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Population Ecology

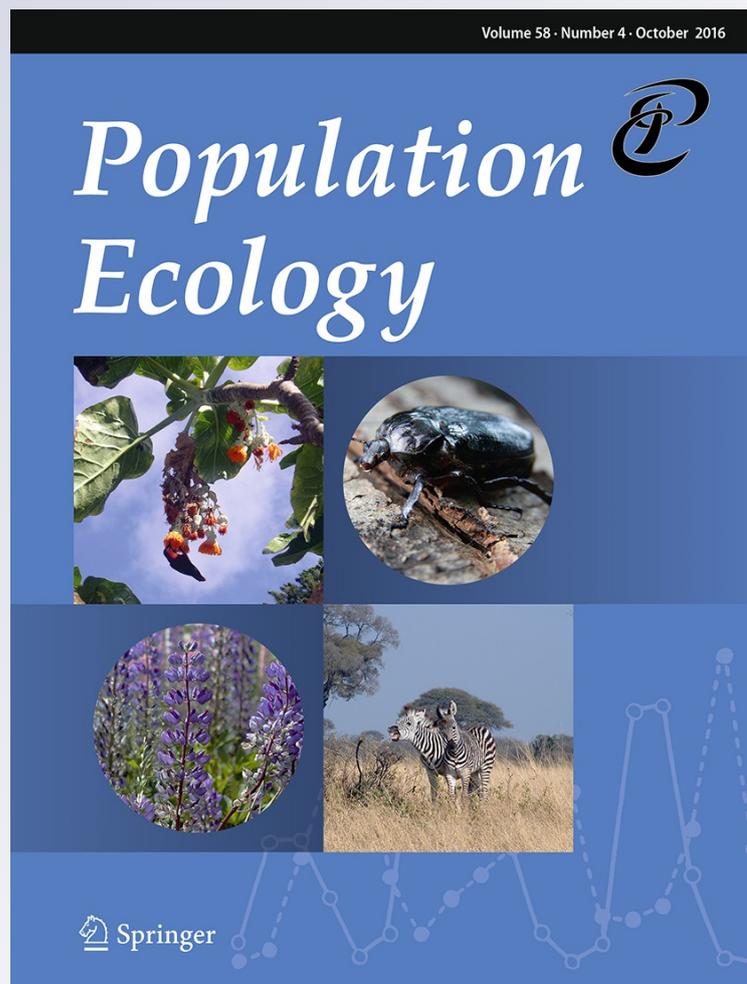
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Vertical stratification of an avian community in New Guinean tropical rainforest

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Abstract Vertical stratification of avian communities has been studied in both temperate and tropical forests; however, the majority of studies used ground-based methods. In this study we used ground-to-canopy mist nets to collect detailed data on vertical bird distribution in primary rain forest in Wanang Conservation Area in Papua New Guinea (Madang Province). In total 850 birds from 86 species were caught. Bird abundance was highest in the canopy followed by the understory and lowest in the midstory. Overall bird diversity increased towards the canopy zone. Insectivorous birds represented the most abundant and species-rich trophic guild and their abundances decreased from the ground to canopy. The highest diversity of frugivorous and omnivorous birds was confined to higher vertical strata. Insectivorous birds did not show any pattern of diversity

along the vertical gradient. Further, insectivores preferred strata with thick vegetation, while abundance and diversity of frugivores increased with decreasing foliage density. Our ground-to-canopy (0–27 m) mist netting, when compared to standard ground mist netting (0–3 m), greatly improved bird diversity assessment and revealed interesting patterns of avian community stratification along vertical forest strata.

Keywords Bird abundance · Canopy · Diversity of birds · Forest strata · Trophic guilds · Understory

Introduction

Tropical forests are characterised by vertical distribution of plant biomass that includes wood, leaves, fruits and flowers, leading to stratification of microhabitats and resources for avian communities (Allee 1926; Smith 1973; Parker and Brown 2000). In general, forests with higher vertical heterogeneity are expected to host more diverse avian communities (MacArthur and MacArthur 1961; Goetz et al. 2007; Huang et al. 2014). The main assumption of the hypothesis is that stratification of microhabitats allows the coexistence of bird species exploiting the same resources (and thus having similar morphology) due to reduced interference competition (Koen 1988; Styring and bin Hussin 2004; Böhm and Kalko 2009; Kwok 2009). A structurally complex mature tropical forest with high vertical heterogeneity therefore represents a suitable environment to study habitat partitioning within an avian community as a mechanism for maintaining high species diversity (Cody 1974; Schoener 1974). Forest bird communities are known to be vertically stratified in terms of species composition (Turček 1951; Dickson and Noble

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1978; Terborgh 1980; Koen 1988; Böhm and Kalko 2009) overall abundance (Pearson 1971; Bell 1982) and species diversity (Jayson and Mathew 2003). Therefore, preferences for certain strata can be one of the main factors leading to the separation of avian guilds (Holmes and Recher 1986). For example, the canopy of tropical primary forest is typically dominated by frugivorous birds (e.g., Shanahan and Compton 2001; Naka and Stouffer 2004).

Foliage density (i.e., habitat volume) is thought to be one of the main factors shaping the distribution of birds along the vertical forest gradient. In agreement, foliage density was positively correlated with bird diversity (MacArthur 1964; Jayson and Mathew 2003) and abundance (Pearson 1971; Bell 1982) in several tropical regions. Walther (2002a) found that species recorded in strata with dense vegetation had narrower vertical foraging niches than species from strata with lower vegetation density. Therefore, foliage density is likely linked to food resource availability, although we realize that a close relation to vegetation density may not apply to all of the particular food resources (Basset et al. 2003). For instance, insect abundance depends primarily on the biomass of young foliage, rather than on total plant biomass (Whitfeld et al. 2012). Nevertheless, correct assessment of available food density is extremely difficult to perform for the entire avian community (Hutto 1990). This applies especially to the New Guinean bird community due to poor description of diet composition for many species. Hereafter we therefore focused only on the effect of vegetation density on vertical distribution without sampling of food resources.

Surveys on the stratification of avian communities in tropical forests are generally difficult to perform. Observations from the ground may be biased against canopy dwelling species, as they are often concealed by thick vegetation and may be detected at a lower rate (Blake and Loiselle 2001). Ground-based methods can be transferred to the canopy using canopy cranes (Walther 2002b, 2003) or walkways. However, it should be noted, that the latter method has, so far, only been used for studies on stratification of different taxa (Schulze et al. 2001) or for mist netting birds only at the same height as the walkways (Stokes et al. 1995). Moreover, although canopy cranes or canopy walkways provide access to higher forest strata, this is only over a limited area of the forest, usually up to 1 ha. Mist netting is another well-established method for bird community studies providing conditions for precise identification (including cryptic species), sampling of genetic material, collecting parasites and morphological data on captured birds. Although this method enables precise determination of the vertical position of caught birds it has rarely been used in higher forest strata and has not been used to assess the vertical stratification for the entire community along all strata (for examples see

Humphrey et al. 1968; Meyers and Pardieck 1993; Derlindati and Caziani 2005; Vecchi and Alves 2015). Here we developed a method of mist net sampling along the vertical forest gradient to explore the stratification of a bird community in lowland tropical rainforest in Papua New Guinea. Apart from ground-to-canopy mist netting optimization, we tested the following hypotheses: (1) forest bird abundances and diversity differ among different strata and change during the day; (2) main dietary groups show different patterns of abundances and diversity along the vertical gradient; and (3) foliage density is linked with the vertical distribution of the avian community.

