Animal Conservation (2002) **5**, 201–216 © 2002 The Zoological Society of London
DOI:10.1017/S1367943002002251 Printed in the United Kingdom

Responses of tropical rainforest birds to abandoned plantations, edges and logged forest in the Western Ghats, India

T. R. Shankar Raman and R. Sukumar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore – 560 012, India

(Received 30 July 2001; accepted 25 March 2002)

Abstract

This study examined the effects of alteration of tropical rainforest vegetation structure and composition on bird community structure and the influence of life-history traits on species persistence in the Kalakad-Mundanthurai Tiger Reserve, Western Ghats. Systematic sampling for vegetation and point count surveys for birds were carried out in cardamom plantations abandoned for 5 and 15 years, plantation–rainforest edges, a selectively logged forest patch and adjoining undisturbed rainforest sites. Principal components analysis of vegetation variables revealed clear differences between undisturbed and altered sites in woody plant and cane densities, canopy cover and vertical stratification. Bird species richness was lowest in cardamom plantations abandoned for 5 years and highest in logged and undisturbed forest. Bird species richness and similarity with undisturbed forest were significantly positively related to the vegetation component representing woody plant and cane (*Calamus* spp.) densities. Sites that were more similar in tree species composition had more similar bird communities whereas similarity in foliage profile between sites did not influence bird community similarity. Birds that were rare, were large-bodied and belonged to the carnivore, omnivore, bark-surface feeder and terrestrial insectivore guilds were adversely affected by habitat alteration. Restoring woody plant and cane densities and rainforest floristic composition in disturbed habitats may be required for management and conservation of bird communities typical to the region.

INTRODUCTION

Secondary forests are now ubiquitous in tropical landscapes. This is particularly evident in regions of tropical rainforest, valued by conservationists for their remarkable species diversity. In south Asia, as in the neotropics, central Africa and southeast Asia, tropical rainforests have been logged for timber, cleared and cultivated, exploited for non-timber natural products, submerged under reservoirs, and converted to plantations and other land uses. Such transformation of natural landscapes by human action has created over 400 million hectares of secondary forest (31% of total forest land) in tropical closed forest formations (Brown & Lugo, 1990). As secondary forests increase in area in the tropics, there is a clear need to assess their conservation values through studies of their vegetation and animal communities (Brown & Lugo, 1990; Richards, 1996; Johns, 1997).

Bird communities have been frequently used for conservation assessment and monitoring (Daniels, 1989; Furness & Greenwood, 1993). Past studies from tropical rainforest regions have shown that agroforestry plantations, logged forests and secondary successional forests generally harbour fewer bird species and have altered community composition as compared to primary forest (Daniels, Hegde & Gadgil, 1990; Johns, 1992; Thiollay, 1995; Raman, Rawat & Johnsingh, 1998). The relationship between degree of habitat alteration and change in bird communities is, however, not precisely understood. The observed effects may be a non-linear function of disturbance intensity (Johns, 1992) with the degree of change in bird community structure and composition being strongly related to the magnitude of alteration of rainforest vegetation structure and floristic composition (Raman *et al.*, 1998).

Within the community, individual bird species differ in their responses and susceptibility to habitat alteration. Habitat changes have been reported particularly to affect rare and restricted-range birds, rainforest habitat specialists and altitudinal migrants (Raman, 2001*a*). Other factors that influence susceptibility include body size, fecundity, diet-guild and foraging stratum (Terborgh & Winter, 1980; Brash, 1987; Kattan, Alvarez-López & Giraldo, 1994; Thiollay, 1995; Sieving & Karr, 1997;

All correspondence to: R. Sukumar. Tel: + 91 (80) 3600382, 3600985; Fax: +91 (80) 3602280, 3601428;
E-mail: rsuku@ces.iisc.ernet.in.

Castelletta, Sodhi & Subaraj, 2000), and abundance or rarity in undisturbed habitat (Diamond, Bishop & van Balen, 1987; Soulé *et al.*, 1988; Warburton, 1997; but see Marsden, 1997). The generality of these patterns can be assessed by studies of various forms of habitat alteration in different tropical forest regions.

Within peninsular India, tropical evergreen rainforests are distributed along the Western Ghats mountain range in southwest India (Champion & Seth, 1968). This region is among the world's biodiversity hotspots, global 200 ecoregions and endemic bird areas (Olson & Dinerstein, 1998; Stattersfield *et al.*, 1998; Myers *et al.*, 2000). Over the last century, in particular, the Western Ghats has seen significant transformation of its landscapes by human impact. Exploitation of forests during the British colonial period for timber, and land conversion for plantations such as teak, tea, coffee, cardamom, pepper and *Eucalyptus*, continued after independence in 1947. Besides creating new, anthropogenic habitats in the landscape, many secondary forest areas were also created as a result of logging and abandonment of plantations (Chandran, 1997). Chronic, low-intensity extractive use of forests also continues along the Western Ghats, with significant effects on the tropical rainforest vegetation (Daniels, Gadgil & Joshi, 1995).

This study focused on the responses of tropical rainforest birds to disturbed forest habitats by documenting changes in bird abundance and community structure. Sites representing cardamom (*Eletteria cardamomum*) plantations abandoned for 5 and 15 years, plantation–rainforest edges and a selectively logged patch were compared with adjacent primary tropical evergreen rainforest in the Kalakad-Mundanthurai Tiger Reserve in southern India. The main questions of the study were: (1) What are the changes in vegetation and bird community structure in disturbed forest sites? (2) Does bird community structure vary predictably with degree of alteration of forest vegetation structure or tree species composition? (3) What are the species correlates of susceptibility to habitat alteration? The results are compared with earlier findings from other tropical rainforest bird communities. In addition, the results are used to discuss the conservation values of abandoned plantations and logged sites and the need for habitat management and rainforest restoration for bird conservation.

STUDY AREA

Location and extent

The study was carried out in the Kalakad-Mundathurai Tiger Reserve (KMTR), a 895 km^2 sanctuary located between 8°25′ to 8°53′ N and 77°10′ to 77°35′′ E at the southern end of the Western Ghats. The Reserve ranges from 50 to 1600 m above mean sea level (asl), with rainforests occurring chiefly above 600 m. In the Western Ghats, KMTR and adjoining areas have one of the largest remaining contiguous tracts (over 400 km^2) of relatively undisturbed tropical rainforest (Ramesh, Menon & Bawa, 1997). The vegetation at mid-elevation is tropical wet evergreen forest (Champion & Seth, 1968) of the *Cullenia exarillata – Mesua ferrea – Palaquium ellipticum* type that has about 43% plant endemism (Pascal, 1988). KMTR contains around 2000 of the 3500 plant species found in the Western Ghats (Ganesh *et al.*, 1996). More details of the vegetation are available elsewhere (Ganesh *et al.*, 1996; Parthasarathy, 1999, 2001)

The mean monthly temperature (average of mean daily maximum and mean daily minimum calculated across all days in the month) in the rainforest ranges between 19°C in January and 24°C in April–May at mid-elevations (Sengaltheri, 1040 m). The average annual rainfall is over 2200 mm. There are three distinct seasons: dry season (February to May), southwest monsoon (June to September) and northeast monsoon (October to January). KMTR receives most (> 50%) of the rainfall during the northeast monsoon. The average relative humidity ranges from about 60% in March to about 90% in November–December.

The intensive study sites were located in Sengaltheri (8°31′ N and 77°26′ E) and Kakachi (8°33′ N and 77°24′ E). These areas contain rainforests ranging in altitude between 800 m and 1400 m, which are contiguous with rainforests elsewhere in the Reserve. The terrain is rugged, mountainous and drained by many perennial streams. All bird sampling reported in this paper was restricted to between 1040 m and 1300 m asl.

Avifauna

Although 278 bird species have been seen in and around KMTR, only about 80 species occur regularly in the rainforests here (Johnsingh, 2001; Raman, 2001*b*). The remaining species occur mainly in drier forests, water bodies and other habitats. This pattern of relatively low bird species richness in the rainforests is typical of other hill ranges (e.g., Anamalai hills, Kannan, 1998) as well as the entire Western Ghats (Daniels, Joshi & Gadgil, 1992). This pattern is not a consequence of recent anthropogenic changes; instead, it is a biogeographic legacy due to the restricted area occupied by rainforests and their isolation from the large tracts of rainforests in northeast India and southeast Asia. Similar areas of rainforest in northeast India tend to have nearly three times the number of bird species (Ali, 1977; Daniels *et al.*, 1992). In the rainforests of KMTR, 13 species of winter migrants arrive around October and stay until April or early May. Other rainforest species are resident year-round, and include 12 of the 15 species endemic to the Western Ghats. A majority of species breed between late January and May (Ali & Ripley, 1983; Raman, 2001*b*). Common and scientific names in this paper follow Inskipp, Lindsey & Duckworth (1996) and Grimmett, Inskipp & Inskipp (1998).

Study strata and selected sampling sites

The following strata and sites were selected for study:

(1) Cardamom plantation abandoned for 5 years

Three sites (P1, P2 and P3) were selected in this stratum (henceforth referred to as 5-year abandoned plantation) at Sengaltheri, where the plantations were abandoned upon expiry of lease in 1995. P1 and P2 were less than 200 m apart and adjoined each other and primary forest, although P3 was about a kilometre away and separated by a stream and a section of secondary growth. When the plantation was established, most understorey trees had been cleared, although large native trees were retained and a few exotic trees (*Erythrina indica*) were planted as canopy shade trees. During the study, the shrub and sapling layer was virtually absent and still dominated by surviving cardamom clumps, and also contained weeds, ferns, some grasses and herbaceous plants. The three sampled sites were surrounded by relatively undisturbed primary rainforest.

(2) Cardamom plantation abandoned for 15 years

A single site (P7, henceforth referred to as 15-year abandoned plantation), abandoned around 1983, was sampled in Kakachi. Superficially, this site resembled the 5-year abandoned plantation but the tree canopy appeared much sparser. Pioneer (*Macaranga indica, Debregesia longifolia*) and rainforest trees were growing in the understorey. The ground layer was still dominated by surviving cardamom plants, weeds, ferns, grasses and herbs.

