the primary and selectively-felled areas, vegetation density was highest in the understorey and the canopy, and lowest in the midstorey. The clear-felled areas have high vegetation density till a height of about 8 m due to luxuriant regrowth and very low density till the canopy level (Fig. 3).

Consequently, vegetation density at the mean absolute height of each species is negatively correlated with the standard deviation of the species' absolute foraging height for all the habitats (Figs 5a-c), meaning that species in dense vegetation have narrower foraging strata across all habitats. In the clear-felled areas and selectively-felled areas, there is a stronger negative relationship compared to the primary habitats, as the species in these secondary habitats have a broader foraging breath (Figs 5a-c).

Guilds

An analysis of vertical distribution of species in the four guilds showed that that the diversity of foraging guilds was also much higher in the canopy than in the other two strata for the selectively-felled and primary areas. In the clear-felled areas, due to the absence of a well defined canopy, guild membership was greatly reduced.

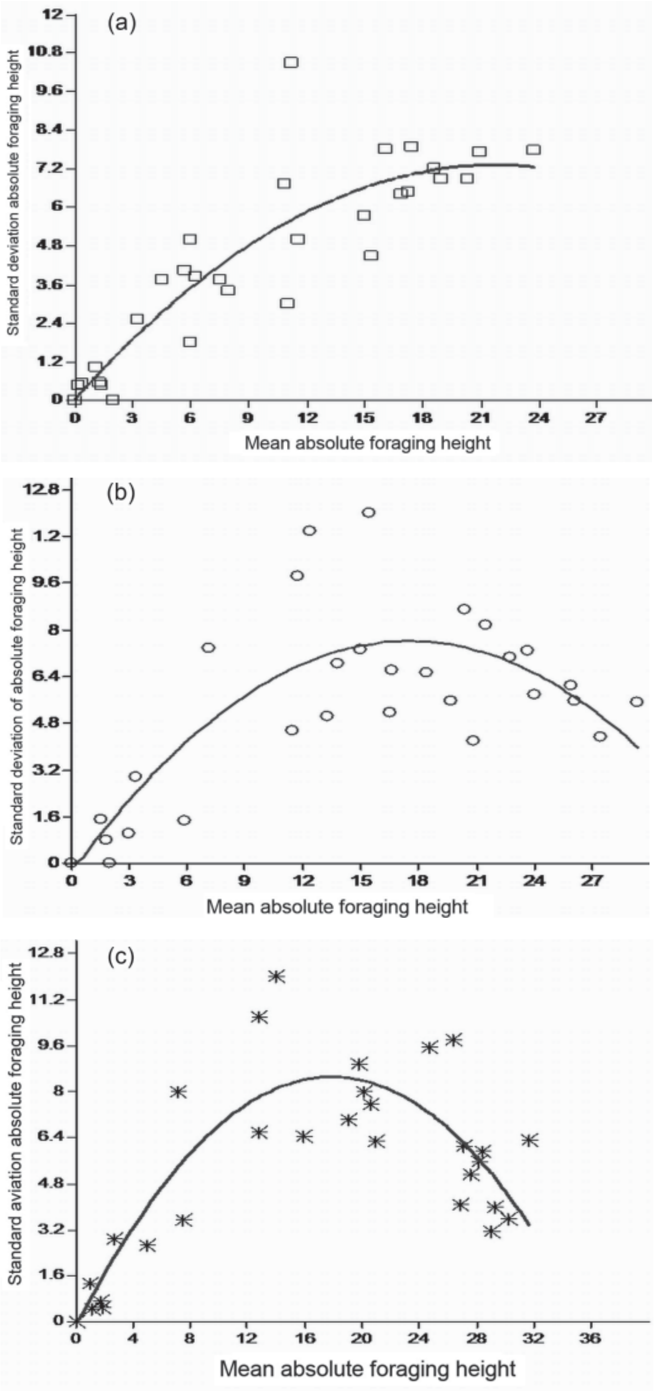

Fig. 4: Plots of the mean versus the standard deviation of absolute height for 31 tropical forest bird species. Species with n = 5 observations depicted with squares (clear-felled), circles (selectively-felled) and astrics (primary). All weighted least-squares regression models fits were significant at the p > 0.0001 level.

a) Clear-felled: $y=0.054x^2+ 0.67x-0.015$, $r^2= 0.80$, F=57.72, df=(2,31), $p<0.0001$

b) Selectively-felled: $y=-0.30x^2-0.90x-0.02$, $r^{2=}0.68$, F=30.53, df= (2, 31), $p<0.0001$

c) Primary: $y= -0.15x^2+0.97x-0.02$, $r^2= 0.74$, F=41.28, df=(2,31), $p<0.0001$