Methods

Study site

Field work was carried out from June to November 2013 in the vicinity of the Swire Research Station located in the center of the Wanang Conservation Area, Madang Province, Papua New Guinea (5°6'49"S; 145°2'19"E, approximately 120 m a.s.l.). The conservation area covers 10,000 ha of primary forest and is surrounded by more than 100,000 ha of continuous primary and selectively logged forest. The annual rainfall is around 3,400 mm, with a mild dry season from July to September; mean monthly air temperature around 26 °C (Anderson-Teixeira et al. 2015). The mean maximum height of trees at the study site was 31 m (excluding scattered emergent trees reaching over 40 m). The best description of local forest vegetation characteristics has been provided by a survey in adjacent Wanang 50 ha forest dynamic plot (located approximately 0.5 km from our study site), comprising of 288,000 stems with DBH >1 cm from 550 species and 211 tons per ha of live aboveground plant biomass (Anderson-Teixeira et al. 2015; Vincent et al. 2015). So far, 135 species of birds have been recorded in Wanang Conservation Area (K. Chmel, unpublished data). The vertical temperature profile of the forest was obtained from three data loggers installed at 1, 14 and 27 m above the ground in shaded locations avoiding direct sunlight. Temperature data were collected at 30 min intervals from 6th of August to 23rd of November 2013 at one of the mist netting sites.

Mist netting

The vertical distribution of the forest bird community was studied by installing mist nets from the ground to the canopy. The method of installation was similar to that of Humphrey et al. (1968). We selected a site in primary forest where we could stack a series of 3 m high and 18 m long mist nets one above the other, thus creating a large

mist net stretching from the ground to the lower canopy. Smaller trees, branches and lianas (<10 cm in diameter) were cut in order to make room (approximately 1.5 m wide vertical space free of vegetation) for the mist nets. Thus, only the presence of larger trees (>10 cm in diameter) in the 18×1.5 m area limited mist net site selection. In three cases mist nets were installed along a fallen tree (between 5–15 years ago) that created just enough space for the panel of mist nets. We used a catapult to shoot guiding ropes for the mist nets over branches of large canopy trees, allowing us to open and close the entire stack of mist nets as needed (Fig. 1). Mist netting was carried out at 12 primary forest sites (Fig. 1) spaced 59–147 m apart (mean 103 m). We were able to stack nine mist nets, each of height 3 m, one above another, reaching a total height of 27 m above the ground at four sites. At the remaining eight sites, mist nets were installed up to 24 m above the ground

(eight mist nets, each of height 3 m). We used mist nets with 19 mm mesh size, securing a good capture rate for small passerines to middle size birds. The largest species captured were Great Cuckoo-Dove (*Reinwardtoena reinwardtii*) and Eclectus Parrot (*Eclectus roratus*). Nevertheless, mist nets were not suitable for capturing large birds: e.g., Victoria Crowned Pigeon (*Goura victoria*), Papuan Hornbill (*Rhyticeros plicatus*), Sulphur-crested Cockatoo (*Cacatua galerita*), Palm Cockatoo (*Probosciger aterimus*), Grey Crow (*Corvus tristis*) and birds of prey (Accipitriformes). In addition, large terrestrial species such as Northern Cassowary (*Casuarus unappendiculatus*) and Red-legged Brush Turkey (*Talegalla jobiensis*) were not present in our dataset.

Mist nets were opened at 6:00 and closed before 18:00 depending on weather conditions (mean 8.9, range 1–11.7 h). The mist nets were closed during strong winds

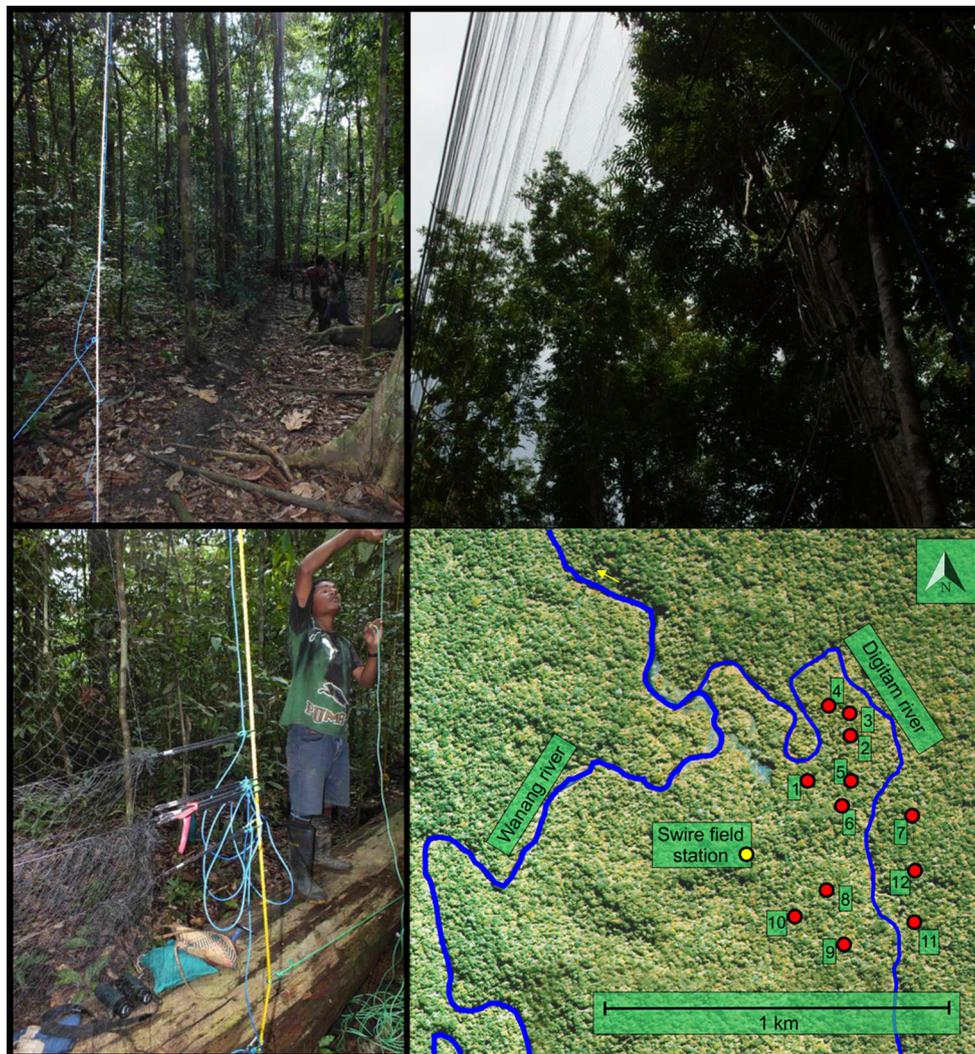


Fig. 1 Mist netting site showing position and operation of ground-to-canopy mist nets. *Bottom right* map with positions of mist netting sites (1–12), Swire field station and small rivers (Wanang and Digitam rivers, approximately 3 m wide)

or rains to prevent captured birds from injury or hypothermia. We were able to carry out mist netting simultaneously at three out of 12 sites, this was usually done for two consecutive days. On average, mist netting was carried out for a total of 89 h (range 75–93 h) on 10 different days (9–11 days) at each site (Table 1) and the total exposure reached was 1,918,152 net-meter-hours.