(3) Plantation–rainforest edges

Two sites (P4, P5) at the edges of the 5-year abandoned plantations in Sengaltheri and one (P6) between an abandoned *Eucalyptus* plantation and secondary rainforest vegetation in Kakachi were sampled. These sites appeared intermediate in structural and floristic alteration between the abandoned cardamom plantations and rainforest and were chosen to see if they were intermediate in bird community attributes. A key difference was the occurrence of woody shrubs in the understorey in this stratum.

(4) Logged forest

One site (T7) representing a selectively logged (probably at low intensity) patch of forest was sampled in Kakachi, near Kodeyar. This site had few large trees and a sparse canopy. The pioneer tree *Macaranga indica* was quite common, as was bamboo in the understorey. The site was otherwise similar in many respects to primary rainforest. The logging was probably carried out when the nearby Kodeyar reservoir was being constructed (1968–78). Since then the site has been abandoned and undisturbed except for limited fuelwood and timber removal by local people.

(5) Primary rainforest

Six undisturbed rainforest sites were sampled (T3, T4 and T5 in Sengaltheri and T8, T9 and T10 in Kakachi). These had tree and liana (> 20 cm girth at breast height, 1.3 m) densities of over 900/ha, with a maximum canopy height of about 30 m. The sites had a dense undergrowth of shrubs, herbs and canes (*Calamus* spp.). The common canopy trees were *Cullenia exarillata, Palaquium ellipticum, Mangifera indica, Syzigium* spp., *Holigarna nigra, Aglaia eleagnoidea* and *Cryptocarya bourdilloni*. Understorey trees included *Antidesma menasu, Agrostistachys borneensis, Epiprinus mallotiformis, Drypetes* sp., *Acronychia pedunculata, Eugenia* sp. and *Nothopegia racemosa*.

The exact area of each patch could not be estimated because of lack of detailed maps; however, the sampling in each site covered approximately 12 ha relatively uniformly in order to enable comparisons.

METHODS

Vegetation sampling

In each of the 14 sites, densities and basal areas of trees greater than 30 cm girth at breast height (GBH at 1.3 m) were estimated using the point-centred quarter method (PCQ, Krebs, 1989). Thirteen PCQ plots, with successive plots spaced 50 m apart along the central trail or transect, were measured in each site, giving a sample of 52 trees per site. The plot centres were located about 10 m off the trail into the forest interior. All trees in the PCQ plots were identified to species, or in a few cases to genus level, using an available flora (Gamble, 1935) and field guide (Pascal & Ramesh, 1997). At each of the 13 PCQ plots, 2 m radius plots were laid around the centre point to enumerate shrubs. In addition, the number of cane plants and the presence or absence of bamboo within a 5 m radius were recorded.

Altitude, canopy and leaf litter variables were measured at 25 points, evenly spaced 25 m apart along the trail or transect in each site. Canopy height was measured using a rangefinder. A canopy overlap index was given as described elsewhere (Daniels *et al*., 1992; Raman *et al*., 1998). Percentage canopy cover was measured using a spherical densiometer at the 25 points in each site. Vertical stratification was assessed at these 25 points following Raman *et al*. (1998). The presence or absence of foliage was noted in the following height intervals (in metres): 0–1, 1–2, 2–4, 4–8, 8–16, 16–24, 24–32 and > 32, directly above and in a 0.5 m radius around each point. Leaf litter depth on the forest floor was measured using a calibrated wooden probe at each point. As ground vegetation and litter were disturbed along trails, the samples were taken 10 m away from trails in the forest interior.

Bird surveys

The fixed-radius point count method was used to survey bird populations at each site (Verner, 1985; Hutto, Pletschet & Hendricks, 1986; Bibby, Burgess & Hill, 1992; Ralph, Sauer & Droege, 1995). Details of the field techniques are available elsewhere (Raman, in press).

Point count surveys of 5 minutes duration were carried out on clear days during the first 3 hours after sunrise when bird activity was highest. All birds seen, heard or flying under the canopy up to a fixed radial distance of 50 m were recorded. Densities estimated by the fixed-radius approach were highly correlated to variable-radius point count estimates and were therefore used to obtain a simple and comparable density estimate across all species (Buckland *et al.*, 1993; Raman, in press). At each site, 25 point count surveys (yielding 122–245 detections and an estimated 265–577 individual birds per site) were carried out, excluding the logged forest patch in which only 18 point counts were sampled because of logistical difficulties. Survey points sampled on a given day were spaced at least 100 m apart along narrow trails or transects through the site. All sampling was carried out by a single observer (TRSR) with over 2 years' experience in identifying birds of the region by sight and calls. Aural detections were included for all analyses for two reasons. First, most (83%) detections were by calls. Second, sound attenuation effects are negligible below 30 m for many species (Waide & Narins, 1988) and for greater distances for birds with loud calls, making it feasible to use the fixed-radius data to compare across sites.

Sampling was carried out mostly between February and May 1998 (the 15-year plantation was sampled in March 1999), when resident birds and winter migrants were present in the plots. Some sampling was also carried out on bright, sunny days between June and August 1998 when winter migrants were absent but resident bird activity and detectability were high. Therefore, for comparisons of bird species richness and abundance across sites, only data on resident birds (excluding seven migrant species) were used. Data from the sampling in March 1999 were included in the study, as environmental conditions were very similar between years with low rainfall and high detectability of both resident bird species (a majority of which were breeding and singing during that time in both years) and migrants (all seven species). Nevertheless, results from the 15-year plantation site need to be interpreted with caution.

Analyses

Average values across replicate sampling points in each site were calculated for altitude measurements and vegetation variables: shrub, cane and cardamom densities, leaf litter depth, and canopy height, cover and rank. Vertical stratification was measured as the average number of strata with foliage across the 25 points sampled in each site. The coefficient of variation of this index reflected variation in foliage distribution across points and was used as an index of horizontal heterogeneity (following Raman *et al.*, 1998). The total number of tree species recorded in the PCQ plots was recorded as a measure of tree species richness. The vegetation variables were summarized using principal components analysis in order to identify sets of inter-correlated variables as components, with each component orthogonal and not correlated to the others. The fewer components representing the vegetation gradient could then be related to bird responses (Pielou, 1984). The analysis was performed using SPSS and the resulting factor matrix was rotated by the Equamax method to enable easier interpretation.

Bird species richness at each site was estimated using the cumulative total bird species recorded, and indexed by the average number of bird species recorded per point count. In addition, Coleman rarefaction curves (random placement procedure, Coleman *et al.*, 1982; Colwell & Coddington, 1994) were constructed using the program EstimateS, Version 6.01 (Colwell, 1997). The number of species detected after 17 point count surveys was estimated using 100 random permutations of the data set (sampling with replacement) and compared across sites. We used only 17 point count surveys (even though we had 25 point counts on most of our transects) because one of our transects had only 18 point count surveys, and we wished to obtain standardized estimates of diversity (Shannon–Weiner index, 100 random permutations of the counts, sampling with replacement) across all the transects.

For aural bird detections, the number of individual birds could not be counted in the field. For each species, however, information on flock sizes (a flock representing one to many individuals for this purpose) was collected during surveys and opportunistic observations. For species with fewer than ten detections, the number of birds comprising a given detection was assumed to be the mean flock size of the species, rounded to the nearest integer. For more frequently detected species, a flock size was randomly assigned to each detection through a Monte-Carlo procedure from the sampling distribution of flock sizes for that species. The average number of individual birds per point was used as an estimate of bird abundance. Differences between sites in bird species richness, number of detections and bird abundance were tested using repeated-measures analysis of variance (Sokal & Rohlf, 1981).

Similarity in bird community and tree species composition between sites was computed using the Morisita index that is least sensitive to sample size effects (Wolda, 1981). An index of similarity in foliage profile was also computed using the Morisita index, based on the data on number of points with foliage in different vertical strata (following Raman *et al.*, 1998). The matrix of pairwise similarities in bird community composition was related to corresponding matrices of similarity/distance in tree species composition and foliage profile, and difference in elevation (elevational distance) between sites using Mantel tests (Manly, 1994). Statistical significance of the Mantel tests was assessed through 10,000 random permutations. To examine the independent effects of different variables, partial Mantel tests derived from the Kendall *tau* approach were used (Hemelrijk, 1990). Relationships between bird community and vegetation components (PCs) were assessed using Kendall correlations (Siegel & Castellan, 1988).

Bird responses to the different habitat changes (study strata i to iv) were assessed using a simple persistence index (PI, modified from the response index of Davies, Margules & Lawrence, 2000). The persistence index was defined as the ratio of the average density of the species in the stratum to its average density in rainforest. The PI can be considered as an index of population decline or increase as species that declined in the stratum relative to rainforest had PI < 1, while those that increased had PI > 1. PI values were calculated for all species in each stratum (5-year and 15-year abandoned plantations, edges and logged) excluding five species that did not occur in primary rainforest samples. Species were classified into eight diet-guilds and three broad foraging strata categories (terrestrial, understorey and canopy) using natural history information from Ali & Ripley (1983) and personal observations. The body mass of each species was obtained from means (or mid-points if only range was available) given by Ali & Ripley (1983). In a few cases, body mass was approximated using values available for similar species. In order to see if persistence was related to rarity and body mass, Kendall partial rank-order correlation coefficients were calculated (Siegel & Castellan, 1988). Difference in PI values of species belonging to different diet-guild and foraging strata categories were tested using non-parametric Kruskal–Wallis analysis of variance (Siegel & Castellan, 1988).

RESULTS

Vegetation changes across strata

There were noticeable differences in vegetation across strata. The most obvious and visible changes were in foliage profile. The percentage of points with foliage in the eight height intervals was significantly different across the five strata ($\chi^2 = 75.63$, d.f. = 28, $P < 0.001$; Fig. 1).

In comparison with primary rainforest, the 5-year and 15-year abandoned cardamom plantations had substantially lower percentage of points with foliage in the height intervals below 16 m owing to the relative paucity of shrubs and understorey trees. The 5-year plantations, however, had a greater proportion of points with foliage above 24 m compared to rainforest, indicating the well-developed canopy of large, remnant shade trees in the plantation. Interestingly, the 15-year abandoned cardamom plantation had a greater percentage of points with foliage than the 5-year plantation in the height intervals between 2 m and 8 m, indicating the contribution of regenerating shrubs and pioneer trees in these vertical strata. In contrast, the logged patch showed a similar foliage profile to primary rainforest at heights below 16 m. However, the logged patch had substantially lower percentage of points with foliage in the height intervals between 16 and 32 owing to the removal of large trees. The plantation–rainforest edges showed a foliage profile similar to primary rainforest, but with a lower percentage of points with foliage in all height classes (Fig. 1).

