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Biology of Tropical Birds

Bird species richness, assemblage density, and feeding guild composition in human-modified lowland rainforests of Papua New Guinea

Riqueza específica, densidad de ensambles y composición de gremios tróficos de aves en selvas tropicales bajas modificadas por actividades humanas en Papúa Nueva Guinea

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ABSTRACT. The island of New Guinea is home to the third largest continuous rainforest in the world, which is increasingly threatened by large-scale deforestation and forest conversion. Despite this, there is little scientific data on the highly biodiverse local avifauna and in particular on its response to anthropogenic disturbances. We seek to address this problem by examining bird assemblages in human-altered rainforests in lowland Papua New Guinea. We surveyed birds using point counts (N = 160 over 90 survey days) in four forest types: a continuous primary forest control site; secondary forests regrown after small-scale agriculture; primary forest fragments isolated by logging; and secondary forests regrown after clear-cutting. We employed generalized linear mixed-effects models to analyze bird species richness, assemblage density, and community structure. We found that total bird species richness decreased significantly in all human-modified forests, while total density did not. Moreover, we found that different feeding guilds showed contrasting response to disturbances. Small-scale agriculture resulted in slight decreases of insectivore species richness but did not impact other guilds. However, in primary forest fragments, habitat isolation and loss of forest connectivity severely impacted both insectivores and frugivores. Moreover, in secondary forests regrown after clear-cutting, fragmentation was compounded with changes to forest structure, resulting in collapse of insectivore species richness and density. On the other hand, nectarivores responded positively to forest alteration, with increased assemblage density in all human-modified forests. Our results show that changes to forest structure come second to fragmentation in their negative effects on bird species. Retaining connectivity with contiguous primary forests is crucial for maintaining the bulk of avian biodiversity. As logging concessions expand across Papua New Guinea, conserving large, intact forest reserves will be essential for sustaining the region's unique avifauna.

RESUMEN. La isla de Nueva Guinea alberga la tercera selva tropical más grande del mundo, la cual se encuentra cada vez más amenazada por deforestaciones a gran escala y la conversión de las selvas. A pesar de ello, la información científica sobre la gran biodiversidad local de aves y, en particular, sobre su respuesta a los disturbios antropogénicos es insuficiente. Buscamos investigar sobre este problema examinando los ensambles de aves en selvas tropicales bajas alteradas por actividades humanas de Papúa Nueva Guinea. Censamos aves mediante puntos de conteo (N = 160 durante 90 días de censos) en cuatro tipos de selvas: selva primaria continua, como sitio control; selva secundaria regenerada después de agricultura a pequeña escala; fragmentos de selva primaria aislados por la tala; y selvas secundarias regeneradas tras la tala rasa. Empleamos modelos lineales mixtos generalizados para analizar la riqueza específica, la densidad de los ensambles y la estructura de la comunidad de aves. Encontramos que la riqueza específica total de las aves disminuyó significativamente en todas las selvas modificadas por actividades humanas, mientras que la densidad total no lo hizo. Además hallamos que diferentes gremios tróficos exhibieron respuestas contrastantes a los disturbios. La agricultura a pequeña escala resultó en ligeros descensos en la riqueza de especies insectívoras, pero no impactó sobre otros gremios. Sin embargo, en fragmentos de selva primaria, el aislamiento del hábitat y la pérdida de conectividad afectaron gravemente tanto a los insectívoros como a los frugívoros. Además, en selvas secundarias que han vuelto a crecer tras la tala rasa, la fragmentación se combinó con cambios en la estructura de la selva, resultando en el colapso de la riqueza y densidad de especies insectívoras. Por otro lado, los nectarívoros respondieron positivamente a la alteración de la selva, con un aumento en la densidad de sus ensambles en todas las selvas modificadas por el hombre. Nuestros resultados muestran que los cambios en la estructura de la selva se sitúan en segundo lugar, después de la fragmentación, en cuanto a sus efectos negativos sobre las especies de aves. Mantener la conectividad con selvas primarias contiguas es crucial para conservar la mayor parte de la biodiversidad de aves. A medida que las concesiones de tala se expandan en Papúa Nueva Guinea, la conservación de grandes reservas selváticas intactas será esencial para sostener la avifauna única de la región.