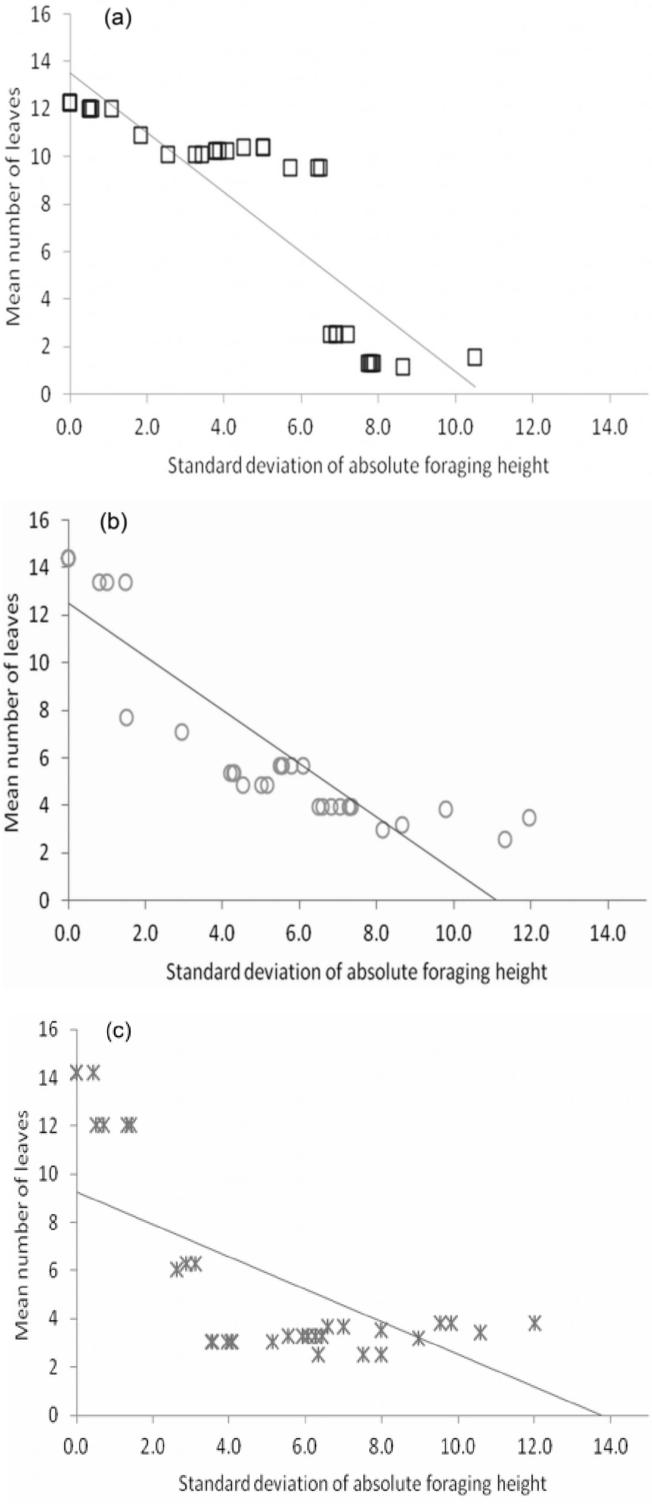

Fig. 5: Plot of vegetation density (mean number of leaves) versus the standard deviation of absolute height for 31 bird species (model I linear regression)

a) Primary: y= -0.67x+9.27, r^2= 0.42, F=22.6, df=(1,31), p<0.0001

b) Selectively-felled: y=-1.22x +12.49, $r^{2=}$0.79, F=120.63, df= (1, 31), p<0.000

c) Clearfelled: -1.22x+13.53, r^2= 0.77, F=105, df=(1,31), p<0.0001

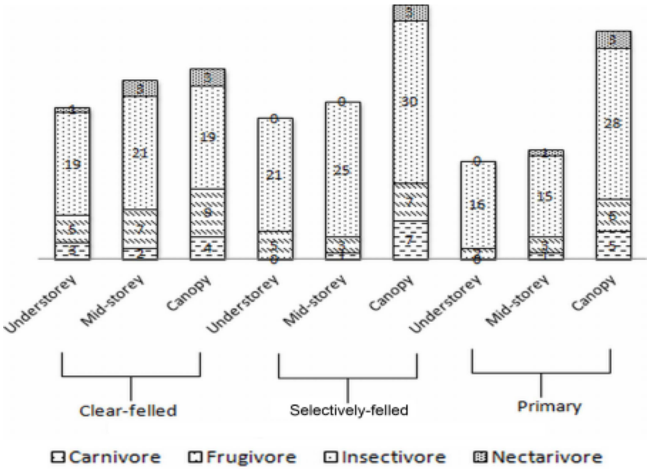

Fig. 6: Species richness of four guilds in vertical space across the three habitats