There were notable differences in other vegetation attributes. Average canopy cover was above 92% (92.9–95.8%) in all the primary rainforest sites. In the other strata, average canopy cover was lower, being 90.6–91.4% in 5-year plantation, 72.1% in the 15-year plantation, 79.3–91.2% in edges and 90.4% in the logged site. The primary rainforest sites also had higher vertical stratification, litter depth and basal area, and lower horizontal heterogeneity as compared to three sites (*Eucalyptus*-rainforest edge, 15-year abandoned plantation and logged sites), while the other sites had intermediate values. Tree and shrub densities were also higher in primary rainforest, lower in 5-year and 15-year plantations and intermediate in the edges. Notably, the logged site and *Eucalyptus* edge had high tree and shrub densities, although the basal area was low.

Cane was present at high densities (average of 2.4–25.2 plants/plot) in the primary forest and logged sites, but absent in the abandoned cardamom plantations, and occurring at intermediate abundance in the edges (0.6–2.4 plants/plot). A converse pattern was found in the distribution of cardamom. Cardamom was absent in primary rainforest (except for one clump recorded in T3), the logged site and the *Eucalyptus* edges. Cardamom densties were high in the 5-year (average of 2.5–3.5 clumps/plot) and 15-year plantations (2.9 clumps/plot) and intermediate in two edge sites (P4 and P5, 0.4–1.3 clumps/plot). Bamboo occurred patchily in the logged site, primary rainforest sites and edges, and, like cane, was absent from the abandoned plantations. For the standardized sample of 52 trees, tree species richness was lowest in *Eucalyptus* edge (14 species), intermediate in the abandoned cardamom plantations and logged site (20–21 species), and highest in primary rainforest and the other two edge sites (23–31 species, except T9 that had 13 species).

Cluster analysis and ordination using vegetation parameters

To examine similarities between sites in their vegetation structure, principal components analysis and ordination were used. Principal components analysis extracted three components representing 81.9% of the total variation in the data set (Table 1). The first component (PC1), explaining 34.6% of the variation, was related strongly positively to tree, shrub and cane densities, weakly to canopy rank and negatively to litter depth and density of cardamom clumps. PC1 can thus be taken to indicate woody plant densities. PC2, explaining 34.2% of the variation, was related to forest structural attributes; it was correlated positively with canopy variables, vertical stratification and basal area, and negatively with horizontal heterogeneity. PC3 (13.1% of the variation) was positively related only to tree species richness.

The major changes along the vegetation gradient are clearly encapsulated when the sites are plotted in the ordination diagram using their PC1 and PC2 scores (Fig. 2). The primary rainforest sites have relatively high PC1 values, reflecting high woody plant densities, and high PC2 values, indicating well-developed forest structural attributes and low horizontal patchiness. The

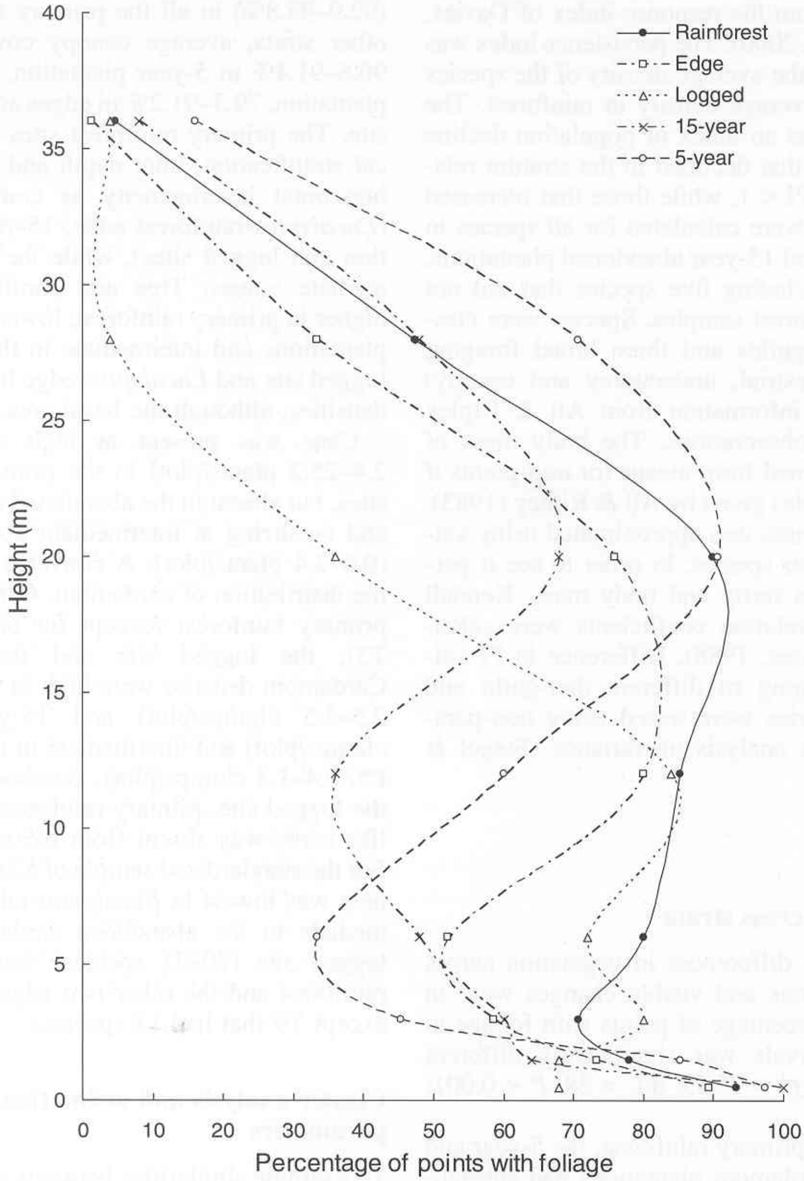

Fig. 1. Foliage profile in the different disturbed rainforest strata and primary rainforest. For strata with replicate sites, percentage of points with foliage in each height interval was averaged across sites. Smoothed curves are used to join percentage values plotted against mid-points of the height intervals sampled.

logged and *Eucalyptus* edge sites have high PC1 scores owing to relatively high woody plant density, but low PC2 scores because of low basal area, canopy cover and vertical stratification. Two primary rainforest sites (T4 and T5) had low PC1 values similar to the edge sites. The abandoned cardamom plantations are at the lower end of the gradient on PC1 owing to very low woody plant densities and an understorey still dominated by cardamom clumps. Two edge sites (P4 and P5) were intermediate between plantations and rainforest. Within the abandoned cardamom plantations, the 15-year plantation site was lower on the PC2 axis than the 5-year sites, indicating sparser canopy, lower vertical stratification and higher horizontal patchiness (Fig. 2).

Trends in bird species richness and abundance

A total of 2431 detections comprising an estimated 6045 individual birds belonging to 52 species was obtained during the study (see Appendix for species and Latin names). Seven (13.5%) bird species were not detected in any of the abandoned plantations and rainforest edges. These were grey-breasted laughingthrush (endemic to Western Ghats), rufous woodpecker, white-bellied woodpecker, oriental dwarf kingfisher, crested serpent eagle, and Eurasian blackbird. All of these species were relatively rare in primary rainforests. Species detected only in the disturbed habitats and absent in primary rainforests were the red-whiskered bulbul (resident), and

Table 1. Results of principal components analysis of forest vegetation variables in disturbed and undisturbed rainforest sites

	Principal components		
	PC1	PC2	PC3
Eigen value	4.2	4.1	1.6
Variance explained (%)	34.6	34.2	13.1
Cumulative variance (%)	**34.6**	**68.8**	**81.9**
Factor matrix[a]			
Tree (> 30 cm girth at breast height) density	**0.907**	0.002	–0.007
Shrub density	**0.933**	0.178	–0.001
Cane density	**0.750**	0.301	–0.320
Density of cardamom clumps	**–0.870**	0.008	–0.306
Litter depth	**–0.604**	0.508	0.348
Canopy rank	**0.595**	**0.578**	0.413
Canopy height	–0.283	**0.929**	–0.002
Canopy cover	0.391	**0.597**	0.524
Vertical stratification	0.272	**0.917**	0.161
Horizontal heterogeneity	–0.311	**–0.784**	–0.156
Basal area of trees > 30 cm GBH	–0.002	**0.839**	0.005
Tree species richness	–0.139	0.002	**0.866**

[a] Pearson's correlations with original variables (d.f. = 12); significant correlations ($P < 0.05$) are given in bold.

Blyth's reed warbler and pied thrush (migrants). Two other resident species detected occasionally in point count surveys in disturbed habitats but not in primary rainforests were the hill myna and white-bellied treepie. These two species were, however, seen frequently in rainforests during opportunistic observations.

Comparison of bird species richness using rarefaction showed discernible, although relatively moderate, differences between strata (Fig. 3). Bird species richness was lowest in 5-year abandoned cardamom plantations and highest in the primary rainforest and logged sites (Fig. 3). The number of resident bird species, detections and individuals per point showed a similar pattern, with the 5-year plantations having lowest and logged and primary rainforests having highest values (Fig. 4). Repeated-measures analysis of variance indicated significant effects of stratum on these three variables ($F > 3.93$, d.f. = 4, $P < 0.05$). The within-subject or repeated-measures (points) effect was not significant ($F < 1.10$, d.f. = 17, $P > 0.35$). There was also no significant interaction effect between point and stratum ($F < 0.92$, d.f. = 68, $P > 0.66$). When the full data set (including migrants) was analyzed, nearly identical results were obtained.