Captured birds were extracted from mist nets and capture time, site number, and height above ground (at 3 m intervals) were recorded. Each bird was ringed with an individual color code or nail-varnish paint code (specific dots on the beak) for a few species where suitable size of color ring was not available. The birds were then measured and released.

Additional ground level mist netting, which served as a comparison with the ground-to-canopy technique, was conducted in 2015 (between 12 March and 10 April and between 28 November and 4 December) at 6 different sites in Wanang conservation area. All sites were located in primary forest. Mist netting was carried out for 3 days at each site resulting in a total of 18 mist netting days

(138.5 h). Mist nets (mean length per site 174.2 m, range 120–252 m) were opened for a mean of 7.7 h per day (range 5.25–10 h) resulting in the total of 457,632 net-meter-hours of exposure. We used mist nets with identical dimensions to those used for ground-to-canopy mist netting (length 18 m, height 3 m, mesh-size 19 mm). These nets were installed only at ground level (reaching 3 m above ground).

Vegetation survey

The heights of the tallest trees in the vicinity of each capture site were measured. Further, we estimated the foliage density profile according to Radtke and Bolstad (2001), who assessed the vegetation structure from its intercepts with multiple vertical laser beams. The final values of foliage density (leaf area index) between two heights (h_1 , h_2) were computed using the following equation: $FD_{h_1, h_2} = \ln(\varphi(h_1)/\varphi(h_2))$, developed by (MacArthur and MacArthur 1961; MacArthur and Horn 1969), where $\varphi(h)$ is the number of intercepts with vegetation

Table 1 Mist netting sampling effort

Site	Mist nets exposure (h)	Number (dates) of mist netting days	Reached height (m)	Total number of caught birds	Total number of caught species	Number of caught birds (0–3 m)	Number of caught species (0–3 m)
1	89.88	10 (7, 10, 30 and 31 July; 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	67	28	1	1
2	89.28	10 (7, 10, 30 and 31 July; 20 and 21 August; 25 and 26 October; 6 and 7 November)	24	62	26	2	2
3	88.02	9 (29 June; 1, 30 and 31 July; 20 and 21 August; 25 and 26 October; 7 November)	27	78	27	20	9
4	91.68	11 (7, 10 and 30 July; 1, 2, 20 and 21 August; 25 and 26 October; 6 and 7 November)	27	104	41	17	11
5	92.33	10 (29 June; 1 July; 1, 2, 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	101	41	11	7
6	92.30	11 (28 and 29 June; 1 July; 1, 2, 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	62	28	14	10
7	82.07	9 (12 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	27	72	25	3	3
8	93.65	10 (9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1, 12 and 13 November)	27	124	44	15	9
9	93.38	10 (9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1, 12 and 13 November)	24	61	25	10	7
10	75.55	9 ((9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1 and 12 November)	24	45	23	13	8
11	86.63	10 (12 and 13 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	24	145	42	9	7
12	90.87	10 (12 and 13 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	24	87	37	6	5

At each site 8 or 9 mist nets (each 3 m high) were used to reach the corresponding total height, 24 or 27 m. Area covered by mist nets equals height reached \times 18 m (length of individual mist nets). Numbers of birds and species caught are shown separately for ground-to-canopy and ground (0–3 m) mist nets

exceeding height h . We calculated foliage density for each 3 m vertical interval (0–3, 3–6, 6–9, 9–12, 12–15, 15–18, 18–21, 21–24, 24–27 m) at each of the 12 sites separately.

Vegetation measurements were taken with a Leica Disto D5 laser range finder (range 0.05–200 m with measuring accuracy ± 1.5 mm). The range finder was fixed in a horizontal position to ensure vertical laser beams. Measurements of intercepts with vegetation were performed along four transects parallel to mist nets at each capture site, laid out at 1 and 2 m distances on each side of the mist net. The measurements were taken at approximately 25 cm intervals along the transects, resulting in approximately 70 measurements per transect and 280 measurements per one mist net site.

Statistical analyses

Spearman rank correlation was used for relationships between bird and environmental variables. Two-way ANOVA was used to test the differences in temperature between forest zones and time of day. The effect of capture site and repeated mist netting on abundance of caught birds was analyzed by Generalized linear model (GLM). An identical method was also used for the analyses of seasonal differences in abundances of trophic guilds along the vertical gradient, where two mist netting periods: 28 July–4 September and 16 October–13 November were compared. We also tested the interactions between height above ground and mist netting period. The influence of temperature (daily means per hour) on total abundance (pooled for twelve sites) was tested by linear regression models separately for three 9 m vertical bands (0–9, 9–18 and 18–27 m above ground). The temperature measurements were carried out at one site only, therefore its effect was analyzed separately from the following model. Changes in abundance and diversity of captured birds with height above ground and foliage density and time of day were analyzed for the whole community and individual trophic guilds by Generalized linear mixed models (GLMM) with Gaussian distribution of dependent variables and using capture site as a random factor. We also tested interactions among explanatory variables as well as adding quadratic polynomial functions to the model to test if those significantly improved the process of finding the best fitting model. Models were fitted using R package Lme4 based on AIC values. Post-hoc pair-wise comparisons among different day times were made using Tukey contrasts (multcomp package in R). All the above mentioned tests and data visualization were performed in the programs: R 3.1.1 and STATISTIKA 12.

Canonical correspondence analysis (CCA) was performed for each trophic guild in order to assess the effect of height above ground and time of day (explanatory

variables) on species abundances (response variables). Statistical significance was obtained by Monte Carlo permutation tests with 999 permutations, using software Canoco5 (ter Braak and Smilauer 2012). Singletons and doubletons ($n = 29$) were excluded from these analyses.

In all models, abundance of birds was represented by standardized net-meter-hour capture rate: [number of caught birds (n)/length of mist net (m)/mist nets exposure (hours)]. Alternatively, we used a Shannon–Wiener diversity index (Shannon 1948) to analyze community and trophic guilds' diversity. The effect of individual sites was eliminated by setting site as a random factor in GLMM and as a covariate in CCA. In GLMM and CCA height above ground (in 3 m intervals) was used as a continuous explanatory variable. In contrast, time of day was divided into four 3-h intervals (between 6:00 and 18:00) and was considered as a categorical variable.