The understorey and mid-storey avifauna were predominantly insectivores in all habitats, whereas the canopy had all guilds, especially frugivores and nectarivores (Fig. 6).

To discern the patterns of guild variation, the four basic guilds were further divided according to foraging modes. This revealed that the primary forest was dominated by habitat specialists, secondary forest harboured both specialists and generalists, while clear-felled held either none, or very few, habitat specialists. Most foraging and dietary guilds that were recorded in sufficient numbers to be tested exhibited significant differences in their abundance between habitats (Fig. 7).

For example, arboreal gleaning insectivores were most abundant in the primary forest and the selectively-felled areas as the foliage volume in these areas is much higher than in clear-felled areas. Arboreal sallying insectivores also showed a similar trend. Arboreal omnivores were consistently most abundant in secondary growth habitats. Terrestrial gleaning insectivores were also more abundant in these habitats. Arboreal frugivores were attracted to the clear-felled habitats due to the abundance of drupes offered by the secondary vegetation, mainly *Elaeocarpus munronii*, *Elaeocarpus serratus*, and *Persea macrantha*.

Differences between habitats

Bird community structure was different in each of the three habitat types for all data sets, with each forest forming a distinct cluster on an MDS plot (ANOSIM global R=0.69, p=0.001; and all pair-wise habitat comparisons were significant, p=0.01) (Fig. 8). Species abundance in primary forest proved to be a poor predictor of its abundance in other habitat types. Within habitats, community dissimilarity among sites was similar for all habitat types, but slightly lower in

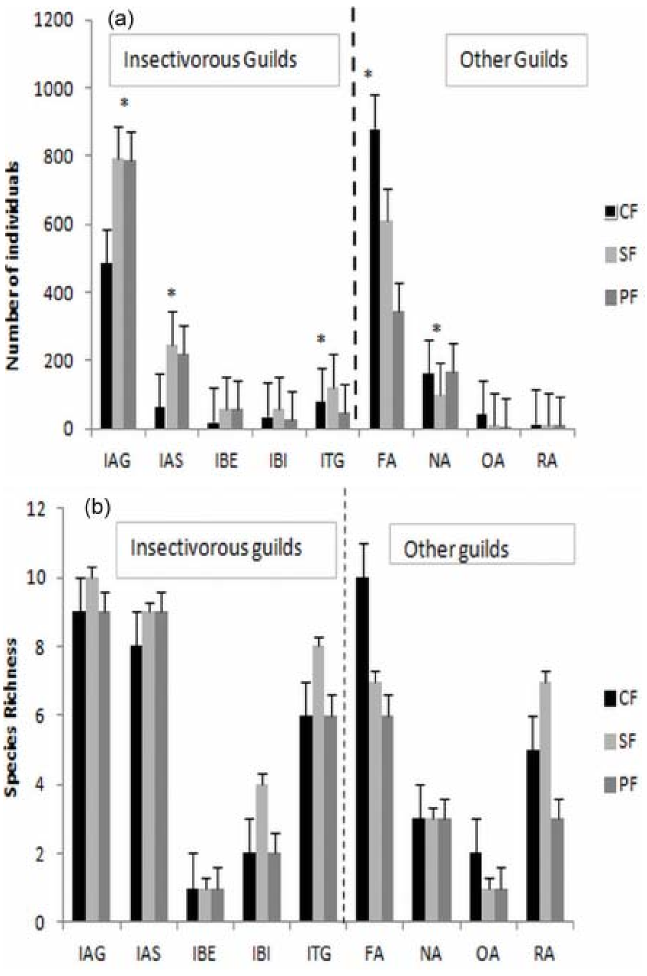

Fig. 7: Changes in the (a) abundance of birds and (b) species richness grouped by foraging and dietary guilds across habitat. [Guild codes are: IAG – arboreal gleaning insectivore; IAS – arboreal sallying insectivore; IBI – bark-searching insectivore (internal); IBE – bark-searching insectivore (external); ITG – terrestrial gleaning insectivore; FA – arboreal frugivore; NA – arboreal nectarivore; OA – arboreal omnivore; RA – diurnal raptor] Significance tests were made using Kruskal-Wallis tests, with p-values indicated by *=<0.05.

clear-felled areas. Geographic distance between sites and community dissimilarity did not show any significant relationship (Rho= -0.1, p=0.4).