Correlations between bird community and vegetation

To examine relationships between vegetation structure (represented by the principal component scores) and bird community attributes, non-parametric Kendall correlations were used. Total bird species richness (rarefaction value after 17 point counts surveys) was correlated to the site scores representing woody plant density (PC1, Kendall $\tau = 0.582$, $N = 14$, $P = 0.004$). The rarefaction estimate of resident bird species richness was also correlated to PC1 scores ($\tau = 0.597$, $P = 0.003$). Other indices of resident bird species richness (overall, number of resident species detected at least twice, and average resident species detected per point) were also significantly positively correlated to PC1 ($\tau > 0.540$, $P < 0.01$; Fig. 5(a)). Total bird abundance, measured as the number of individual birds per point, was also significantly positively correlated to PC1 ($\tau = 0.429$, $P =$

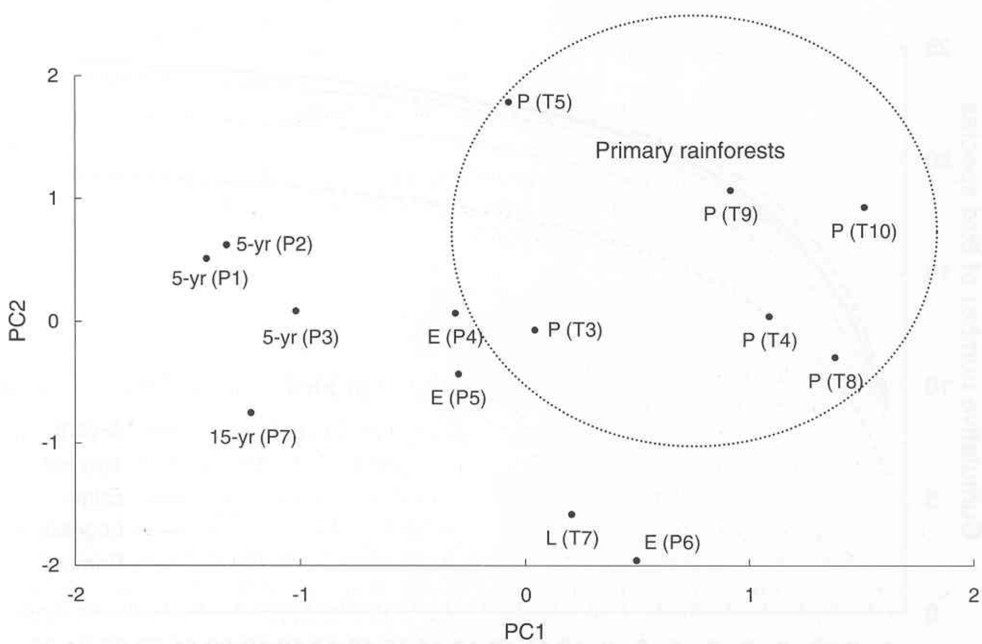

Fig. 2. Ordination of sampled sites using the principal component scores PC1 and PC2. PC1 was related positively to woody plant and cane density and negatively to density of cardamom clumps and leaf litter depth. PC2 was related positively to forest structural attributes (canopy cover, vertical stratification, basal area) and negatively with horizontal heterogeneity. The ellipse is drawn by eye to indicate primary rainforest sites.

0.033), although the correlation between resident bird abundance and PC1 was not highly significant (τ = 0.363, P = 0.071). PC1 was also significantly positively correlated to endemic bird species richness (τ = 0.524, P = 0.017) and endemic bird abundance (τ = 0.729, P < 0.001) across sites. The correlation between bird species diversity (Shannon–Weiner index) and PC1 was not statistically significant (all birds: τ = 0.354, P = 0.079; resident birds: τ = 0.287, P = 0.154). None of the bird community parameters was significantly correlated to PC2 or PC3 scores or the altitude of the sites.

The above bird community indices do not reflect changes in relative abundance of individual species as a consequence of habitat changes. Changes in bird community composition in the study sites were thus assessed by comparing all sites to one of the primary rainforest sites (T9) that was virtually undisturbed and had highest bird species richness. Similarities in bird community composition between each site and T9 (Morisita index) were computed and correlated with the PC scores. Again, similarity in bird community composition with primary forest was significantly positively correlated only to PC1 (τ = 0.606, N = 13, P < 0.01). Thus, sites with higher scores of PC1 reflecting higher woody plant densities were more similar in bird community composition to primary rainforest (Fig. 5(b)).

Bird species turnover and similarity between sites

A dendrogram illustrating similarities in bird community composition between sites was produced using average linkage (between groups) cluster analysis (Fig. 6). The input for the cluster analysis was a matrix of pairwise similarities between sites (Morisita index) in bird community composition. The dendrogram shows four primary rainforest sites clustering together and being distinct from the other sites. Two primary rainforest sites (which had lower PC1 scores, see Fig. 5(b)) were, however, linked to some of the disturbed habitats (Fig. 6).

Mantel tests were used to determine if bird species compositional similarity between sites was related to similarities in tree species composition and foliage profile, and elevational distance between sites. Similarity in bird community composition was significantly positively correlated with similarity in tree species composition (Mantel test, K_r = 246, P = 0.0076), but not with similarity in foliage profile (K_r = 22, P = 0.38). Elevational distance between sites was not significantly correlated to bird community similarity (K_r = 111, P = 0.13), tree species similarity (K_r = 68, P = 0.23) or foliage profile similarity (K_r = 111, P = 0.12) between sites.

Mantel tests between the predictor variables revealed that only similarity in tree species composition and similarity in foliage profile were correlated (K_r = 280, P = 0.0021). Partial Mantel tests were used to examine the influence of each variable controlling for the other. Bird community composition was still not correlated to similarity in foliage profile when tree species similarity was controlled for (partial Mantel test, T = – 0.045, P = 0.69). Conversely, bird species composition continued to be significantly correlated with similarity in tree species composition after controlling for similarity in foliage profile (T = – 0.236, P = 0.0063), further indicating the influence of tree species composition on bird community composition.

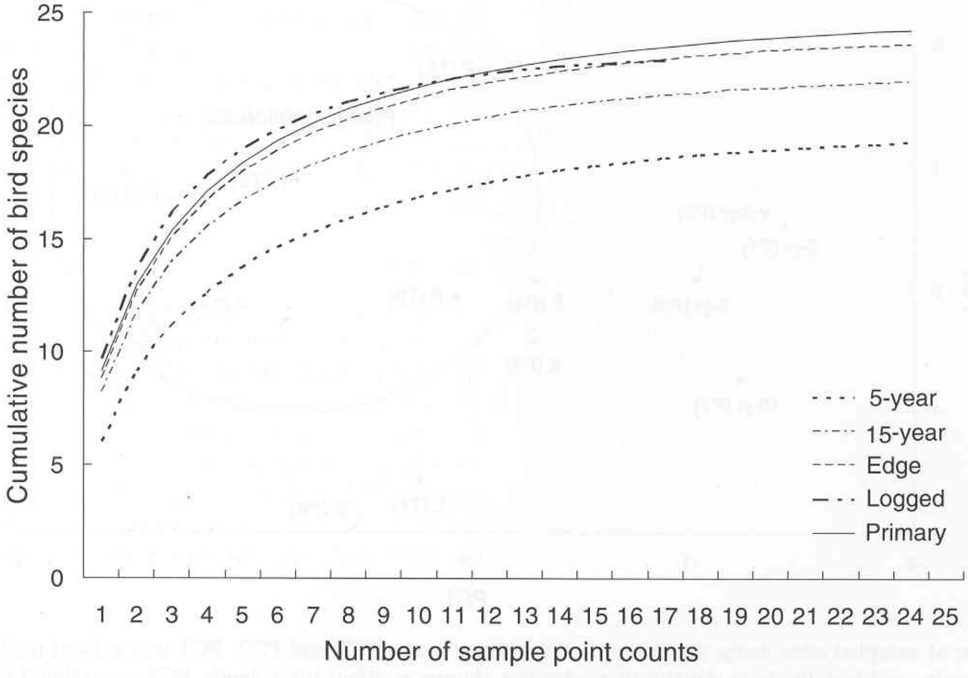

Fig. 3. Rarefaction curves of resident bird species richness with sampling effort in the different strata. For strata with replicate sites, estimated resident species richness curves were averaged across sites.

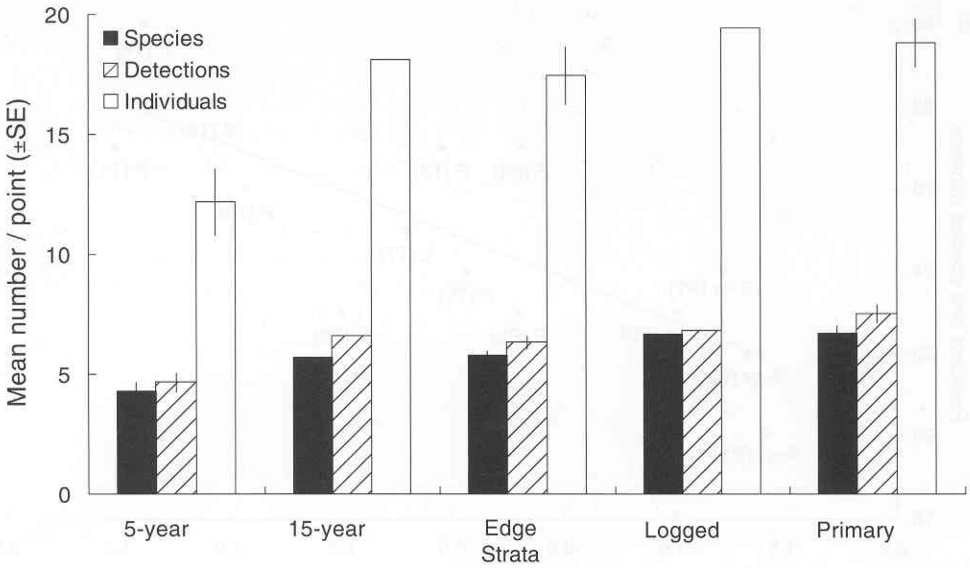

Fig. 4. Variation in resident bird species richness, detections and abundance in point count censuses in the different strata. For the three strata with replicate sites, the mean and standard error (error bars) were calculated using the average values for each site ($N = 3$ for 5-year plantation and edge, $N = 6$ for primary rainforest).

Species attributes and persistence in disturbed habitats

Persistence index (PI) values were compared among different species categories to assess the influence of these species attributes on the susceptibility of birds to habitat changes. Most species categories in most strata have average PI values less than 1 (Fig. 7). This suggests that the different forms of habitat alteration result in generally lowering the abundance of bird species as compared to rainforest. There was, however, wide variation among species and some categories appeared more sensitive.

