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Research Article

Bird abundances in primary and secondary growths in Papua New Guinea: a preliminary assessment

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Abstract

Papua New Guinea is the third largest remaining area of tropical forest after the Amazon and Congo basins. However, the growing intensity of large-scale slash-and-burn agriculture and logging call for conservation research to assess how local people's traditional land-use practices result in conservation of local biodiversity, of which a species-rich and diverse component is the avian community. With this in mind, I conducted a preliminary survey of birds in small-scale secondary plots and in adjacent primary forest in Wanang Conservation Area in Papua New Guinea. I used mist-netting, point counts, and transect walks to compare the bird communities of 7-year-old secondary growth, and neighboring primary forest. The preliminary survey lasted 10 days and was conducted during the dry season (July) of 2008. I found no significant differences in summed bird abundances between forest types. However, species richness was higher in primary forest (98 species) than in secondary (78 species). The response of individual feeding guilds was also variable. Two habitats differed mainly in presence of canopy frugivores, which were more abundant (more than 80%) in primary than in secondary forests. A large difference (70%) was found also in understory and mid-story insectivores. Species occurring mainly in secondary forest were Hooded Butcherbird (*Cracticus cassicus*), Brown Oriole (*Oriolus szalayi*), and Helmeted Friarbird (*Philemon buceroides*). Examples of primary forest species were Red-bellied Pitta (*Pitta erythrogaster*), Little Kingfisher (*Alcedo pusilla*), and Zoe's Imperial Pigeon (*Ducula zoeae*). My results suggest that changes in bird assemblages occur even in relatively undisturbed landscapes in response to small-scale shifting agriculture that is crucial for local people's livelihood; it also seems that traditional land use by local people favors the persistence of a rich bird species pool in the forested and traditionally managed landscape.

Keywords: Shifting-culture, secondary growth, bird, feeding guilds, Papua New Guinea

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Introduction

Birds are one of the best known faunal group in the tropics. They are ecologically highly diverse and occupy a wide range of habitats. They have therefore been frequently used taxa indicating the effects of environmental change [1]. Changes in bird communities may reveal successional processes going on in cleared forest. For example, analysis of bird-species inventories from 10 studies revealed that up to 70% of mature forest bird communities may recover in successional sites, and that species composition is about 55% similar to that of mature forests within 25 years [2].

Whatever changes in habitat structure may influence habitat selection and foraging efficiency of all birds, one of the most notable impacts has been the disproportionate effect within different foraging guilds. Studies in Canada, the United States, France, and Papua New Guinea report, that insectivores have consistently declined and are often the most heavily impacted [1, 3-6]. They seem to be particularly sensitive to different forms of disturbance, including selective logging [7-8], forest degradation and fragmentation [9-12], slash-and-burn agriculture [13], and surface fires [14]. A summary study in agricultural landscapes in Amazonia has also documented declines in insectivorous birds [15].

In Papua New Guinea, shifting (slash-and-burn) agriculture has occurred for at least 5,000 years and is likely to remain the economic base of a large proportion of the population [16]. In the past, shifting agriculture has had limited environmental impact and much primary rainforest has survived. Shifting agriculturalists valued forests as the source of materials and animal and vegetable foodstuffs. Rapid population growth and involvement in cash economies caused a shortening of rotation times, the clearing of much greater areas of primary forest, and in some cases the unintended conversion of secondary forests to grasslands [17]. However, this is not the case in Wanang Conservation Area in Upper Ramu, Papua New Guinea, where most of the cleared areas are small (0.5-1.5 ha) and rotation times long (~10 years). This is due to the fact that the area of forested land (~110 km²) belongs to a small community (~90 people) who clear small new plots of land for gardening, rather than maintaining a large existing one, abandoning their gardens for more than 10 years before coming back (personal communication from community members).

Here I report preliminary results from a rapid survey of avian species richness and diversity in areas of second-growth and primary forest in Wanang Conservation Area in Papua New Guinea. I further describe differences in the distribution of foraging guilds in the two forest types.

Methods

Study area

My study took place in the lowlands (200 m asl.) of Wanang (Papua New Guinea, Wanang Conservation Area in Upper Ramu, Fig.1 and 2). The bird survey was conducted between July 20 and July 30, 2008. Two replicate transects were established in primary (S5°14.234', E145°10.661', Fig. 2) and secondary (S5°13.903', E145°10.729', Fig. 2) sites. Transects were located as far as possible from other surrounding habitats and were both spatially independent (distances between primary and secondary sites was ca. 4 km) and 1 km from each other within one forest site. The first site was primary forest (10,081 ha) and the second was 7-year-old secondary growth (about 10 ha). Transects in primary forests were selected to reflect region-scale differences in soil type and topography, thereby capturing the highest amount of diversity.

Habitat features

Habitat characteristics were measured in two 1-hectare plots. Both vegetation plots were placed close (approximately 100 m) to the bird census transects. Data collection procedures within plots are described elsewhere [18]. Habitat characteristics used as explanatory variables in this study were canopy openness and height, tree density, and plant family richness.