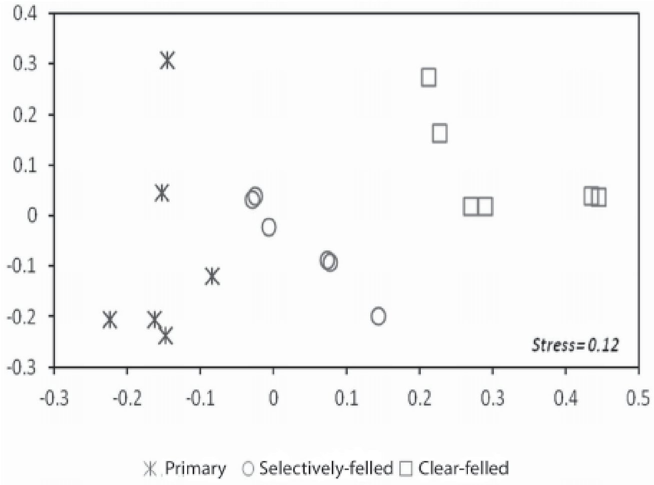

Fig. 8: Non-metric multidimensional scaling (MDS) ordinations of the bird community in three forest types. Ordination analyses are based on quantitative dissimilarity matrices.

DISCUSSION

Tropical bird community composition is constrained and determined by habitat structure (Terborgh 1985). Bird species richness and community structure is strongly correlated with closed canopy and complex habitat structure in regenerating forests (Andrade and Rubio-Torgler 1994; Blankespoor 1991; Bowman *et al.* 1990; Dunn 2004; Raman *et al*. 1998). There were statistically significant differences in vegetative structure between the forest types sampled. The primary and the selectively-felled areas were more similar than the short statured clear-felled areas. It can be postulated that the regeneration in selectively-felled areas had reached a level where the overall differences in vegetative structure, compared to the (control) primary forest, were not biologically or ecologically significant, and thus did not exert differential effects on their associated avifauna. Also important was the contiguity of our selectively-felled and clear-felled forest areas, which is critical in the re-colonisation of such forests (Lambert 1992). Contiguity or proximity increases the chance that vagrants or transient birds dispersing through secondary

Table 2: Vegetation structure in unlogged Primary, Selectively-felled and Clear-felled sites (F= One-way ANOVA)

	Clear-felled Mean ±SD	Selectively-felled Mean ±SD	Primary Mean ±SD	Statistic	df	P
Stem density/plot (>10 cm DBH)	11.42 ±5.8	10.18 ±1.27	8.21 ±0.034	F= 1.44	174	Ns
Stem density/plot (<10 cm DBH)	12.96 ±1.89	10.79 ±2.54	7.77 ±1.94	F = 33.34	174	< 0.001
% Canopy cover	87.42 ±6.53	90.07 ±4.69	92.75 ±1.49	F= 10.29	174	< 0.001

habitats will be detected (Terborgh and Weske 1969). Some authors have proposed that avian re-colonisation in such forests requires the presence of a mosaic of unlogged and selectively-logged forests (Johns 1996; Lambert 1992; Wong 1985), and is inversely related to the distance between them (Wong 1985).

We found that the primary forest canopy was species rich as compared to the mid-storey and understorey. In the tall primary forest, the vertical development of canopy structure provides a diversity of habitat elements and microclimatic conditions, which are crucial to vertical canopy use by birds. This general relationship of bird species diversity and forest height diversity is well known in forest-avian research (MacArthur and MacArthur 1961; Willson 1974). This study provides evidence that midstorey species of tropical rainforests forage in a broader stratum than understorey or canopy species. This was generally true for the primary and selectively-felled areas, but the clear-felled areas had a completely different pattern with species expanding their foraging niches. Dead leaf gleaning insectivores that are restricted to the forest floor in the primary areas were seen foraging at heights of 3–7 m in the clear-felled areas. The observed results may not hold true for rare species, as they were excluded from the analysis and phylogenetic relationships were not taken into account. It remains to be investigated if rare and other open-forest species have an influence on the foraging niches of the core avifauna in the clear-felled and selectively-felled areas through competition.