Rarity and body mass

The abundance of bird species in primary rainforest was negatively correlated to body mass ($\tau = -0.28$, $N = 47$, $P = 0.006$). In each stratum, avian persistence was significantly positively correlated with abundance when the effects of body mass were controlled for. The correlation was weaker in 5-year and 15-year abandoned plantations (Kendall partial rank-order correlations, $T = 0.17$ and 0.18, respectively, $N = 47$, $P < 0.05$) compared to edge and logged sites ($T = 0.31$ and 0.40, respectively, $P < 0.01$). Body mass did not have a significant independent effect on persistence in 5-year abandoned plantations and edge sites ($T = -0.10$ and -0.01, respectively, $P > 0.05$), although it was significantly negatively related to persistence in 15-year plantations and logged sites ($T = -0.30$ and -0.25, respectively, $P < 0.01$). The results indicate a higher susceptibility of rare species to habitat disturbance.

Diet-guild

Diet-guild also had an influence on PI values. These differences between diet-guilds in PI values were significant in the 15-year abandoned plantations (Kruskal–Wallis ANOVA by ranks, $H = 17.46$, $N = 47$, $P = 0.015$) and almost significant ($H = 13.66$, $P = 0.058$) in logged forest (Fig. 7(a)). Terrestrial insectivores and carnivores had low average PI values in all strata except in logged forest. Bark-surface feeders had low PI values, except in the 15-year plantation. Omnivores had relatively low average PI values in all strata (Fig. 7(a)).

Foraging strata

Terrestrial birds appeared to be related to low average PI values in all strata, whereas understorey birds had relatively low average PI values in 5-year plantation and edge strata only. Canopy birds had relatively higher average PI values, particularly in 15-year plantations. Only in 15-year plantations, however, were the differences statistically significant ($H = 6.49$, $P = 0.04$, Fig. 7(b)).

Endemism

Average persistence index of endemics ($N = 7$ species) was compared with that of non-endemics ($N = 40$ species) in each stratum using Mann–Whitney U-tests. The average PI of endemics was lower than that of non-endemics in 5-year plantation (0.31 ± 0.16 SE *vs.* 0.71 ± 0.15), 15-year plantation (0.49 ± 0.40 *vs.* 1.24 ± 0.28), edge (0.49 ± 0.19 *vs.* 0.73 ± 0.10) and logged sites (0.56 ± 0.25 *vs.* 0.68 ± 0.11). However, these differences were not statistically significant (Mann–Whitney U-tests, $P > 0.20$).

DISCUSSION

Alteration of rainforest habitat had discernible effects on the bird community. These included reductions in bird

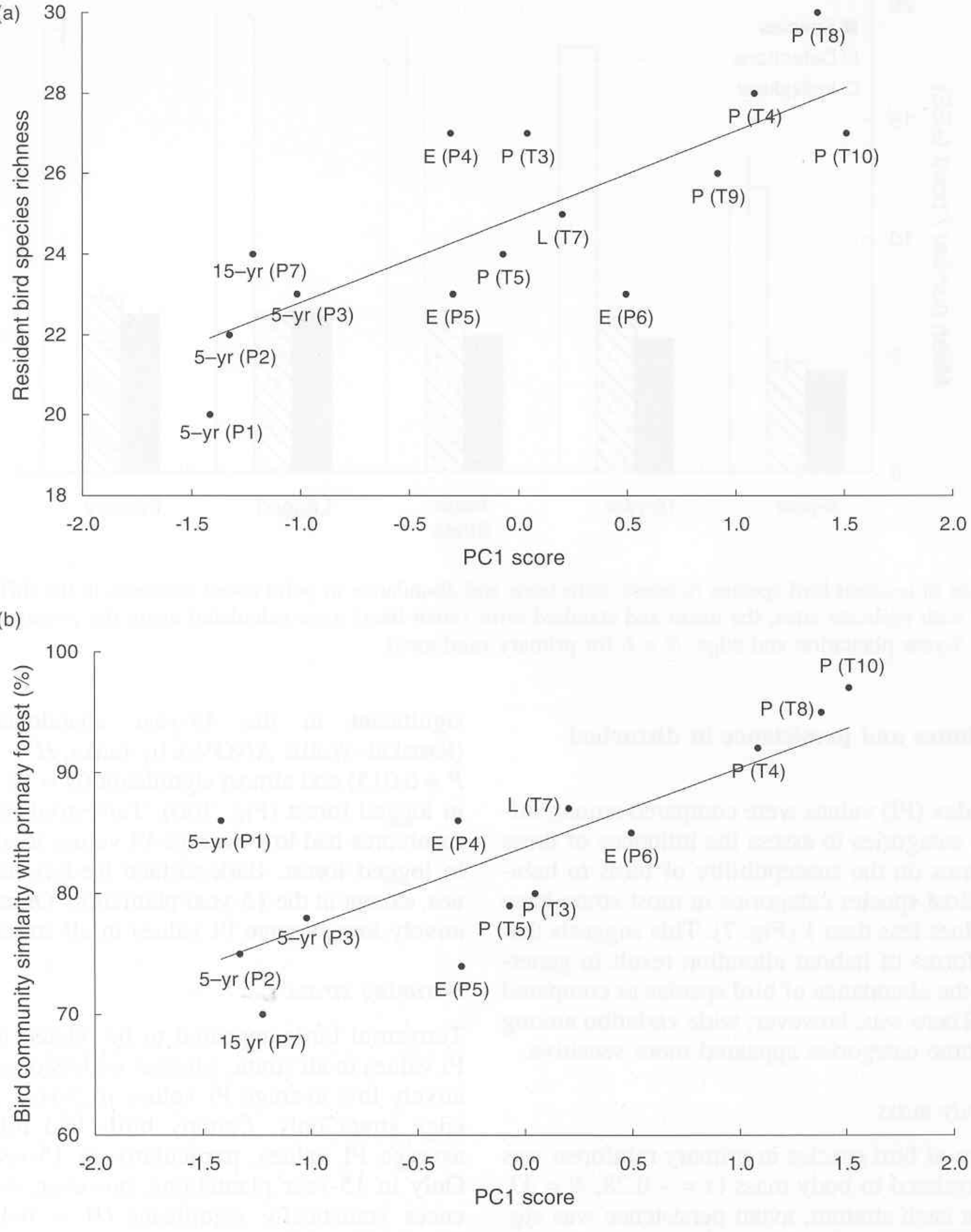

Fig. 5. Relation between the vegetation component representing woody plant density (PC1) and (a) resident bird species richness across sites, and (b) bird community similarity (Morisita index) of sampled sites with one reference primary forest site.

species richness, abundance and diversity, and changes in species composition, particularly in the abandoned cardamom plantations. Most species tended to occur at lower densities in the altered habitats, but a few appeared to decrease substantially in abundance or disappear altogether. In contrast, few species appeared to increase in abundance in altered habitats and only three species were recorded solely from these habitats. Of these, two (Blyth's reed warbler and red-whiskered bulbul) are widespread common species occurring abundantly in disturbed second-growth and more open forest habitats, and the other (pied thrush) was detected only once during the study.

Several factors are possibly involved in the relatively moderate effects noticed in this study. A primary factor is the rainforest-dominated landscape of the study area. All the plantation and logged sites in the study area were adjacent to and contiguous with primary rainforest or surrounded by it. The Agasthyamalai range of mountains, of which the study area forms a part, contains one of the last remaining large tracts of continuous rainforest (over 400 km^2) in the Western Ghats (Ramesh *et al.*, 1997; Johnsingh, 2001). It is plausible that logged sites or plantations in a landscape dominated by disturbed and secondary habitats and containing only rainforest fragments will have more altered bird communities (Andrén, 1994). In addition, the sites were relatively undisturbed after being abandoned (5–15 years

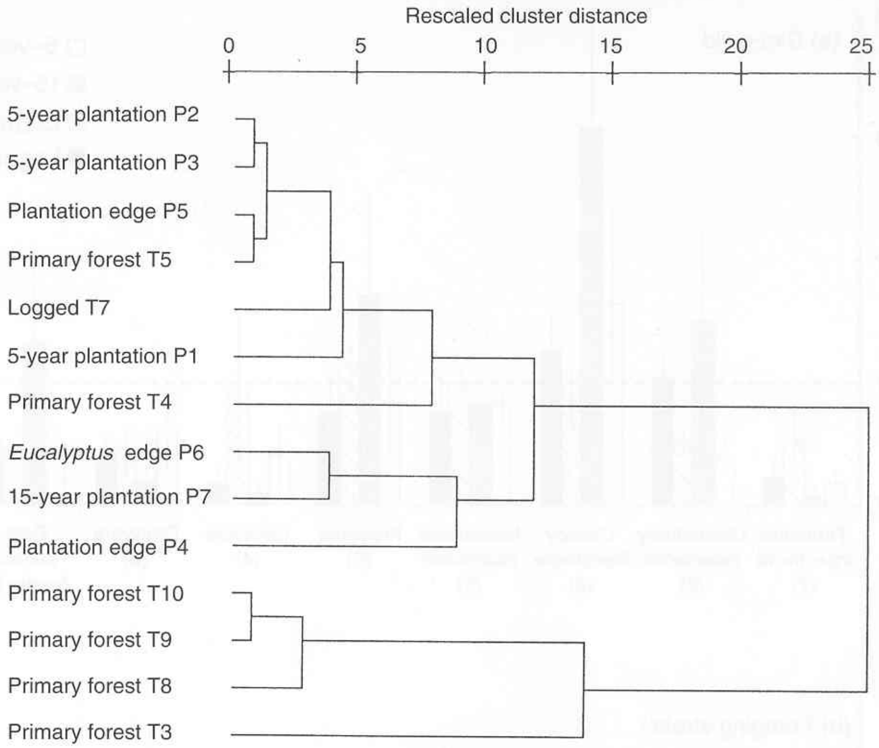

Fig. 6. Cluster analysis dendrogram illustrating similarity between sites in bird community composition.

for plantations and >30 years for the logged site) and did not suffer from chronic human impacts that can lead to further vegetation changes (Daniels *et al.*, 1995). Another influential factor is that most rainforest birds in the Western Ghats appear to be generalist or adaptable species capable of thriving in a variety of habitats (Daniels, 1989). The study may also provide only a conservative assessment of the impacts of habitat changes because of the use of a fixed-radius point count survey method. Better detectability of species in the relatively more open disturbed sites could have contributed to a bias against primary forest in estimates of abundance and species richness, although other analyses are unlikely to have been substantially affected by the slight bias.