Survey of avifauna

The avifauna at each site was examined using point counts, line-transect walks, and mist-netting (Fig.2). These methods, as applied elsewhere [19-21], were used with minor modifications. In each site, one 750-m transect was established, with six 50-m radius points separated by 150-m intervals. Transects were located at least 300 m away from the forest type edge to diminish edge effect [22]. All fieldwork and censuses were carried out by six observers (randomly divided into two groups every day). Each group was constantly accompanied by an experienced ornithologist from Papua New Guinea. Detections were predominantly of birds heard only, followed by birds both seen and heard; hence we use the term “detectability” only. Records of less-known songs and calls were determined and discussed in laboratory. All over-flying birds and uncertain (5.8%) identifications were removed from the analysis.

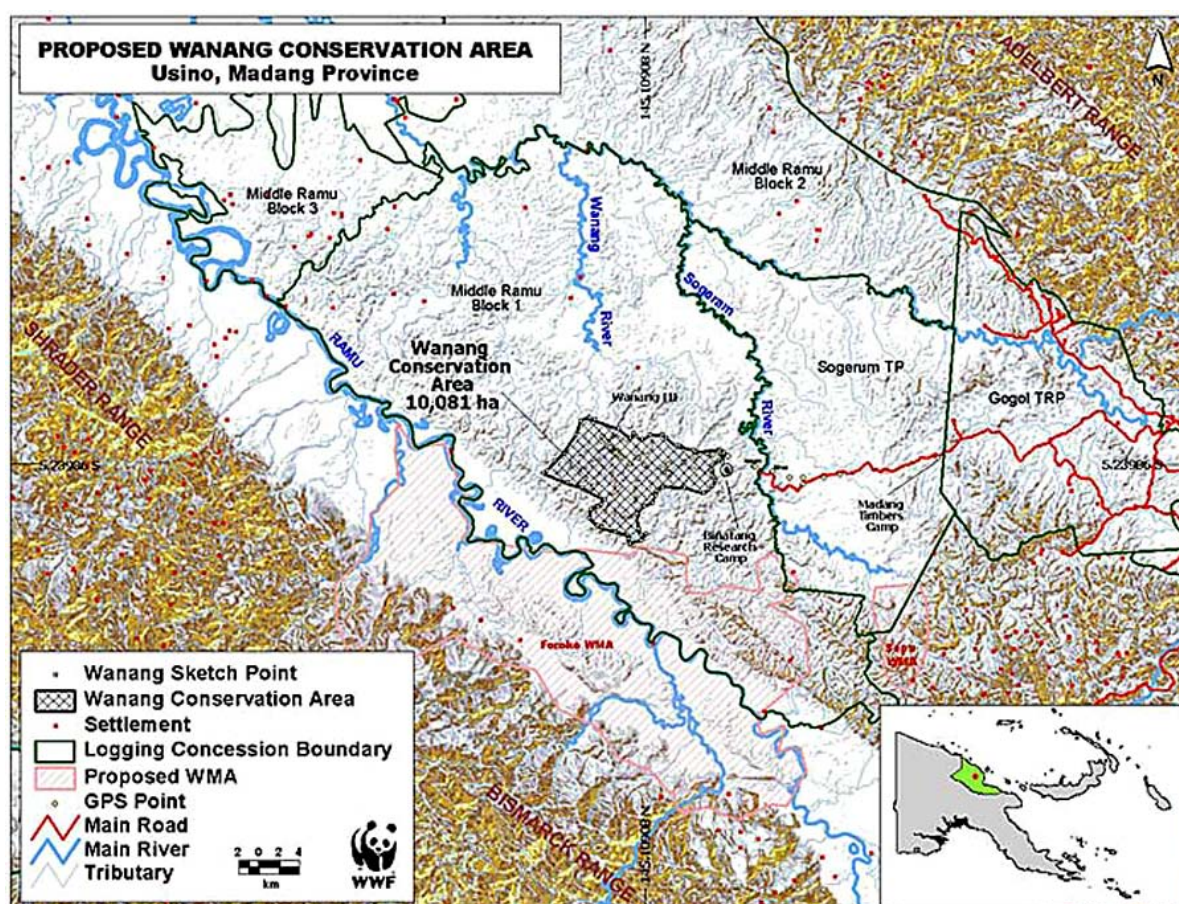


Fig. 1. Location of Wanang Conservation Area in Papua New Guinea.

The line transect was walked slowly (750 m in 1 hour) twice a day (beginning at sunrise and pre-sunset) for the bird census. All detected birds (both seen and heard) were specified and recorded into the following meter classes: 0-20 and 20-50 meters. Point-count censuses were carried out twice a day along the same transects as the line method [13]. The survey at one point lasted 10 minutes and all detected birds were recorded similarly as in line transect (with the same distance classes).