Species were divided into three main trophic guilds [frugivores, insectivores and omnivores; Table S1 in Electronic Supplementary Material (ESM)] according to information on diet obtained from Tvardíková (2013) and del Hoyo et al. (2016). Among omnivores there were subgroups of birds feeding on a combination of fruit/nectar, fruit/insect or insect/nectar. However, in order to avoid misleading interpretation caused by small sample size, in statistical models these subgroups were pooled into omnivores only. Birds of prey with less than four recorded individuals (*Accipiter poliocephalus*—3 individuals, *Uroglaux dimorpha*—1 individual) were excluded from the analyses of trophic guilds. Small vertebrate prey that is part of the diet of several species (e.g., Alcedinidae) was classified as insect prey. The functional difference between large insect and small vertebrate prey was negligible for our purposes.

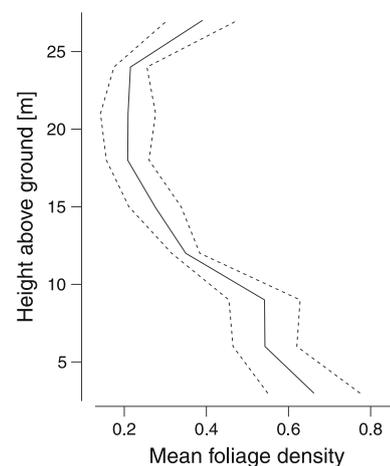


Fig. 2 Vertical profile of mean foliage density from 12 capture sites (*dashed lines* represent standard error)

Table 2 Results of the best GLMM models testing the influence of time of day (time), foliage density (FD) and height above ground (height) on the abundance (captures per net-meter-hour) and diversity (Shannon diversity index) of the avian forest community and three different trophic guilds (*FR* frugivores, *IN* insectivores, *OM* omnivores)

	<i>n</i>		Model	AIC	χ^2	<i>P</i> value		
Abundance of birds	400		~ 1	-4001.8				
			~ Time	-4094.7	98.92	<0.001		
			~ Time + FD	-4093.2	0.45	0.4983		
			~ Time + height	-4109.9	17.15	<0.001		
			~ Time + height + height ²	-4115.7	7.778	0.005		
Abundance of trophic guilds	400	FR	~ 1	-4853.9				
			~ VFD	-4850.1	14.07	<0.001		
			~ Height	-4897.4	45.50	<0.001		
			~ Height + time	-4904.7	13.25	0.004		
		IN	~ 1	-4385.7				
			~ Time	-4481.5	89.82	<0.001		
			~ Time + FD	-4489.8	10.30	0.001		
			~ Time + height	-4488.3	8.76	0.003		
		OM	~ 1	-4502.6				
			~ Time	-4530.7	34.10	<0.001		
			~ Time + FD	-4532.3	3.56	0.059		
			~ Time + height	-4564.3	35.59	<0.001		
		Diversity of birds	100		~ 1	321.1		
					~ FD	321.3	1.85	0.174
					~ Height	298.4	24.73	0.011
	~ Height + height ²			295.1	5.32	0.021		
Diversity of trophic guilds	100	FR	~ 1	152.3				
			~ FD	141.3	13.05	0.003		
			~ Height	107.2	117.62	<0.001		
			~ Height + height ²	100.7	8.53	0.003		
		IN	~ 1	179.8				
			~ FD	173.5	5.30	0.021		
			~ Height	177.7	1.08	0.299		
		OM	~ 1	190.0				
			~ FD	190.1	1.18	0.176		
			~ Height	170.2	21.77	<0.001		

In all models, the capture site was used as a random factor. Quadratic polynomial functions are shown only when it improved the models. Significant models (*P* < 0.05) are typed in bold

Results

The vertical foliage profile of forest surrounding the mist netting sites was characterized by very high foliage density in the lower strata (0–9 m) and at the vertical band between 24–27 m above the ground. Other vertical zones (between 9–24 m above ground) had much lower values of foliage density (Fig. 2). However, we found a significant negative correlation between height above ground and foliage density at mist netting sites (Spearman rank correlation, $r_s = -0.55, n = 100, P < 0.001$), therefore foliage density was not used in individual models as an explanatory

variable together with height above ground. Forest air temperature, measured at 1, 14 and 27 m above ground, differed vertically and temporally (two-way ANOVA; height above ground: $F_2 = 480.8, P < 0.001$; day-time: $F_9 = 304.7, P < 0.001$). The highest temperatures were reached around 13:00 at 27 m above ground (Fig. S1 in ESM).

In total, 850 individual birds (from 84 species) were captured, some of them repeatedly, resulting in 1008 captures (Table S1 in ESM) Abundance of birds (capture rate) differed significantly among the 12 sites but did not decrease or increase with repeated controls at the same

study site (GLM; $n = 120$; site: $F = 6.62$, $P < 0.001$; repeated controls: $F = 0.29$, $P = 0.590$).

Apart from foliage density, both time of day and net height affected the capture rates (Table 2). The highest abundance of birds was recorded during the morning with a gradual decrease towards the evening (Fig. 3). However,

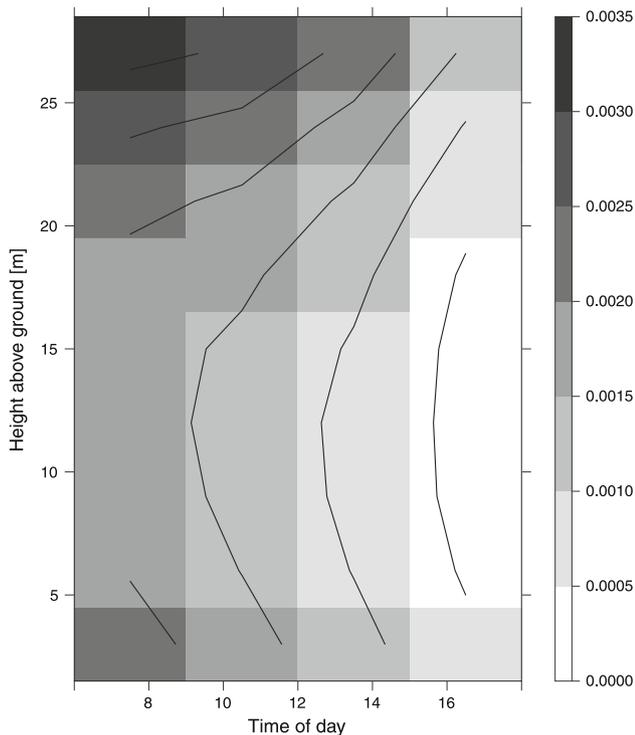
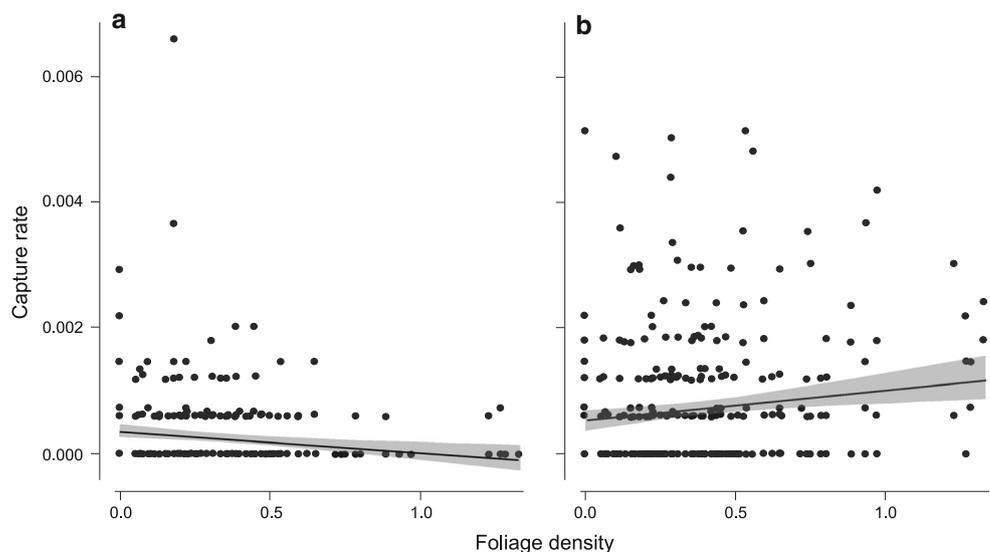