Species varied widely in their responses to habitat alteration. This variation, even within particular categories or guilds, suggests that species responses may be idiosyncratic. That responses may be dependent substantially on the unique natural history and ecology of individual species has been recognized earlier (Wiens, 1989; Simberloff, 1994). In addition, part of the variation may be due to chance and sampling effects, especially for infrequently detected species. This may apply in particular to the 15-year plantation site as it was sampled in a different year and therefore may represent a sampling-time effect rather than a site effect. Although environmental conditions as well as bird species occurrence and detectability were similar between years, this possibility cannot be overlooked. Thus, higher persistence of some species categories noted in this site may at least partly be due to sampling effects and therefore the results need to be regarded as tentative or indicative and need verification by sampling of replicate sites.

Some species attributes did, however, appear to be related to increased susceptibility to habitat alteration. Birds that were rare and those that were large-bodied tended to be more susceptible to habitat changes, a pattern consistent across the different forms of habitat disturbance studied here. The influence of both attributes, abundance and body size, is not surprising since these two variables are usually negatively correlated, with larger birds tending to be rarer (Carrascal & Telleria, 1991; Silva, Brown & Downing, 1997). When the effects of body size were statistically controlled, abundance continued to have a consistent effect, although the reverse was true (controlling abundance) for only two strata. That rare birds are relatively more affected by habitat alteration is significant from a conservation perspective, since the value of disturbed habitats is diminished if they contain predominantly common or widespread species (Usher, 1986). Endemic species appeared to persist in the secondary habitats in this study, although they tended to show slight declines in abundance. The lack of statistically significant differences between endemics and non-endemics is probably due to high variation across species and small sample size (only seven endemic species). A similar pattern of widespread, common species benefiting from habitat disturbances at the cost of rare, specialized or restricted-range species has been noted in other studies (Leck, 1979; Raman, 2001*a*).

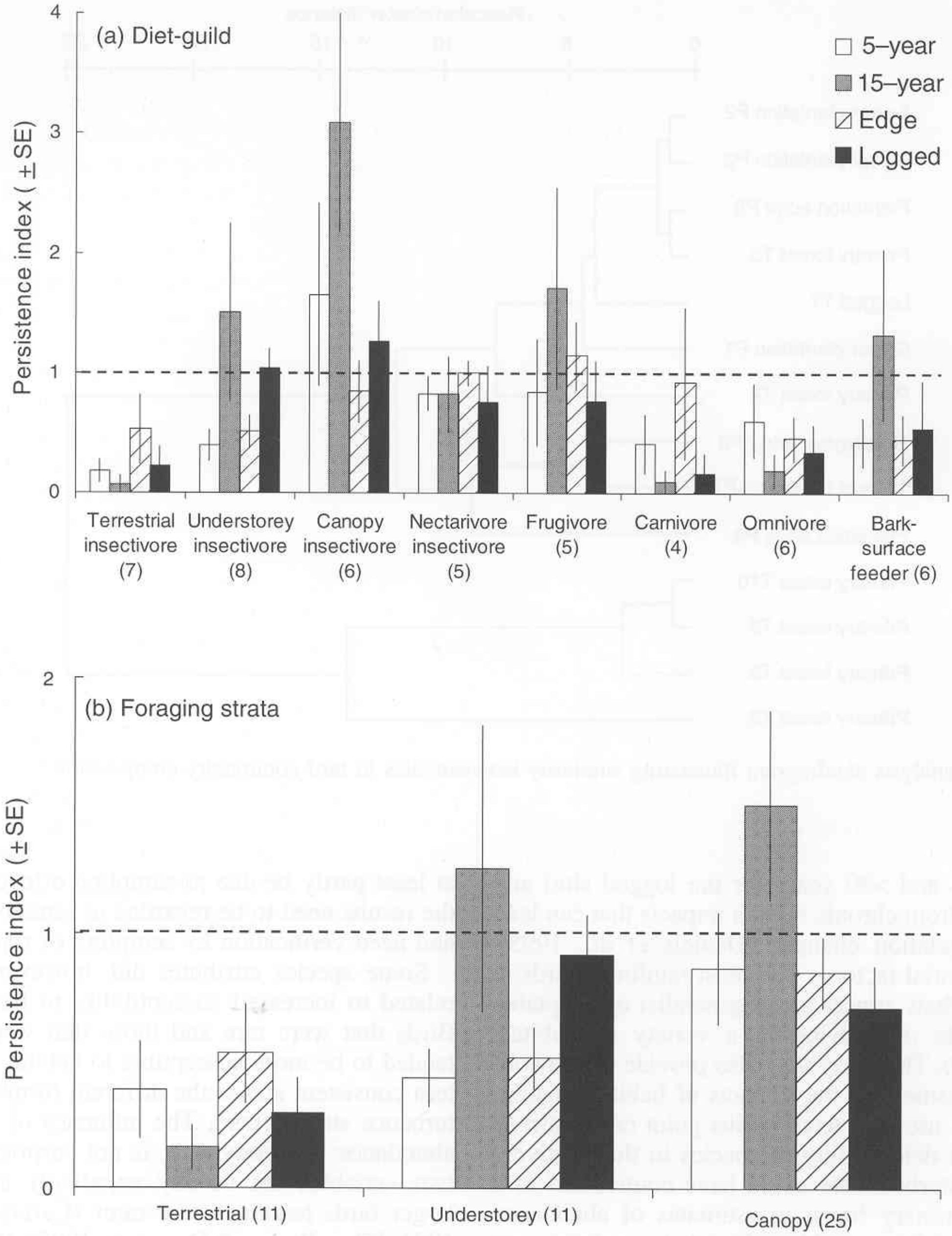

Fig. 7. Persistence of rainforest bird species in the different strata in relation to (a) diet-guild and (b) foraging strata. The error bars indicate standard error of the persistence index calculated across all species in each category. Figures in parentheses refer to number of species in each category.

Birds that are rare in rainforest are so mostly because of their need for larger areas for ranging and specific resources or niches that are naturally scarce in the habitat (Thiollay, 1994). Rare and large-bodied birds decline disproportionately in abudance in altered habitats possibly because of diminution of the available habitat area as well as available niche-resources. Besides rarity, other factors such as foraging stratum and diet-guild also affected the persistence of species in disturbed habitats, with terrestrial insectivores apparently particularly susceptible to habitat alteration. The low PI values, especially in the abandoned cardamom plantations, may be attributed to the relatively sparse understorey vegetation, largely owing to the paucity of shrubs, saplings and cane plants. Absence of cane may have particularly affected understorey species such as dark-fronted babbler and black-and-orange flycatcher that often use cane as a foraging and nesting substrate with cane leaves being frequently used for nest construction. Johns (1989) also noted declines in terrestrial and understorey insectivorous birds after logging in peninsular Malaysia. It is not known, however, whether it is the paucity of vegetation itself (serving as cover from predators and nesting or foraging substrate) or indirect, negative effects on arthropod availability, or both, which lead to declines in insectivorous birds. Lowered tree density is likely to have had negative consequences for populations of bark-surface feeders such as woodpeckers and nuthatches, as noted in other studies (Johns, 1989; Thiollay, 1995; Raman *et al.*, 1998). As a consequence of their wider dietary flexibility, omnivores could be expected to do better in disturbed habitats than more specialised birds (May, 1982). A contrary pattern was observed here. A possible explanation is that although omnivores may find some kinds of food in the disturbed habitats, the quantities available are lower than in primary rainforest. The persistence of carnivores appeared to be low in some habitats, although low sample sizes precludes firm conclusions or inference of possible causes.

Canopy-insectivores, frugivores, and nectarivores-insectivores showed relatively high persistence, in contrast to patterns observed in studies of other forms of habitat disturbance (Terborgh & Winter, 1980; Bowman *et al.*, 1990; Thiollay, 1995; Raman *et al.*, 1998). The frugivores and nectarivore-insectivores were all canopy birds and, as a class, canopy birds showed high persistence. This pattern is linked to the retention of native trees in the canopy in all the sites. Even within sites with low tree density (abandoned plantations), most of the large trees were retained for shade and basal areas remained high (Parthasarathy, 2001; this study). These large canopy trees contribute to most of the fruit crop (and possibly flower abundance) in the rainforest (T. R. S. Raman, unpublished data). Thus, unlike under disturbance regimes which lead to severe reductions of large trees and change in species composition, the frugivore, nectarivore-insectivore and canopy insectivore guilds did not suffer major reductions in the present study.

Overall, it is clear that the retention or maintenance of key attributes of the rainforest vegetation structure and composition is needed to maintain a relatively intact bird community structure and composition. A higher density of trees, shrubs and cane plants, as reflected by PC1 in this study, appears to be particularly important in augmenting bird abundance and species richness and increasing the similarity of disturbed sites with primary rainforest. Past studies, including the classic work of MacArthur & MacArthur (1961), and others (Terborgh, 1985; Raman *et al.*, 1998) have highlighted the positive effects of forest structure on bird species diversity. Forest structure as indexed by canopy measures, vertical stratification and foliage profile did not appear to influence bird species richness, abundance or community composition in this study. This is possibly because the range of variation in these attributes was less than that observed in other attributes such as tree species similarity. It is possible that alteration of forest structure may be tolerated by most bird species up to a threshold level and only more drastic changes (such as forest clearing and succession, Raman *et al.*, 1998) will effect changes in bird communities. In contrast to foliage profile, the present study suggests a greater influence of tree species composition on the bird community composition. The influence of floristic composition has been relatively neglected in bird community studies (Wiens, 1989). While plant-dependent guilds such as frugivores and nectarivores may depend directly on floristic composition, other guilds such as insectivores too may be affected by species-specific variation in foliage structure and foraging substrate (Robinson & Holmes, 1984). The recovery of floristic composition may thus have a key role to play in the recovery of bird communities after habitat disturbances.