Line transects and point counts were surveyed simultaneously on the same day, both in secondary and primary forest. One group carried out one census using one sampling method (e.g. line transects) in early morning at a sampling transect in secondary forest, and a second method (e.g. point counts) was used on the way back (immediately after finishing the first one). The second group did the same in the primary forest plot. The pre-sunset survey was carried out in a similar way. Thus, two line transects and two point counts were completed per day in both forest types.

Mist-netting was standardized at 100 m of nets within each forest type, and nets were operated for eight days (6:00-11:00 and 15:00-17:00). I used one 10-m, three 12-m, and three 18-m long nets. All were of 16 mm mesh and were 2.5 m in height. All the nets were set up in one line at least 300 m from the forest type edge.

Data analyses

Almost all census techniques sample animal populations imperfectly, and it is highly unlikely that all the individuals will be recorded during a rapid assessment [23]. References to abundance in this paper therefore refer to the indices of abundance derived from my sample techniques (abundance/sample effort) rather than density, which is not known. For tropical forest avifauna, point counts tend to be a more effective sampling method in mature forests, while line transects tend to be more effective in disturbed forests [24-25]. Mist-netting was very ineffective in my study area despite the extent of my sampling effort (5,600 net-hours). In order to limit any systematic bias between habitats, due to sensitivity of detection rates to particular combinations of sampling method and forest type, I treat line-transect and point-count data separately across sites. Similar results from these two very different methods should be seen as providing strong support for the validity of my conclusions.

To test difference in bird abundances between primary and secondary forest, generalized linear mixed models (GLMM, package lme4, function lme) were fitted to the data. Species abundances from each survey were coded as the responsible variable and type of forest (secondary, primary), time of day (sunrise, pre-sunset), observer (group 1 or 2), and method (point count, line transect) as fixed effects. Transect was treated as a nested random effect. The GLMMs were fitted in R version 2.10.1 [26] by specifying a logit link function. The effect of each predictor variable was evaluated separately. Step-wise selection was performed after that.

To compare the bird composition in the plots, multivariate analysis (Canoco 4.5, [27]), and ANOSIM analysis (PAST 2.01, [28]) were used. RDA analysis with a split-plot specified design was performed in Canoco. The variance partitioning was counted afterward.

Data from all three sampling techniques were gathered together for further analyses. Patterns of species richness between forest types were compared using sample-based rarefaction curves (EstimateS 8.2, [29]). Program EstimateS 8.2 was used to calculate similarity indices between individual samples, and Morista-Horn and Jackard indexes were used [30]. Comparisons between forest types were standardized by of the number of individuals, as I was interested in patterns of species richness and not in species density.

Species were assigned to feeding guilds. Necessary information was extracted from literature [31] and from direct observations. More accurate feeding guilds were established from the beginning but were merged for figure and analysis simplification later, as it did not affect result significance.

Comparison of individual feeding guilds across forest types was computed as ANOVA in Statistica 9 [32].

Results

The data analyzed here are the result of 48 one-hour transect and point-count surveys and 5,600 meter-hours of mist-netting. I identified 2,569 individuals comprising 98 species during the observations. Point counts recorded 94 species from 1,699 records; the transect method recorded 82 species from 679 records. Mist-netting (2,800 meter-net hours in one habitat) recorded 19 new species from 68 captures, and added 6 new species to the total number of recorded species. Appendix 1 shows the complete list of species recorded in each habitat.



Fig. 2. Wanang Conservation Area – A) Wanang field station with primary plot in background, B) Primary forest, C) Secondary forest, D) Mist-netted Variable Pitohui (*Pitohui kirhocephalus*) is measured E) Hooded Pitohui (*Pitohui dichrous*) F) Variable Dwarf Kingfisher (*Ceyx lepidus*) G) Common Paradise Kingfisher (*Tansyiptera galatea*). Photos by K. Tvardíková

Point counts recorded more birds than line transect overall, and the rarefaction curve shows that primary forest always had a higher number of species. On the other hand, the transect method recorded slightly more birds in secondary growth (Fig. 3) after certain sampling effort. The effect of method, and interaction between forest type and method, was also significant (Appendix 2). Moreover, the GLMM model and RDA analysis revealed significant effects regarding time of census for both methods. The observer and forest type (without interaction) did not have a significant effect on bird abundances for either survey method (Appendix 2). Total variability explained by time of survey and forest type was 8.4%. Forest type explained more than half of this variability (6%), and time of survey only 2.4% (Canoco, RDA, variance partitioning, [33]).

Similarity indices between samples taken at different time periods were quite low (Morista-Horn index = 0.68) indicating that the effect of time of day on apparent species composition and abundance was quite high. The survey beginning at sunrise yielded higher densities (68 %) than the pre-sunset survey. Moreover, there were some species detectable in the morning (or in the evening) only. Examples of birds recorded mainly in the morning are Hooded Pitohui (*Pitohui dichrous*, Fig.2) and King Bird of Paradise (*Cicinnurus regius*). On the other hand, Lowland Mouse Warbler (*Crateroscelis murina*) and Brush Cuckoo (*Cacomantis variolosus*) were recorded during the evenings only.