Fig. 3 Abundance of birds (captures per net-meter-hour) in relation to height above ground (3-m intervals) and time of day (3-h intervals). Post-hoc comparison showed that abundances differed significantly among all time intervals except between the first two, 3 h intervals (6:00–8:59 \times 9:00–11:59)

the abundance of birds did not differ significantly between the first two morning 3-h intervals (6:00–8:59 vs. 9:00–11:59, $P = 0.120$). Between the rest of the 3-h time intervals the difference in abundance was significant ($P < 0.001$). The highest capture rate was recorded in the top strata (21–27 m) and the lowest in the vertical band between 9 and 18 above ground. Capture rate near ground level (0–9 m) was slightly higher compared to midstory vertical bands (9–18 m, Fig. 3). This explains why the best fitting model contained the quadratic polynomial function of height above ground (Table 2). Analysis of temperature and its effect on abundance of birds (compared for three 9 m vertical bands) showed a significant relationship only for the lowest strata (0–9 m), where abundance decreased with increasing temperatures (Fig. S2 in ESM).

Caught birds consisted mainly of insectivores (364 individuals, 449 including recaptures, 40 species) and omnivores (344 individuals, 411 including recaptures, 28 species) followed by frugivores (137 individuals, 144 including recaptures, 14 species). Abundance of frugivorous and insectivorous birds was related to foliage density (Table 2). Frugivorous birds showed a negative response to foliage density, while insectivorous birds were more abundant in strata with thicker vegetation (Fig. 4). In all trophic guilds, the overall abundance of birds responded significantly to the time of day (Table 2; Fig. 5a–c). Insectivores were most frequently caught between 6:00 and 8:59 contrary to omnivorous and frugivorous birds with highest frequency later in the morning between 9:00 and 11:59 (Fig. 5a–c). Abundance of frugivores and omnivores increased significantly towards the canopy zone (Fig. 5d, f) in contrast with insectivores that exhibited the highest density at the 0–3 m ground level (Table 2; Fig. 5e). Interaction of time and height above ground did not

Fig. 4 Linear relationship between abundance (captures per net-meter-hour) of trophic guilds (**a** frugivores, **b** insectivores) and foliage density (shaded area represents standard error)



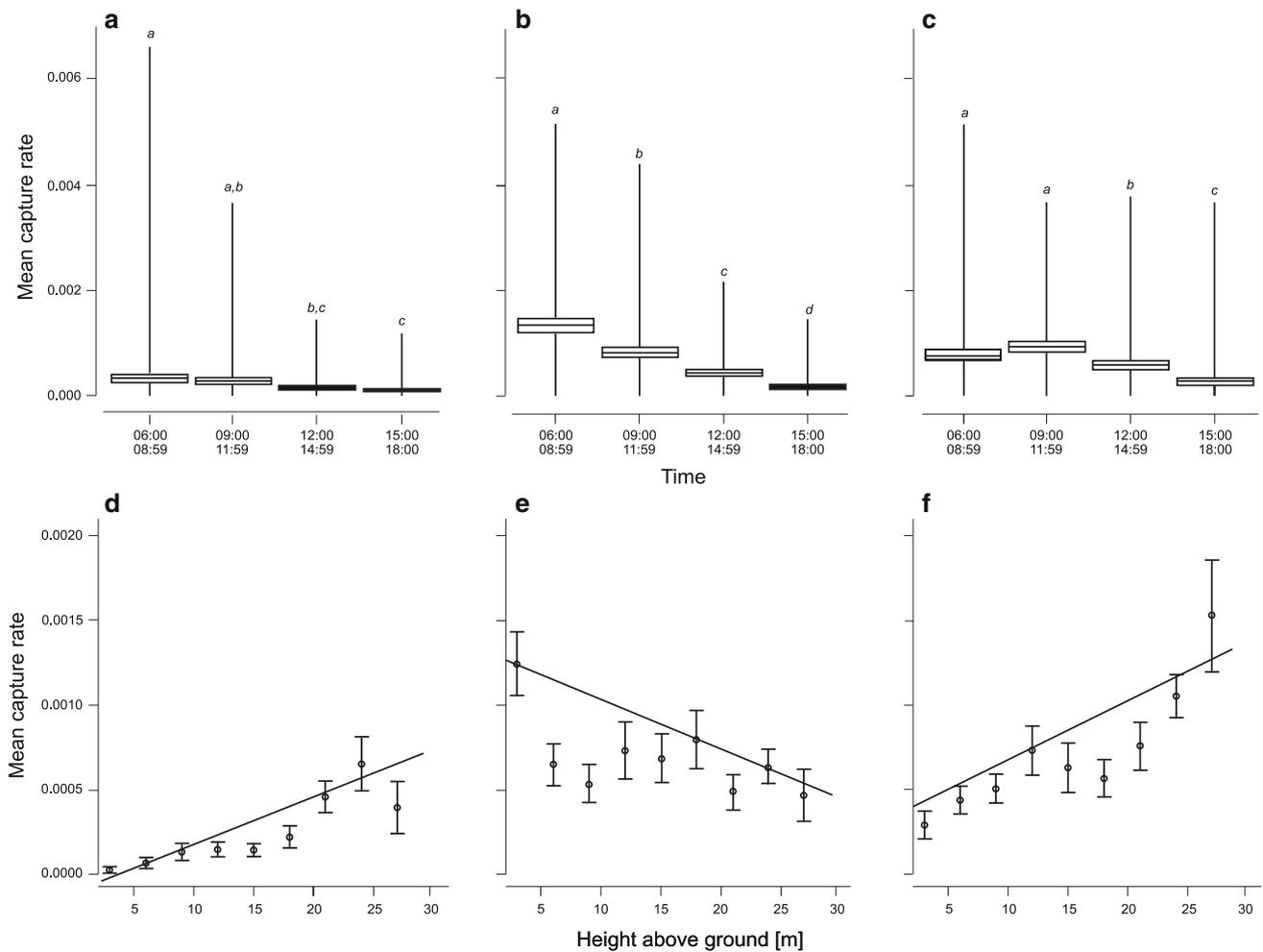


Fig. 5 Abundance (mean captures per net-meter-hour \pm SE, min., max.) of trophic guilds (frugivores: **a, d**; insectivores: **b, e**; omnivores: **c, f**) in response to time of day (*top row*) and height