A noteworthy result is that, despite being in a rainforest-dominated landscape, the abandoned plantations and logged sites do not appear to have recovered substantially over time, even in the absence of major disturbances. A similar result was noted by Johns (1989, 1992) of incomplete recovery of rainforest bird community structure even 12 years after logging in Malaysian rainforests. In the present study, the bird species richness in 5-year abandoned cardamom plantations differed very slightly from the 15-year stratum. This was associated with vegetation differences in the latter stratum, such as establishment of some pioneer trees in the understorey, although the ground layer was still covered by surviving cardamom plants. Although some birds, such as understorey and canopy insectivores appeared to increase in abundance, bird community composition changed to the extent that the 15-year plantation was less similar to the adjacent undisturbed primary rainforest site (T9) than the more distant 5-year plantations were to T9 (Fig. 5(b)). Although this result could be due to a greater level of initial disturbance or alteration in the 15-year site, the results do suggest that leaving the abandoned plantations for natural regeneration may not necessarily lead to recovery of typical rainforest communities, at least in the short term.

CONCLUSIONS

In a rainforest-dominated landscape, sites that have faced moderate habitat alteration continue to support a large complement of the rainforest bird community, although many species decline in abundance and there are changes in community composition. Rare and large-bodied species, and species belonging to the terrestrial insectivore, bark-surface feeder, omnivore and carnivore diet-guilds appear particularly susceptible to habitat alteration and such species may be targeted for monitoring efforts. Direct intervention, in the form of restoration and augmentation of key attributes such as woody plant and cane density and tree species composition, is needed for conservation and maintenance of rainforest bird communities in sites that have faced such habitat alteration.

Acknowledgements

We are grateful to the Ministry of Environment and Forests, India, and the John D. and Catherine T. MacArthur Foundation for financial support. We thank the Tamil Nadu Forest Department, particularly the Chief Wildlife Warden, for permits and V. K. Melkani for his interest and support in the field. We thank A. Ganapathy for cooperation and allowing us access to sampling sites within the estates. We are grateful to N. V. Joshi for advice and useful discussions. N. M. Ishwar, Divya Mudappa and K. Vasudevan were wonderful and inspiring colleagues to work with in the field and we thank them and Ravi Chellam for unstintingly lending their support and sharing the field station resources. Divya Mudappa also helped enormously in fieldwork, in data collection, and in review and preparation of this manuscript. We are grateful to P. Jeganathan for assistance with vegetation data collection and Rohan Arthur and M. D. Madhusudan for help with analysis and figures. M. Jeyapandian, A. Silamban, Sashikumar, and many others are thanked for their assistance in the field. The Editor and referees provided useful suggestions to improve the manuscript.

REFERENCES

Ali, S. (1977). *Field guide to the birds of the eastern Himalaya.* Delhi: Oxford University Press.

Ali, S. & Ripley, S. D. (1983). *Handbook of the birds of India and Pakistan.* Delhi: Oxford University Press.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**: 355–366.

Bibby, C. J., Burgess, N. D. & Hill, D. A. (1992). *Bird census techniques.* London: Academic Press.

Bowman, D. M. J. S., Woinarski, J. C. Z., Sands, D. P. A., Wells, A. & McShane, V. J. (1990). Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. *J. Biogeog.* **17**: 227–239.

Brash, A. R. 1987. The history of avian extinction and forest conversion on Puerto Rico. *Biol. Conserv.* **39**: 97–111.

Brown, S. & Lugo, A. E. (1990). Tropical secondary forests. *J. Trop. Ecol.* **6**: 1–32.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. (1993). *Distance sampling: estimating the abundance of biological populations.* New York: Chapman & Hall.

Carrascal, L. M. & Tellería, J. L. (1991). Bird size and density: a regional approach. *Am. Nat.* **138**: 777–784.

Castelletta, M., Sodhi, N. S. & Subaraj, R. (2000). Heavy extinctions of forest avifauna in Singapore: lessons for biodiversity conservation in southeast Asia. *Conserv. Biol.* **14**: 1870–1880.

Champion, H. G. & Seth, P. K. (1968). *A revised survey of the forest types of India.* Delhi: Manager of Publication.

Chandran, M. D. S. (1997). On the ecological history of the Western Ghats. *Curr. Sci.* **73**: 146–155.

Coleman, B. D., Mares, M. A., Willig, M. R. & Hsieh, Y.-H. (1982). Randomness, area, and species richness. *Ecology* **63**: 1121–1133.

Colwell, R. K. (1997). EstimateS: Statististical estimation of species richness and shared species from samples. Version 6.01b. Source URL: http://viceroy.eeb.uconn.edu/estimates.

Colwell, R. K. & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. Ser. B* **345**: 101–118.

Daniels, R. J. R. (1989). *A conservation strategy for the birds of Uttara Kannada district, south India.* Ph.D. thesis. Bangalore: Indian Institute of Science.

Daniels, R. J. R., Gadgil, M. & Joshi, N. V. (1995). Impact of human extraction on tropical humid forests in the Western Ghats in Uttara Kannada, south India. *J. Appl. Ecol.* **32**: 866–874.

Daniels, R. J. R., Hegde, M. & Gadgil, M. (1990). Birds of man-made habitats: the plantations. *Proc. Indian Acad. Sci. (Anim. Sci.)* **99**: 79–89.

Daniels, R. J. R., Joshi, N. V. & Gadgil, M. (1992). On the relationship between bird and woody plant species diversity in the Uttara Kannada District of south India. *Proc. Natl. Acad. Sci. (USA)* **89**: 5311–5315.

Davies, K. F., Margules, C. R. & Lawrence, J. F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**: 1450–1461.

Diamond, J. M., Bishop, K. D. & van Balen, B. (1987). Bird survival in an isolated Javan woodland: island or mirror? *Conserv. Biol.* **1**: 132–142.

Furness, R. W. & Greenwood, J. J. D. (1993). *Birds as monitors of environmental change.* London: Chapman & Hall.

Gamble, J. S. (1935). *Flora of the Presidency of Madras.* Reprint. Dehra Dun: Bishen Singh Mahendra Pal Singh.

Ganesh, T., Ganesan, R., Devy, M. S., Davidar, P. & Bawa, K. S. (1996). Assessment of plant biodiversity at a mid-elevation evergreen forest of Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India. *Curr. Sci.* **71**: 379–392.

Grimmett, R., Inskipp, C. & Inskipp, T. (1998). *Birds of the Indian subcontinent.* Delhi: Oxford University Press.

Hemelrijk, C. K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Anim. Behav.* **39**: 1013–1029.

Hutto, R. L., Pletschet, S. M. & Hendricks, P. (1986). A fixed-radius point count method for nonbreeding and breeding season use. *Auk* **103**: 593–602.

Inskipp, T., Lindsey, N. & Duckworth, W. (1996). *An annotated checklist of the birds of the Oriental region.* Sandy, Bedfordshire: Oriental Bird Club.

Johns, A. D. (1989). Recovery of a Peninsular Malaysian rainforest avifauna following selective timber logging: the first twelve years. *Forktail* **4**: 89–105.

Johns, A. D. (1992). Vertebrate responses to selective logging: implications for the design of logging systems. *Phil. Trans. R. Soc. Lond. Ser. B* **335**: 437–442.

Johns, A. D. (1997). *Timber production and biodiversity conservation in tropical rain forests.* Cambridge: Cambridge University Press.

Johnsingh, A. J. T. (2001). The Kalakad-Mundanthurai Tiger Reserve: a global heritage of biological diversity. *Curr. Sci.* **80**: 378–388.

Kannan, R. (1998). Avifauna of the Anaimalai hills (Western Ghats) of southern India. *J. Bombay Nat. Hist. Soc.* **95**: 193–214.

Kattan, G. H., Alvarez-López, H. & Giraldo, M. (1994). Forest fragmentation and bird extinctions: San Antonio eighty years later. *Conserv. Biol.* **8**: 138–146.

Krebs, C. J. (1989). *Ecological methodology.* New York: Harper & Row.

Leck, C. F. (1979). Avian extinctions in an isolated tropical wet forest preserve. *Auk* **96**: 343–352.

MacArthur, R. A. & MacArthur, J. W. (1961). On bird species diversity. *Ecology* **42**: 594–598.

Manly, B. F. J. (1994). *Multivariate statistical methods: a primer.* Second edition. London: Chapman & Hall.

Marsden, S. (1997). Changes in bird abundance following selective logging on Seram, Indonesia. *Conserv. Biol.* **12**: 605–611.

May, P. G. (1982). Secondary succession and breeding bird community structure: patterns of resource utilisation. *Oecologia* **55**: 208–216.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Olson, D. M. & Dinerstein, E. (1998). The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.* **12**: 502–515.

Parthasarathy, N. (1999). Tree diversity and distribution in undisturbed and human-impacted sites of tropical wet evergreen for-