The most commonly captured species in the mist-nets were Yellow-bellied Longbill (*Toxorhamphus novaeguineae*), Variable Dwarf Kingfisher (*Ceyx lepidus*, Fig.2), Mimic Meliphaga (*Meliphaga analoga*) and Common Paradise Kingfisher (*Tanysiptera galatea*, Fig.2). The majority of captures (68%) occurred in early morning (6:00-9:00).

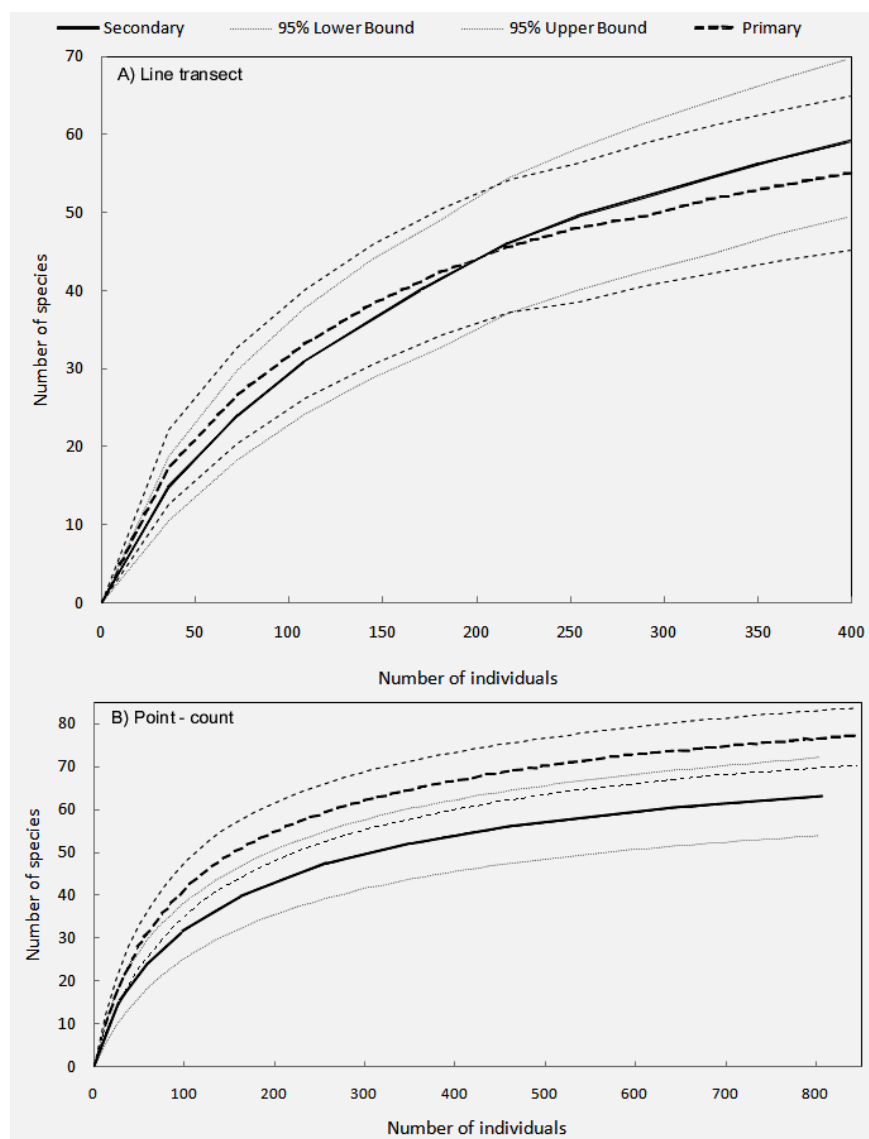


Fig. 3. Rarefaction curves for species recorded by A) transect and B) point-count method in both forest types.

Between-habitat comparison

Significantly more species was recorded in primary forest (n = 91) than in second-growth (n = 68) using point counts, but primary forest had a similar level of richness to second-growth when using the transect method only (Fig. 4). Most of the species (n = 60) were recorded in both habitats. Thirty-one species were recorded only in primary forest and 7 only in secondary growth. Species occurring mainly in secondary forest were Hooded Butcherbird (*Cracticus cassicus*), Brown Oriole (*Oriolus szalayi*), and Helmeted Friarbird (*Philemon buceroides*). Examples of primary forest species were Red-bellied Pitta (*Pitta erythrogaster*), Little Kingfisher (*Alcedo pusilla*), and Zoe's Imperial Pigeon (*Ducula zoeae*).

The communities in both plots were significantly different (Canoco, RDA, $F=6.155$, $p=0.026$) according to RDA analysis, and the forest type explained 60% of variability. Analysis of similarity was also highly significant (PAST, One-way ANOSIM, $R=0.2046$, $p=0.0001$).