Key Words: *bird species richness; rainforest disturbance, feeding guilds; secondary forests; New Guinea*

INTRODUCTION

Tropical rainforests are home to the majority of the world's bird species, making them the most valuable terrestrial ecosystems for avian conservation. However, deforestation and forest fragmentation threaten to destroy large areas of formerly intact rainforests, endangering many bird species (Morris 2010, Laurance 2015, Turubanova et al. 2018). Despite this threat, the scientific literature dealing with bird biodiversity in human-modified rainforests is subject to significant regional bias. Most studies have been conducted in the Neotropics, while other regions, such as Africa and Oceania, are neglected in comparison (Sodhi et al. 2008, Matuoka et al. 2020). Findings from one

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biogeographical region are not always globally applicable due to the high regional specificity of bird communities and the ecosystems they inhabit (Corlett and Primack 2006, Burivalova et al. 2019, Silva et al. 2020), which often leads to an insufficient understanding of anthropogenic impacts (Sodhi et al. 2008).

The island of New Guinea is home to the third largest contiguous primary rainforest in the world (Brooks et al. 2006), and over five percent of global biodiversity is contained within its boundaries (Sekhran et al. 1995). More than 800 bird species live on the island, their diversity peaks at low and medium elevations (Sam et al. 2019, 2024). Until the beginning of the 20th century, the rainforests in the lowlands of New Guinea were virtually untouched by commercial logging (Fox 2011). In Papua New Guinea (hereafter PNG), which occupies the eastern half of the island, over 70 percent of primary forests have retained their continuity until today (Gamoga et al. 2021). In recent decades, however, forest degradation and deforestation have increased significantly (Bryan and Shearman 2015, Turia et al. 2022). This effect is most pronounced in lowland regions, which have the greatest potential for biodiversity loss (Shearman and Bryan 2011). Despite this alarming trend, the impact of deforestation, forest fragmentation or degradation on birds in New Guinea remains poorly understood.

Several studies have discussed the interaction between agricultural land use and bird diversity in PNG. Elevation-dependent changes in bird community structure were found with increasing agricultural exploitation (Marsden et al. 2006, Marsden and Symes 2008). In addition, a preliminary survey identified decreases in species richness and abundances in secondary forest patches regenerating after subsistence agriculture (Tvardíková 2010). To date, only one study has examined the effects of large-scale forest disturbance on bird communities in New Guinea (Sam et al. 2014). The study found that forest fragmentation reduces the species richness of insectivorous and frugivorous birds in particular. These results show comparable effects of large-scale fragmentation as reported in other tropical regions (Thiollay 1997, Renjifo 1999, Şekercioğlu et al. 2002). However, this study did not consider the full range of altered forest ecosystems in lowland PNG.

In particular, secondary forests form the most widespread human-modified landscape of PNG (Gamoga et al. 2021), yet their bird communities have never been extensively surveyed. Studies from neighboring tropical landscapes have suggested that secondary forests can maintain high bird diversity. Response of large canopy frugivores to selective logging and subsistence agriculture was examined on the island of New Britain, finding mainly that some species sought out gardens and logged forests due to increased proportion of flowering and fruiting trees (Marsden and Pilgrim 2003). In Sulawesi, understory birds were similarly abundant in secondary and primary forests (Waltert et al. 2005), including endemic and red-list species (Martin and Blackburn 2014). Studies from Sumatra and Borneo found similar bird species richness in primary and secondary forests, although this is partially determined by high forest connectivity (Imron et al. 2022, Prabowo et al. 2016).

On the other hand, New Guinean birds are reportedly sensitive to hunting pressure, (Pangau-Adam et al. 2015), as well as changes to habitat structure (Tvardíková 2010), and edge effect (Sam et al. 2014), all of which can be associated with secondary forests (Watson et al. 2004). Many species, such as canopy frugivores or terrestrial insectivores, cannot survive in secondary forests due to limitations associated with variation in habitat structure (Şekercioğlu et al. 2002). Furthermore, secondary forests are often subject to constant disturbance from adjacent human settlements, such as timber gathering, fire, or hunting (Whitworth et al. 2018, Chmel et al. 2018). Researchers should also consider the regional specificity of forest disturbances in PNG.