above ground (*bottom row*). Means with the same letter (positioned above outlines, *top row*) are not significantly different from each other (Tukey test, $P > 0.05$)

improve the models significantly. Finally, we found no seasonal differences in abundance (GLM, P at least 0.312) and vertical distribution (GLM, P at least 0.138) in any of the trophic guilds.

Abundance of individual species changed more with height above ground than with time of day in all trophic guilds. Frugivores showed the strongest response to height as well as time of day (Fig. 6). The division of insectivorous species according to foraging strategies into gleaners and sallying birds (Fig. 6) showed that the group of insectivores found exclusively in the understory is formed only by gleaners (*Rhipidura threnothorax* and *R. rufidorsa*, *Pitta erythrogaster* and *Ptilorhoa caerulescens*). In contrast, sallying species such as Rufous-bellied Kookaburra (*Dacelo gaudichaud*) or Yellow-billed Kingfisher (*Syma torotoro*) preferred higher strata and showed the strongest positive response to height above ground. Frugivorous species were most abundant in the canopy zone, except for the specialised ground-feeding Stephan's Dove

(*Chalcophaps stephani*). Two subgroups of omnivorous birds (foraging on insects/nectar and fruits/insects) included species preferring higher strata as well as species more abundant in lower strata. Birds that feed on nectar and fruits on the other hand preferred mostly higher strata (Fig. 6).

The diversity of the avian forest community expressed by the Shannon index increased with height above ground, but did not change with foliage density (Table 2; Fig. 7a). When we divided the species according to their trophic requirements, we found that the diversity of frugivorous and omnivorous birds changed with foliage density (Table 2). Frugivorous species expressed higher diversity in strata with low vegetation density (Fig. 7b). Insectivores were, in contrast, more diverse in strata with thicker vegetation (Fig. 7c). Finally, diversity of omnivores was not related to foliage density (Table 2). Diversity of frugivores and omnivores increased with height above the ground. Frugivores especially exhibited extremely low diversity in

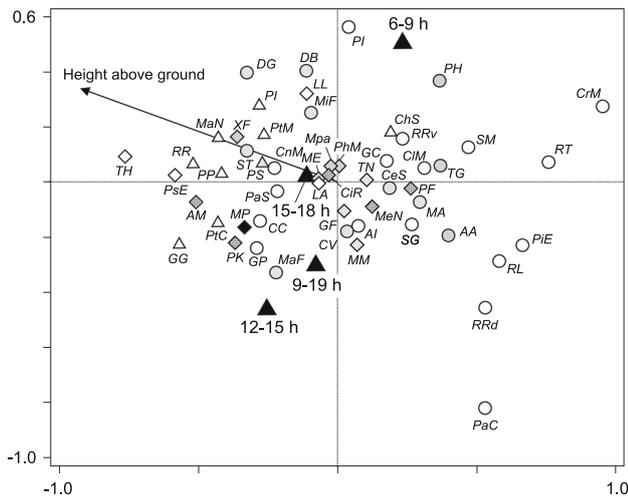


Fig. 6 CCA diagram visualising the abundance of frugivorous (empty triangles), insectivorous (empty circles gleaning species, filled circles sallying species) and omnivorous (bricked diamonds frugivoro-insectivores, grey diamonds nectarivoro-insectivores, empty diamonds nectarivoro-frugivores, black diamond non-classified omnivore) species in relation to height above ground (height) and time of day (6–9, 9–12, 12–15, 15–18 h). The first two ordination axes explained 3.09 % of total variation. Values of explained variation (%), Pseudo- F statistics (F) and P level (P) for explanatory variables (height and time) obtained by Canonical Correspondence Analysis (covariate: capture site, Monte Carlo test with 999 permutations) of trophic guilds: frugivores (height 7.5 %, $F = 6.6$, $P = 0.002$; time 3.3 %, $F = 2.8$, $P = 0.006$), insectivores (height 2.5 %, $F = 4.9$, $P = 0.002$; time 1.6 %, $F = 3.1$, $P = 0.002$), omnivores (height 2.8 %, $F = 5.6$, $P = 0.002$; time 1.3 %, $F = 2.6$, $P = 0.004$). Species codes: AA, *Alcedo azurea*; AI, *Arses insularis*; AM, *Aplonis metallica*; CC, *Carterornis chrysomela*; CeS, *Ceyx solitarius*; ChS, *Chalcophaps stephani*; CiR, *Cicinnurus regius*; CIM, *Colluricincla megarhyncha*; CnM, *Coracina melas*; CrM, *Crateroscelis murina*; CV, *Cacomantis variolosus*; DB, *Dicrurus bracteatus*; DG, *Dacelo gaudichaud*; GC, *Gerygone chrysogaster*; GF, *Glycichaera fallax*; GG, *Geoffroyus geoffroyi*; GI, *Garritornis isidorei*; GP, *Gerygone palpebrosa*; LA, *Loriculus aurantifrons*; LL, *Lorius lory*; MA, *Miagra alecto*; MaF, *Machaerirhynchus flaviventer*; MaN, *Macropygia nigrirostris*; ME, *Myzomela eques*; MeN, *Melanocharis nigra*; MiF, *Microeca flavovirescens*; MM, *Melilestes megarhynchus*; MP, *Micropsitta pusio*; Mpa, *Meliphaga analoga/M. aruensis*; PaC, *Ptilorhoa caerulea*; PaS, *Pachycephala simplex*; PF, *Pitohui ferrugineus*; PH, *Poecilodryas hypoleuca*; PhM, *Philemon meyeri*; PI, *Ptilinopus iozonus*; PIE, *Pitta erythrogaster*; PK, *Pitohui kirhocephalus*; PP, *Ptilinopus pulchellus*; PsE, *Psittaculirostris edwardsii*; PtC, *Ptilinopus coronulatus*; PtM, *Ptilinopus magnificus*; PtS, *Ptilinopus superbus*; RL, *Rhipidura leucothorax*; RR, *Reinwardtoena reinwardtii*; RRd, *Rhipidura rufidorsa*; RRv, *Rhipidura rufiventris*; RT, *Rhipidura threnothorax*; SG, *Symposiachrus guttula*; SM, *Symposiachrus manadensis*; ST, *Syma torotoro*; TG, *Tanysepta galatea*; TH, *Trichoglossus haematodus*; TN, *Toxorhamphus novaeguineae*; XF, *Xanthotis flaviventer*

lower forest zones. In contrast, diversity of insectivorous birds did not change significantly with height above ground (Table 2; Fig. 7d–f).