Most foraging and dietary guilds (4 of 6) exhibited significant differences in their abundance between habitats, with the overall pattern being broadly similar for point-count (Fig. 5) and transect data. Canopy-dwelling frugivore populations were denser in primary forest. A stronger response was found in insectivores, as all (from all forest stories) were denser in primary forest. Similarity indices for individual foraging guilds also differed when compared between forest types. Both forest types contained more frugivorous (Jackard 0.86-0.88 and Morista-Horn 0.86-0.89) than insectivorous (Jackard 0.71-0.73 and Morista-Horn 0.72-0.73) bird species; the comparison of these indices is significant for both guilds (ANOVA, Jackard: $F_1=4.8$, $p=0.04$; Morista-Horn: $F_1=6.165$, $p=0.013$).

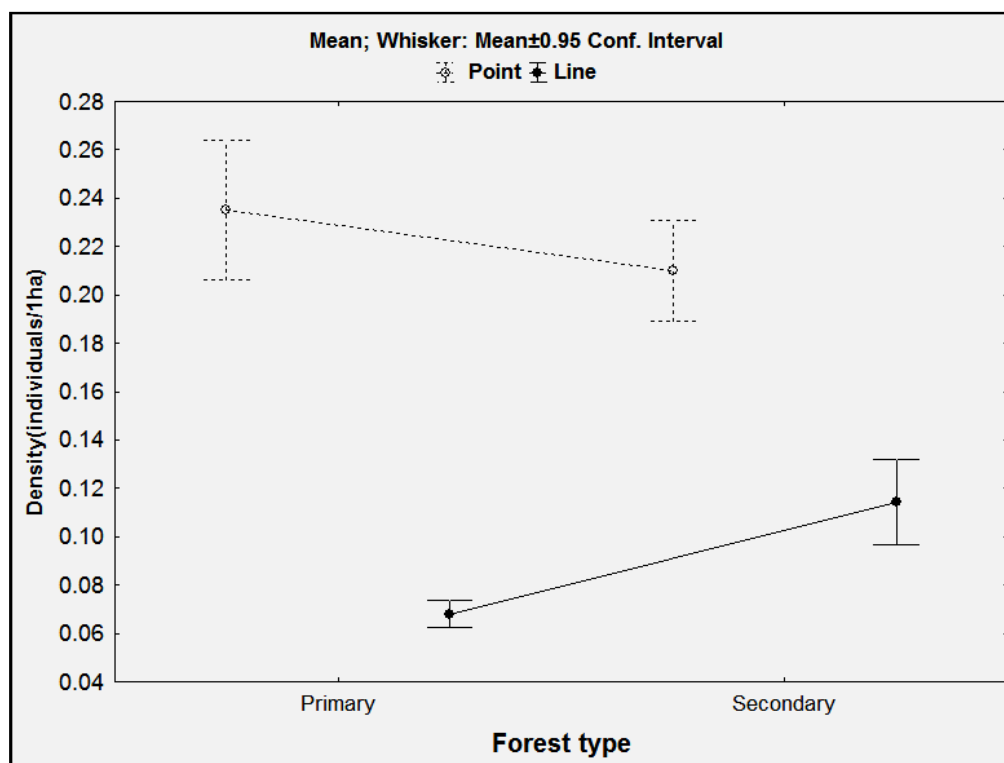


Fig. 4. Comparison of bird densities in primary and secondary forest as gained by point-count and transect methods.

Habitat description

Within the primary 1-hectare plot, the total number of stems at $\text{dbh} \geq 5$ cm was 1,355 and comprised 209 species. The Shannon measure of diversity (H') was 4.53. The most important families were *Meliaceae*, *Euphorbiaceae*, *Myristicaceae*, *Sapindaceae*, and *Rubiaceae*. In the secondary plot, the total number of stems was 1,214 and comprised 87 species. The Shannon measure of diversity was 2.9. The most abundant families in terms of number of stems were *Euphorbiaceae*, *Moraceae*, *Tilliaceae*, and *Lamiaceae*. Canopy openness (%) was similar in primary (25 ± 3.6) and secondary forest (30 ± 1.7) (Wilcoxon test, $n=12$, $p=0.145$). Canopy was much higher in primary (33 ± 3.9) than in secondary (16.4 ± 1.07) forest (Wilcoxon test, $n=12$, $p=0.012$). Tree, shrub, and ground layer diversity did not differ significantly (Spearman's correlation, $n=12$, $p>0.05$).