Studies have shown that relative height is a better measure of stratification in the absence of accurate height measurements and variability of forest height (Terborgh 1980; Walther 2002b). Since the sampling was carried out from the canopy, the height of the platforms was known and all detection heights were measured accurately. Stratification was not measured as stratum which is a crude measure, as it is a categorical variable. The relationship between the mean and the range for absolute height for Peruvian and New Guinean birds had the similar overall shape (see Walther 2002b), the observed relationships would have been impossible to infer without access to the canopy for detailed observations.

Many canopy species are usually invisible from the ground, especially in continuous canopy forests. The use of the platforms in conjunction with traditional ground-based sampling circumvents this problem (Anderson 2009; Walther 2003). The advantages of canopy sampling cannot eliminate the problem of pseudoreplication, especially for territorial species (Munn 1985). To minimise this, a total of 18 platforms were set up across the three habitats to ensure adequate replication and spatial coverage.

Variation in diurnal and seasonal height of foraging has been reported in Pearson (1971, 1977) and Bell (1982). This variation was not substantial enough to influence the overall relationship observed in our study which spanned over three years and seven seasons. The reasons for and the mechanisms that explain the observed parabolic relationships are discussed in Walther (2002b). With the change in structure of the habitat, it seems that species that specialise as understorey and canopy dwellers broaden their foraging niche. But not all species can show such niche plasticity and are forced out of the avian assemblages in areas of disturbance. Understorey babblers (*Rhopocichla atriceps*, *Pellorneum ruficeps*) and laughingthrushes (*Trochalopteron fairbanki*, *Garrulax delesserti*) use the dense band of vegetation found near the ground, which is difficult for sallying flycatchers such as *Culicicapa ceylonensis* and *Eumyias albicaudatus* which are found in the lower midstorey and above. Similarly, woodpeckers (Picidae) and nuthatches (Sittidae), as well as leaf-gleaning warblers (*Phylloscopus* spp.), tits (Paridae) and babblers (*Alcippe* spp.) are found throughout the mid-storey and extend into the understorey and the canopy. The foraging breaths for each species is hence a result of requirements that are found in a narrow band for understorey and canopy species, but in much broader strata for midstory dwellers (Walther 2002b).

The guild composition of the primary forest canopy was more diverse with an abundance of frugivores and nectarivores. Most bird species were confined to specific vertical foraging niches, especially understorey and canopy birds that forage in narrower vertical niches than mid-storey birds (Walther 2002b). The Square-tailed Black Bulbul (*Hypsipetes ganeesa*), Yellow-browed Bulbul (*Iole indica*), Oriental White-eye (*Zosterops palpebrosus*) and Brown-cheeked Fulvetta (*Alcippe poioicephala*) were some of the species that were seen to utilise vertical strata differently across the disturbance gradient. The change in habitat structure had a negative effect on these species as these canopy and mid-storey dwellers are more adversely affected.

Thirty-five years after being felled, the clear-felled areas we examined clearly failed to compensate for the loss of primary habitats and the habitat specialists they contain. Older areas of secondary forest may be more species rich (Dunn 2004) and hold a much higher proportion of primary forest species (see Sodhi *et al.* 2005). Even if forests are left, the post-disturbance recovery of bird communities is non-linear and slows after around 25 years, and regaining the complex microhabitats and structures required by primary forest specialists is likely to take centuries rather than decades (Raman *et al.* 1998).

CONCLUSION

Avian compositional characteristics were generally comparable for primary and selectively logged tropical rainforests, which possibly indicates advanced stages of forest regeneration. Our observation of generally undiminished bird diversity and greater abundance in the selectively-felled areas is an encouraging indication of the potential role of such forests in tropical-forest bird conservation. However, clear-felling had adverse impacts and showed reduction of rare rainforest specialist species because the forest canopy was opened up by logging, which resulted in gaps and changes in the vegetation structure, which were maintained by wind penetration and sustained harvesting of small boles for fuelwood and building material by the local people and by elephant activity. However, these areas were used by frugivorous species because of an abundance of secondary species with drupe fruits, so they may be of seasonal importance to such frugivores.

A complex habitat matrix does have a potential role in biodiversity conservation as they may act as refugia, a seasonal resource, can help to offset species loss, and may also provide landscape connectivity. But the current conservation efforts should concentrate primarily on the preservation of standing primary forests.

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