Traditional mist netting, limited only to ground level, leads to reduced species richness in the sample. Recorded

species richness was significantly lower when ground nets (0–3 m) were compared to the complete set of ground-to-canopy mist nets 0–27 m at the same mist netting sites (numbers of species per site; 0–3 m: median = 7, range 1–11; 0–27 m: median = 28, range 23–44; Mann–Whitney U test, $z_{2,24} = 4.128$, $P < 0.001$). In total, the lowest net captured 100 individuals of 30 species, while the full set of ground-to-canopy nets captured 850 individuals of 84 species. Even with increased sampling effort, the species richness recorded with ground nets remains far lower. This was shown by the ground mist netting (0–3 m) survey that was carried out in 2015 in the same conservation area. In total 427 individuals (485 including recaptures) were captured, but only 46 species were recorded. Moreover, rarefaction curves comparing both sampling techniques showed that ground level mist netting became saturated at a faster rate (Fig. 8). Therefore, even if the sample size of ground-to-canopy mist netting was reduced to the same value as ground mist netting (485 captures), elevated mist nets would capture approximately 24 species more than ground mist nets. The most underscored group of birds caught by ground mist nets were frugivores with only three captured species: *Chalcophaps stephani*, *Gallicolumba rufifigula* and *Ptilinopus coronulatus*; the first two species are ground foraging birds. In contrast, the proportion (both abundance and species richness) of insectivorous birds caught by ground mist nets was much higher compared with ground-to-canopy mist nets (Fig. 8). Insectivorous birds that were caught only in ground-to-canopy mist nets were canopy dwelling cuckoos (Cuculidae, 7 species), other birds preferring higher strata (*Carterornis chrysomela*, *Dicrurus bracteatus*, *Gerygone palpebrosa*, *Microeca flavovirescens*, *Peltops blainvillii*) and aerial species such as Papuan Spinetail (*Mearnsia novaeguineae*). The proportion of omnivorous birds was similar in both ground-to-canopy and ground mist nets. Omnivorous birds that were not captured by ground mist nets were mainly parrots (*Cyclopsitta diophthalma*, *Charmosyna placentis*, *Eclectus roratus*, *Lorius lory*, *Psittaculirostris edwardsii*, *Trichoglossus haematodus*) and other birds that are not often encountered in the understory: *Glycichaera fallax*, *Lalage atrovirens*, *Leptocoma serieca*, *Mino dumontii*, *Paradisaea minor*.

Discussion

The mean foliage density profile from our capture sites resembled profiles from other tropical forests characterized by two peaks of foliage density, one peak in the understory and the second peak in the canopy strata (Pearson 1971; Schemske and Brokaw 1981; Bell 1982; Meir et al. 2000; Walther 2002b). Both Pearson (1971) and Bell (1982)

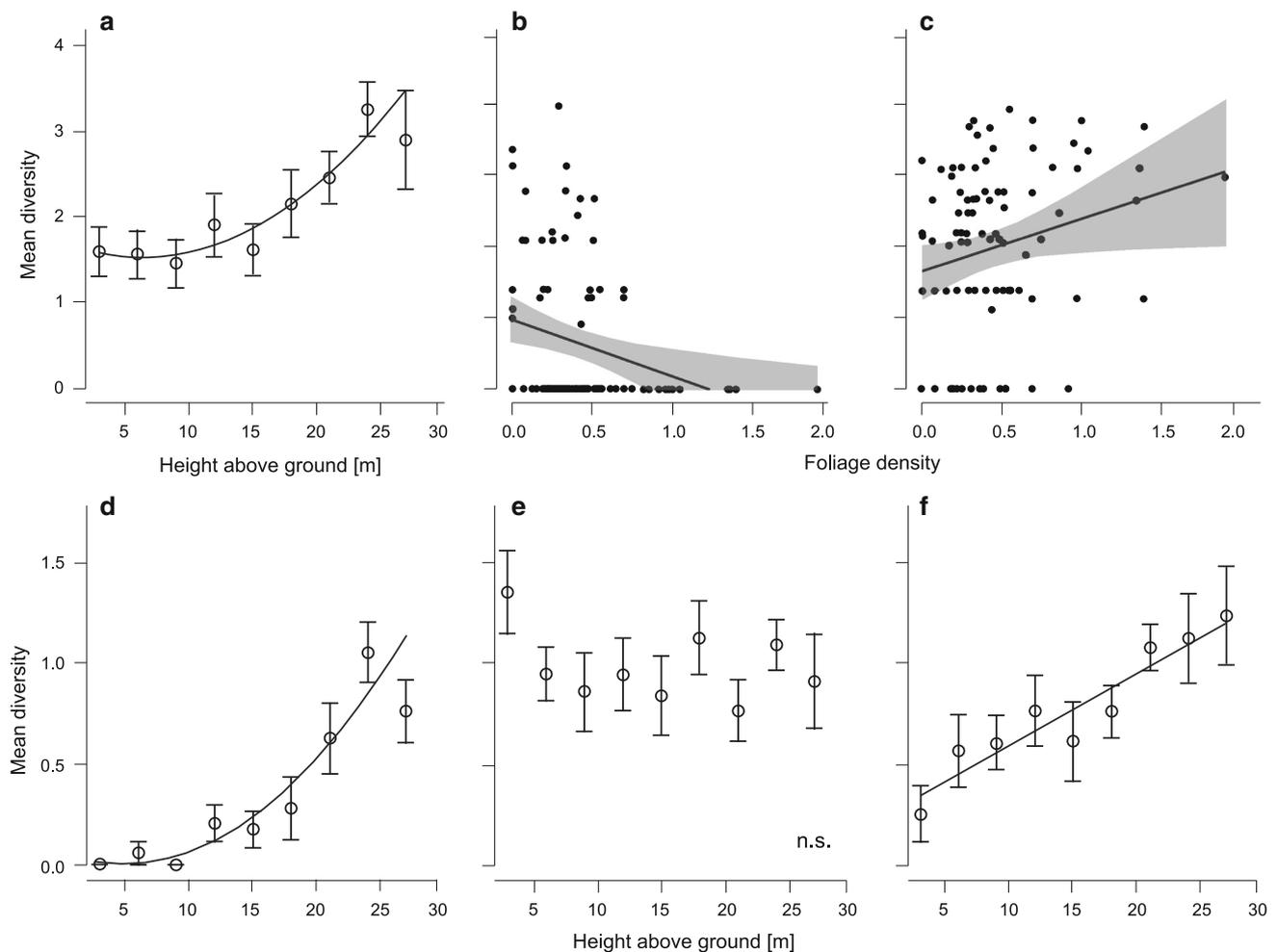


Fig. 7 Diversity (Mean Shannon–Wiener diversity index \pm SE) of avian community (**a**) and trophic guilds (frugivores: **d**, insectivores: **e**, omnivores: **f**) and its profile across vertical forest strata (height above