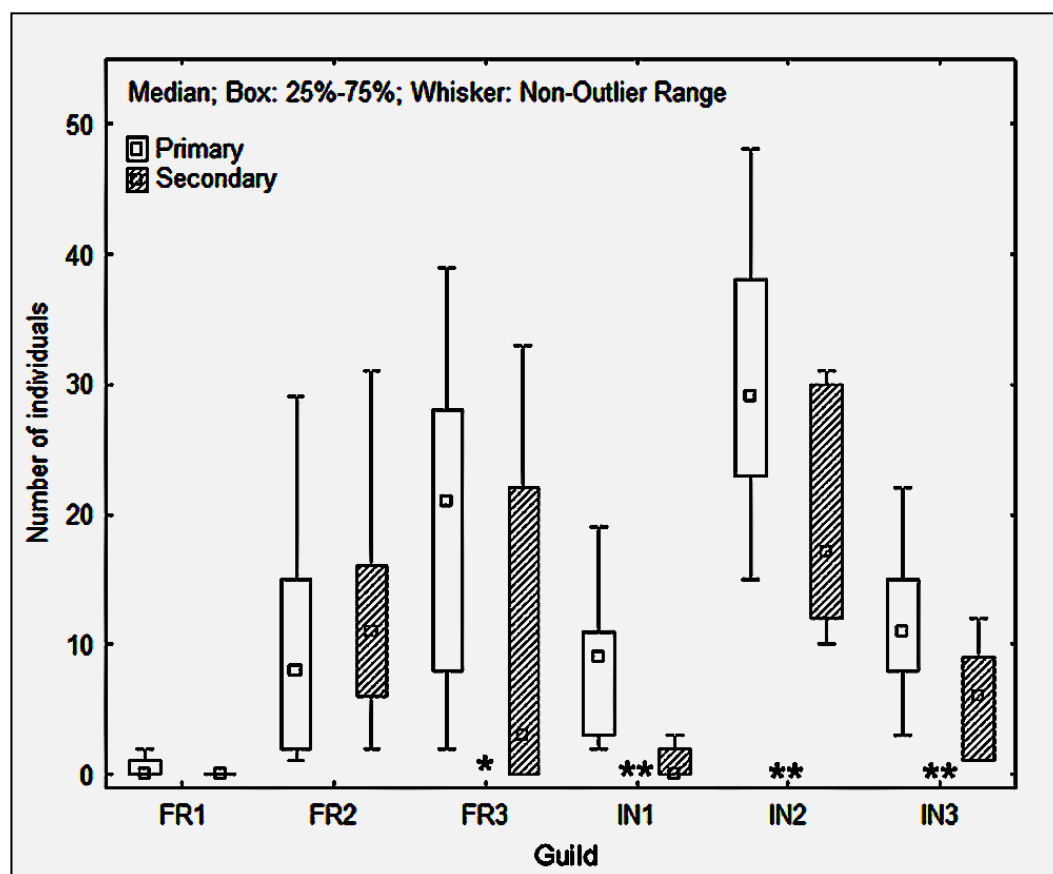


Fig. 5. Number of individuals of individual feeding guilds in primary and secondary forest – results of point-count method only. FR – frugivores, IN – insectivores, 1- understory, 2- mid-story, 3-canopy. Significant difference primary and secondary forest: ** $p<0.01$, * $p<0.05$.

Discussion

Overall, the cross-site comparison suggests that the primary and secondary forest types do not differ in summed bird abundances but only in species diversity. The response of individual feeding guilds to different forest types was also variable. I did not find significant differences between both habitats in avian richness, a finding consistent with patterns reported by Dunn [34] in a review of studies spanning recovery of faunal communities in secondary forests. The author reports that although species richness in a secondary site may recover within 20 years after abandonment, recovery of species composition may take a longer period.

Data show shifts in species abundance within the guild of canopy-dwelling frugivores and significant declines in all insectivorous birds in the Wanang research area. These guilds were adversely affected by habitat modification (canopy and tree density decreased with disturbance), and they seem to be confined to primary or relatively undisturbed forests [35-36]. This trend is supported by reports from other studies in Northeast India and Amazonia [37-38]. In these studies, changes in canopy openness and understory vegetation cover were strongly correlated with changes in bird community structure following surface fires.

Data also suggest that insectivorous birds may be more sensitive than frugivores to shifting cultivation. Further questions to investigate may be an assessment of the importance of mature forests as a source for recolonization of such small secondary plots and a determination whether secondary growths resulting from shifting cultivation may be used by birds as breeding and foraging sites.

It has been pointed out that large sampling scale studies incorporate the effects of surrounding habitat and therefore reflect bird diversity in the agriculture-fallow-forest matrix rather than the diversity in each habitat specifically [2]. This assumption is based on previous large-scale secondary studies indicating a negligible effect on bird diversity [e.g., 39-42], whereas other studies [19, 43] have shown that diversity is affected in small-scale studies that do not make up a matrix of surrounding primary (or close to primary) habitats and edge habitats. While the short duration of our survey and the sampling limitations intrinsic to the sampling design used recommend caution with the interpretation of the data presented, the results suggest that shifting cultivation fallows seem to have similar abundances but different richness of bird species compared to primary forest. One factor responsible for this may be the small scale of the study and close proximity to primary/near-primary forest [44].