est in southern Western Ghats, India. *Biodiv. Conserv.* **8**: 1365–1381.
Parthasarathy, N. (2001). Changes in forest composition and stucture in three sites of tropical evergreen forest around Sengaltheri, Western Ghats. *Curr. Sci.* **80**: 389–393.
Pascal, J. P. (1988). *Wet evergreen forests of the Western Ghats of India: ecology, structure, floristic composition and succession*. Pondicherry: Institut Français de Pondichéry.
Pascal, J. P. & Ramesh, B. R. (1997). *A field key to the trees and lianas of the evergreen forests of the Western Ghats (India)*. Pondicherry: Institut Français de Pondichéry.
Pielou, E. C. (1984). *The interpretation of ecological data*. New York: John Wiley & Sons.
Ralph, C. J., Sauer, J. R. & Droege, S. (Eds). (1995). *Monitoring bird populations by point counts*. Albany, CA: USDA, Forest Service, Pacific Southwest Research Station.
Raman, T. R. S. (2001*a*). Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. *Conserv. Biol.* **15**: 685–698.
Raman, T. R. S. (2001*b*). Community ecology and conservation of tropical rainforest birds in the southern Western Ghats, India. Ph.D. thesis submitted, Bangalore: Indian Institute of Science.
Raman, T. R. S. (in press). Assessment of census techniques for inter-specific comparisons of tropical rainforest bird densities: a field evaluation in the Western Ghats, India. *Ibis*.
Raman, T. R. S., Rawat, G. S. & Johnsingh, A. J. T. (1998). Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, northeast India. *J. Appl. Ecol.* **35**: 214–231.
Ramesh, B. R., Menon, S. & Bawa, K. S. (1997). A vegetation-based approach to biodiversity gap analysis in the Agasthyamalai Region, Western Ghats, India. *Ambio* **26**: 529–536.
Richards, P. W. (1996). *The tropical rain forest: an ecological study*. Second edition. Cambridge: Cambridge University Press.
Robinson, S. K. & Holmes, R. T. (1984). Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* **101**: 672–684.
Siegel, S. & Castellan, N. J., Jr. (1988). *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill.
Sieving, K. & Karr, J. R. (1997). Avian extinction and persistence mechanisms in lowland Panama. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities:* 156–170. Laurance, W. F. & Bierregaard, R. O., Jr., (Eds). Chicago: University of Chicago Press.
Silva, M., Brown, J. H. & Downing, J. A. (1997). Differences in population density and energy use between birds and mammals: a macroecological perspective. *J. Anim. Ecol.* **66**: 327–340.
Simberloff, D. (1994). Habitat fragmentation and population extinction of birds. *Ibis* **137**: S105–S111.
Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. Second edition. San Fransisco: W. H. Freeman.
Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M. & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* **2**: 75–92.
Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. (1998). *Endemic bird areas of the world: priorities for biodiversity conservation*. Cambridge: Birdlife International.
Terborgh, J. (1985). Habitat selection in Amazonian birds. In *Habitat selection in birds:* 311–340. Cody, M. L. (Ed.). Orlando: Academic Press.
Terborgh, J., & Winter, B. (1980). Some causes of extinction. In *Conservation biology: an evolutionary-ecological perspective:* 119–134. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer.
Thiollay, J. M. (1994). Structure, density and rarity in an Amazonian rainforest bird community. *J. Trop. Ecol.* **10**: 449–481.
Thiollay, J. M. (1995). The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. *Conserv. Biol.* **9**: 335–353.
Usher, M. B. (1986). Wildlife conservation evaluation: attributes, criteria and values. In *Wildlife conservation evaluation:* 3–44. Usher, M. D. (Ed.). London: Chapman & Hall.
Verner, J. (1985). Assessment of counting techniques. *Curr. Ornithol.* **2**: 247–302.
Waide, R. B. & Narins, P. M. (1988). Tropical forest bird counts and the effect of sound attenuation. *Auk* **105**: 296–302.
Warburton, N. H. (1997). Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities:* 190–206. Laurance, W. F. & Bierregaard, R. O., Jr. (Eds). Chicago: University of Chicago Press.
Wiens, J. A. (1989). *The ecology of bird communities*. 2 vols. Cambridge: Cambridge University Press.
Wolda, H. (1981). Similarity indices, sample size and diversity. *Oecologia* **50**: 296–302.

Appendix. Bird species and their abundances (individuals/ha) in the different study sites in and around Kalakad-Mundanthurai Tiger Reserve

Species	N[a]	Body mass (g)	5-year abandoned plantations			15-year abandoned plantations	Edges			Logged	Primary rainforests					
			P1	P2	P3	P7	P4	P5	P6	T7	T3	T4	T5	T8	T9	T10
Red spurfowl *Galloperdix spadicea*	2	369			0.10						0.10					
Grey junglefowl *Gallus sonneratii*	11	750				0.10	0.10	0.20			0.10			0.31	0.20	0.10
Speckled piculet *Picumnus innominatus*	3	11.5				0.10						0.20				
Rufous woodpecker *Celeus brachyurus*	4	101									0.10			0.10	0.10	0.10
White-bellied woodpecker *Dryocopus javensis*	1	300														0.10
Common flameback *Dinopium javanense*	9	101	0.10		0.10		0.20					0.10		0.20	0.10	0.10
Greater flameback *Chrysocolaptes lucidus*	37	150	0.20	0.31	0.10	0.31	0.31	0.31	0.10	0.20	0.20	0.41	0.41	0.31	0.51	0.10
White-cheeked barbet *Megalaima viridis*	52	80.5	0.66	0.31	0.41	0.15	0.20	0.05	0.05	0.20	1.02	0.05	0.10			
Malabar trogon *Harpactes fasciatus*	14	82		0.10	0.20		0.10	0.10		0.10		0.20		0.20	0.31	0.10
Oriental dwarf kingfisher *Ceyx erithacus*	1	15										0.05				
Vernal hanging parrot *Loriculus vernalis*	16	20	0.10	0.10	0.05		0.15				0.25	0.05	0.05	0.05		
Malabar parakeet[b] *Psittacula columboides*	5	85			0.15						0.61					
Mountain imperial pigeon *Ducula badia*	3	620					0.10				0.20					
Emerald dove *Chalcophaps indica*	10	132					0.05			0.05			0.05	0.15	0.10	0.10
Crested serpent eagle *Spilornis cheela*	1	1300											0.05			
Besra *Accipiter virgatus*	8	135		0.05			0.10		0.10		0.05	0.10				
Asian fairy bluebird *Irena puella*	13	120				0.20	0.10	0.20			0.81					
White-bellied treepie *Dendrocitta leucogastra*	2	99.3						0.41								
Scarlet minivet *Pericrocotus flammeus*	27	25	0.10		0.10		0.92	0.71	0.10	0.36	0.97	0.20	0.31	0.36	0.20	
Bar-winged flycatcher-shrike *Hemipus picatus*	26	9		0.31	0.31	0.92			0.61	0.31	0.15	0.15	0.15	0.15	0.46	0.46
Greater racket-tailed drongo *Dicrurus paradiseus*	39	79.5		0.25	0.20	0.10	0.56	0.56	0.20		0.51	0.56		0.20	0.41	0.71
Black-naped monarch *Hypothymis azurea*	2	11				0.05					0.05					
Malabar whistling thrush *Myophonus horsfieldii*	136	116.9	0.41	0.46	0.71	0.20	1.07	0.56		0.25	0.20	0.41	1.07	0.31	0.76	0.51
Pied thrush *Zoothera wardii*	1	58.6			0.10											
Orange-headed thrush *Zoothera citrina*	31	53.3	0.05	0.10		0.10			0.05	0.05		0.41	0.05	0.20	0.20	0.36
Eurasian blackbird *Turdus merula*	1	75														0.05
Rusty-tailed flycatcher *Muscicapa ruficauda*	8	13.3	0.15	0.05	0.05	0.05					0.10					
Black-and-orange flycatcher[b] *Ficedula nigrorufa*	76	8.5				0.31			0.51	1.02		0.81	0.20	1.22	1.83	1.83
Nilgiri flycatcher[b] *Eumyias albicaudata*	44	17.5				1.22			0.31	0.41			0.10	0.81	1.22	0.41
White-bellied blue flycatcher[b] *Cyornis pallipes*	28	19.9	0.10	0.05	0.31		0.20	0.31		0.10	0.31	0.25	0.20	0.10		
Grey-headed canary flycatcher *Culicicapa ceylonensis*	192	6.5	1.32	1.53	0.81	0.31	0.71	0.71	0.92	1.32	0.41	2.24	1.83	1.83	2.95	2.65
Indian blue robin *Luscinia brunnea*	8	18			0.10						0.20				0.05	0.05
Hill myna *Gracula religiosa*	1	126						0.15								
Velvet-fronted nuthatch *Sitta frontalis*	27	11.7	0.25	0.36		0.71	0.10	0.25	0.25	0.31		0.25	0.15	0.31	0.25	0.10
Black-lored tit *Parus xanthogenys*	30	14.4	0.20	0.51	0.10	0.41	0.31		0.41	0.10		0.10	0.31	0.20	0.10	0.41
Red-whiskered bulbul *Pycnonotus jocosus*	11	27.4							0.92	0.20						
Yellow-browed bulbul *Iole indica*	165	31	0.87	0.46	0.92	1.73	1.78	2.24	0.87	0.76	2.75	1.07	1.73	0.56	0.97	0.56
Black bulbul *Hypsipetes leucocephalus*	141	42.9	1.07	1.22	1.38	4.74	2.14	1.53	2.60	1.07	0.61	0.15	0.76	1.83	0.76	1.68
Oriental white-eye *Zosterops palpebrosus*	228	8.8	3.97	8.45	6.16	6.62	5.14	11.41	6.11	6.42	3.06	6.21	11.3	5.65	6.06	4.99
Blyth's reed warbler *Acrocephalus dumetorum*	4	10.6							0.15	0.05						
Greenish warbler *Phylloscopus trochiloides*	88	7	0.46	0.51	0.36	1.22	0.05		0.51	0.31	0.41	0.05		0.36	0.10	0.15
Large-billed leaf warbler *Phylloscopus magnirostris*	84	11.5	0.31	0.20	0.20	0.36			0.31	0.36	1.02	0.05		0.56	0.61	0.31
Wynaad laughingthrush[b] *Garrulax delesserti*	4	90						0.81						0.76	0.76	
Grey-breasted laughingthrush[b] *Garrulax jerdoni*	1	55												0.41		
Puff-throated babbler *Pellorneum ruficeps*	39	26	0.20	0.10	0.05		0.25	0.25	0.05	0.31	0.31	0.41	0.15	0.81	0.36	0.10
Indian scimitar babbler *Pomatorhinus horsfieldii*	79	47.8	0.31	0.71	0.36	0.92	1.07	0.15	0.71	0.76	0.56	0.76	0.41	1.07	1.17	0.87
Dark-fronted babbler *Rhopocichla atriceps*	25	16		0.15		0.92	0.15		0.46	0.31	0.15	0.31	0.15	0.46		0.61
Brown-cheeked fulvetta *Alcippe poioicephala*	123	20.7	0.76	0.36	0.56	0.97	1.88	1.88	1.43	2.14	2.70	1.78	1.94	3.46	4.33	4.02
Plain flowerpecker *Dicaeum concolor*	124	6.2	0.15	0.20	0.25	0.51	0.20	0.81	0.76	0.51	1.02	0.10	0.56	0.41	0.56	0.25
Crimson-backed sunbird[b] *Nectarinia minima*	310	4.5	1.38	1.99	1.68	0.61	2.04	1.53	2.44	0.31	2.90	2.85	3.06	1.17	3.00	2.80
Little spiderhunter *Arachnothera longirostra*	134	13	0.36	0.56	0.31	0.87	0.66	0.15	0.71	0.25	0.25	0.20	0.46	0.41	0.92	0.71
Grey wagtail *Motacilla cinerea*	2	16.3							0.05							0.05

[a] Number of detections of species
[b] Species endemic to the Western Ghats