ground). Linear relationship of diversity (Shannon–Wiener diversity index) and foliage profile of frugivorous (**b**) and insectivorous (**e**) birds (shaded area represents standard error)

suggested a positive correlation between foliage density and abundance of birds, but they did not support their assumptions with statistical tests. Further, they both admitted certain deviance from the claimed relationship in some strata. Walther (2002a) reported that birds recorded in lower strata were surrounded by thicker vegetation compared with birds in higher strata. This is in agreement with our study where insectivorous birds with highest abundances in the understory showed positive preference for thicker vegetation, whereas frugivorous birds avoided (both in terms of abundance and diversity) the understory with high vegetation density. However, we did not find a relationship between overall abundance or diversity of the avian community and foliage density. This suggests that foliage density of different forest strata explains the vertical distribution of birds at a finer scale rather than at community level.

Our results showed that birds were most abundant and had highest diversity in the topmost sampled strata. This is in agreement with the general assumption that tropical forest canopy is the center of diversity, although only Pearson (1971) has empirically confirmed this for Neotropical birds. In contrary to our results, Bell (1982) reported from Papua New Guinea that birds were most abundant in the understory. Nevertheless, in agreement with our results, both Pearson (1971) and Bell (1982) reported lowest abundance of birds in the midstory. However, Jayson and Mathew (2003) reported a different pattern of vertical distribution of birds from Indian tropical evergreen forest, where abundance of birds decreased from ground to canopy. Previous studies were based on ground surveys, which may under-estimate bird abundance in the canopy. Moreover, Pearson (1971) and Bell (1982) included only foraging birds while our mist netting allowed

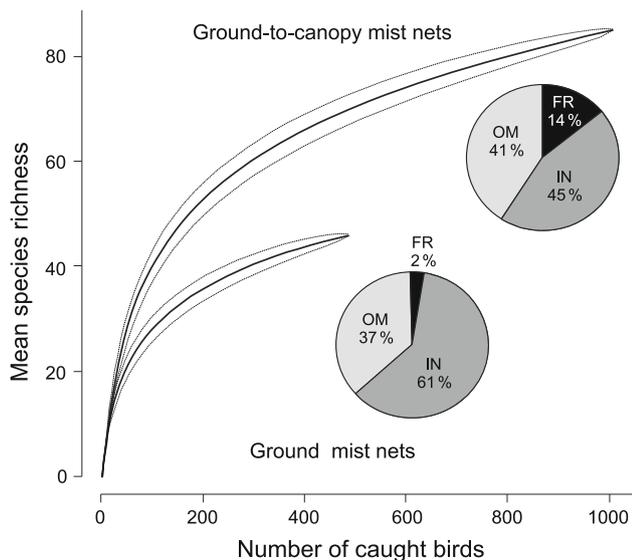


Fig. 8 Rarefaction curves (\pm SE: *dashed lines*) showing species accumulation for ground based (*lower curve*) and ground-to-canopy (*top curve*) mist netting. In total we made 485 captures of 46 species and 1008 captures of 84 species in ground mist nets and ground-to-canopy mist nets, respectively. The following numbers of birds (including recaptures) and species of different trophic guilds were caught by both mist netting techniques: *FR* frugivores (ground 12 birds, 3 species; ground-to-canopy 144 birds, 14 species), *IN* insectivores (ground 296 birds, 28 species; ground-to-canopy 449 birds, 40 species), *OM* omnivores (ground 177 birds, 15 species; ground-to-canopy 411 birds, 28 species)

capture of nearly all birds, independent of whether feeding or just moving through the forest.

The increased diversity and abundance of birds towards the canopy may be explained by high fruit and flower availability in the canopy, which is indirectly supported by the increased diversity of frugivorous and omnivorous birds in higher strata. This result is consistent with studies on vertical distribution of trophic guilds from other tropical sites (Terborgh 1980; Greenberg 1981; Bell 1982; Frith 1984; Koen 1988). However, the diversity of frugivores in the understory might be slightly underestimated in our dataset, because mist nets are not designed to capture large frugivorous birds foraging on the ground (e.g., *Goura victoria*, *Casuaris unappendiculatus*). Insectivorous birds did not exhibit any pattern of vertical distribution of species diversity, although their abundance was slightly higher in the understory. Higher abundance of insectivores in the understory compared with the canopy was also reported from the neotropics (Greenberg 1981) and Africa (Koen 1988). One could expect that the vertical distribution of insectivorous birds may be linked with the abundance and diversity of insects in different strata. Several studies reported higher diversity or abundance of different groups of insects in the canopy (e.g., Sutton et al. 1983; Schulze et al. 2001; Charles and Basset 2005). Other studies have

shown that insects in the understory can be as abundant as in the canopy (Basset et al. 2001; Schulze et al. 2001; Stork and Grimbacher 2006). Our results document an increased abundance of insectivores in the understory, which may indicate that insects in the lowland primary forests of New Guinea are most abundant there. Insect availability may also be higher in the understory due to thicker vegetation and the presence of the forest floor, which provides a microhabitat missing in other strata.

We observed highest abundances of birds during the morning hours with gradual decrease towards the evening. This is in agreement with other studies from tropical forests (Bell 1982; Blake 1992). In contrast, vertical shifts downwards during the midday hot period observed in nectarivorous birds (Bell 1982) or a decrease in bird abundance in the topmost stratum (Pearson 1971) were not confirmed by our results at either community or trophic level. Temporal activity (capture rate) of birds differed among birds with different foraging strategies. Insectivores, in contrast to frugivores and omnivores were caught mainly during the early morning period (6:00–8:59). Thus if mist netting was carried out only during early morning periods, the relative proportion of insectivores would increase. A possible cause for the earlier onset of activity (movements through the forest) in insectivores can be explained by their fast metabolic rate, which is related to their small body size (Nagy 2005). The mean body mass of insectivorous birds caught during our survey was considerably lower compared to frugivorous and omnivorous birds (mean \pm SD: insectivores 30.7 ± 20.1 g, frugivores 115.8 ± 50.5 g, omnivores 40.6 ± 43.7 g). Small insectivores probably start to forage earlier in order to regain energy lost during the long tropical night.

Our results show the efficiency of ground-to-canopy mist netting. Although the installation of mist nets in the canopy was time consuming and mist netting did not acquire behavioral data (e.g., foraging, singing, displaying, resting), this method allowed us to obtain detailed data on the vertical distribution of bird guilds and obtained a fuller picture of bird diversity. Moreover, a considerable number of bird species would not have been recorded by a ground-based census, due to their secretive life-style or preference for higher canopy strata. Finally, we showed that elevated mist nests can be used to survey the stratification of avian forest communities and to the best of our knowledge this is the first study using this method.

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