Implications for conservation

Results of my study stress that some changes in avian diversity occur even in small secondary plots. This would theoretically mean that only the conservation of large, continuous blocks of primary forest would be the ideal course to follow for conserving the diversity of bird species in a given area. However, most of local communities in Papua New Guinea are poor, undeveloped, and thus highly dependent on garden food planted on slash-and-burn plots. To conserve habitat for birds as well as local people, a landscape shared with a large plot of primary forest and land based on shifting agriculture practices would be the best option. Land with semi-permanent agricultural plots and adequate (composting, mulching, plant propagation) agricultural techniques would sustain food production. On the other hand, the conservation of primary forest could conserve extant avian diversity and bring in a sustainable income from ongoing research or tourism.

It seems that in Wanang small secondary plots managed by local people increase bird species diversity. However, when large scale slash-and-burn practice results in the area of secondary plots exceeding that of primary forest, as has been documented in Wanang's neighboring areas and for other areas of Papua New Guinea [45], the conservation benefits of small-scale slash-and-burn

agriculture are lost. Thus, our preliminary survey indicates that the people of the Wanang community have adopted land management techniques for food production which appear to be successful in preserving their forests, including the unique species-rich avian community.

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Appendix 1. List of species recorded during the survey in Wanang area. Presence of species in primary or secondary plot is marked by * and its absence by -. Nomenclature based on Hoyo, J., Elliot, A., Christie, D.A., Sargata, J. (eds.), (1992) Handbook of the Birds of the World. Lynx Edicions, Barcelona, Spain.

English name	Scientific name	Primary plot	Secondary plot
White-eared Catbird	<i>Ailuroedus buccoides</i>	*	-
Common Kingfisher	<i>Alcedo atthis</i>	*	*
Azure Kingfisher	<i>Alcedo azurea</i>	*	-
Little Kingfisher	<i>Alcedo pussio</i>	*	-
Singing Starling	<i>Aplonis cantoroides</i>	*	*
Shining Straling	<i>Aplonis metallica</i>	*	*
Frilled Monarch	<i>Arses telescopthalmus</i>	*	-
Sulphur-crested Cuckatoo	<i>Cacatua galerita</i>	*	*
Brush Cuckoo	<i>Cacomantis variolosus</i>	*	*
Large-tailed Night-jar	<i>Caprimulgus macrurus</i>	*	-
Golden Cuckoo-shrike	<i>Campochaera sloetii</i>	*	*
Northern Cassowary	<i>Casuarius unnapendiculatus</i>	*	-
Lesser Black Coucal	<i>Centropus bernsteini</i>	*	*
Greater Black Coucal	<i>Centropus menbeki</i>	*	-
Pheasant Coucal	<i>Centropus phasianinus</i>	*	-
Variable Dwarf Kingfisher	<i>Ceyx lepidus</i>	*	*
Pygmy Drongo	<i>Cheatorhynchus papuensis</i>	*	*
King Bird of Paradise	<i>Cicinnurus regius</i>	*	-
Shining Bronze Cuckoo	<i>Chrysococcyx lucidus</i>	*	*
Olive-backed Sunbird	<i>Cinnyris jugularis</i>	*	*
Little Shrike-thrush	<i>Colluricincla megarhyncha</i>	*	-
Boyer's Cuckoo-shrike	<i>Boyer's Cuckoo-shrike</i>	*	*
New Guinea Cuckoo-shrike	<i>Coracina melas</i>	*	*
Black-faced Cuckoo-shrike	<i>Coracina novaehollandiae</i>	*	*
White-bellied Cuckoo-Shrike	<i>Coracina papuensis</i>	*	*
Bare-eyed Crow	<i>Corvus tristis</i>	*	*
Hooded Butcherbird	<i>Cracticus cassicus</i>	*	*
Rusty Mouse Warbler	<i>Crateroscelis murina</i>	*	-
Rufous-bellied Kookubara	<i>Dacelo gaudichaud</i>	*	*
Red-capped Flowerpecker	<i>Dicaeum geelvinkianum</i>	*	-
Spangled Drongo	<i>Dicrurus bracteatus</i>	*	*
Pinon Imperial Pigeon	<i>Ducula pinon</i>	*	-
Purple Tailed Imperial Pigeon	<i>Ducula rufigaster</i>	*	-
Zoe Imperial Pigeon	<i>Ducula zoeae</i>	*	-
Eclectus Parrot	<i>Eclectus roratus</i>	*	*
Little Egret	<i>Egretta garzeta</i>	-	*
Common Koel	<i>Eudynamis scolopaceus</i>	*	*
Common Dolarbird	<i>Eurystomus orientalis</i>	*	*
Isidore's Rufus Babbler	<i>Garritornis isidorei</i>	*	-

Appendix 1, continued

English name	Scientific name	Primary plot	Secondary plot
Red-cheeked Parrot	<i>Geoffroyus geoffroyi</i>	*	*
Blue-collared Parrot	<i>Geoffroyus simplex</i>	-	*
Yellow-bellied Gerygone	<i>Gerygone chrysogaster</i>	*	*
Brahminy Kite	<i>Haliastur indus</i>	*	-
Papuan Harpy Eagle	<i>Harpyopsis novaeguineae</i>	*	-
Long-tailed Buzzard	<i>Henicopernis longicauda</i>	*	*
Pacific Swallow	<i>Hirundo tahitica</i>	*	*
Varied Triller	<i>Lalage leucomela</i>	-	*
Black Capped Lori	<i>Lorius lory</i>	*	*
Yellow-breasted Boatbill	<i>Machaerirhynchus flaviventer</i>	*	*
Brown Cuckoo-dove	<i>Macropygia amboinensis</i>	*	*
Black Berrypecker	<i>Melanocharis nigra</i>	*	-
Mimic Meliphaga	<i>Meliphaga analoga</i>	*	*
Hook-billed Kingfisher	<i>Melidora macrorrhina</i>	*	*
White-marked Forest Honeyeater	<i>Meliphaga montana</i>	*	-
Rainbow Bee-eater	<i>Merops ornatus</i>	*	*
Olive-yellow Flycatcher	<i>Microeca flavovirescens</i>	*	*
Buff-faced Pygmy Parrot	<i>Micropsitta pusio</i>	*	*
Yellow Faced Myna	<i>Mino dumontii</i>	*	*
Golden Monarch	<i>Monarcha chrysomela</i>	*	*
Spot-winged Monarch	<i>Monarcha guttula</i>	*	-
Hooded Monarch	<i>Monarcha manadensis</i>	*	*
Shining Flycatcher	<i>Myiagra alecto</i>	*	*
Plumed Longbill	<i>Oedistoma iliolophus</i>	*	*
Brown Oriole	<i>Oriolus szalayi</i>	-	*
Rufous Monarch	<i>Monarcha rubiensis</i>	*	-
Rusty-breasted Whistler	<i>Pachycephala hyperythra</i>	*	*
Grey Whistler	<i>Pachycephala simplex</i>	-	*
Lesser BOP	<i>Paradisaea minor</i>	*	*
Lowland Peltop	<i>Peltops blainvillii</i>	*	*
Helmeted Friarbird	<i>Philemon buceroides</i>	-	*
Meyer's Friarbird	<i>Philemon meyeri</i>	*	*
Rusty Pitohui	<i>Pitohui ferrugineus</i>	*	*
Variable Pitohui	<i>Pitohui kirhocephalus</i>	*	*
Red-bellied Pitta	<i>Pitta erythrogaster</i>	*	-
Black-sided Robin	<i>Poecilodryas hypoleuca</i>	*	*
Palm Cuckatoo	<i>Probosciger aterrimus</i>	*	-
Dusky Lory	<i>Pseudeos fuscata</i>	*	*
Edward's Fig Parrot	<i>Psittaculirostris edwardsii</i>	-	*
Blue Jewel-babbler	<i>Ptilorrhoa caerulescens</i>	*	-
Coronated Fruit Dove	<i>Ptilinopus coronulatus</i>	*	*
Orange-bellied Fruit Dove	<i>Ptilinopus iozonus</i>	*	-

Appendix 1, continued

English name	Scientific name	Primary plot	Secondary plot
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Wompoo Fruit Dove	<i>Ptilinopus magnificus</i>	*	*
Pink-spotted Fruit Dove	<i>Ptilinopus perlatus</i>	*	*
Beautiful Fruit Dove	<i>Ptilinopus pulchellus</i>	*	*
Superb Fruit-dove	<i>Ptilinopus superbus</i>	*	*
Great Cuckoo-dove	<i>Reinwardtoena reinwardtii</i>	*	*
White-bellied Thicket-Fantail	<i>Rhipidura leucothorax</i>	*	-
Sooty Thicket Fantail	<i>Rhipidura threnothorax</i>	*	*
Papuan Hornbill	<i>Rhyticeros plicatus</i>	*	-
Channel-billed Cuckoo	<i>Scythrops novaehollandiae</i>	*	*
Yellow-billed Kingfisher	<i>Syma torotoro</i>	*	*
Northern Fantail	<i>Rhipidura rufiventris</i>	*	*
Brown-collared Brush Turkey	<i>Talegalla jobiensis</i>	*	-
Common Paradise Kingfisher	<i>Tanysiptera galatea</i>	*	*
Sacred Kingfisher	<i>Todiramphus sanctus</i>	*	-
Yellow-bellied Longbill	<i>Toxorhamphus novaeguineae</i>	*	*
Rainbow Lorikket	<i>Trichoglossus haematodus</i>	*	*
Tawny-breasted Honeyeater	<i>Xanthotis flaviventer</i>	*	-

Appendix 2. Single fixed-effect models and forest as nested clustering variables

	Estimate	t	P
Forest	-0.122	-0.754	0.451
Observer	-0.321	-0.883	0.377
Time	1.119	3.354	<0.001 ***
Method	-1.16	-2.381	0.017 *
Forest:Observer	0.197	0.857	0.392
Forest:Time	0.849	0.983	0.326
Forest:Method	-0.429	-1.992	0.046 *