Subsistence agriculture is a key driver of deforestation and secondary succession (Corlett 1994). PNG is no exception, but as the lowland areas of the country have historically been sparsely populated due to the prevalence of malaria, there are significant spatial constraints to agricultural activities (Gamoga et al. 2021). Subsistence agriculture is known to have less severe impacts on bird populations, as it is defined by creation of smaller forest clearings and regrowths, which in PNG is accompanied by selective logging of adjacent forest (Blankespoor 1991, Borges 2007). Another widespread form of disturbance leading to secondary forest regrowth in lowland PNG is large-scale deforestation, which has been introduced in the last century (Shearman and Bryan 2011). This type of disturbance is characterized by clear-cut logging of large swathes of primary forest (Gamoga et al. 2021). Bird colonization is subsequently hampered not only by restricted dispersal but also by the absence of important habitat characteristics for many decades after the onset of succession (Watson et al. 2004). The resulting secondary forest regrowth may, therefore, host severely impoverished bird assemblages (Sodhi 2008)

Conservation efforts in PNG are facing many obstacles associated with the country's natural resources, fractured land ownership, and low level of societal and economic development (Laurance et al. 2012). Furthermore, financial alternatives to the selling of forest land to foreign agents are rare, and mostly unsupported by the national government (Novotny 2010). Education and employment of native para-ecologists is often dependent on non-governmental organizations, as well as researchers bringing expatriate funding (Basset et al. 2000). Moreover, PNG is among the most expensive areas in the world for field research, a problem exacerbated by low forest accessibility and infrastructure development (Bartlett 2018). These issues compound the poorly explored ecosystem functioning with increasing intensity of land use change and deforestation. As especially secondary forests after clear-cutting become a prevalent land cover in the coming decades, it is crucial that their conservation value for birds is quantified.

Our study is the first in-detail examination of bird communities in human-modified lowland rainforests in PNG. We compare key metrics such as bird species richness and density, as well as community structure represented by guild composition, in four forest types: continuous primary forests (P1), isolated primary forest fragments (P2), secondary forests regrown after subsistence agriculture (S1), and secondary forest after large scale clear-cutting deforestation (S2). We aim to test the following predictions:

1) Bird diversity will decrease from P1 forest to P2 forests due to dispersal limitation and loss of microhabitats in forest fragments (Sam et al. 2014). We predict that particularly insectivores will be affected, as they are sensitive to fragmentation (Thiollay 1997).

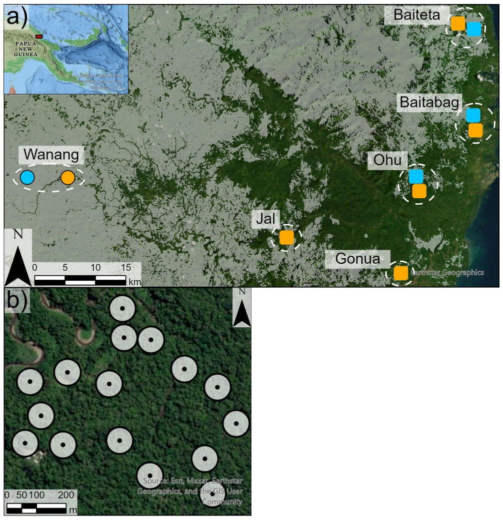
2) Similarly, S1 and S2 forests will feature declines of bird diversity due to changes in habitat structure. We predict that this effect will be associated with habitat loss for many insectivore species, as well as disappearance of frugivores due to hunting, reduced food supply and increased predation (Waltert et al. 2005, Chmel et al. 2018). We predict that this decline will be more severe in S2 forests regrown after clear-cutting.

METHODS

Study sites

The fieldwork was conducted from January 2010 to October 2012. Our study took place in the lowlands (<200 m asl) of Madang province in Papua New Guinea (Fig. 1a). Study sites included: P1) a continuous primary forest area located in the middle of >10,000 ha continuous lowland primary forest in Wanang Conservation Area, which itself is embedded within ~100,000 ha of selectively logged, but largely continuous rainforest, P2) isolated primary rainforest fragments of varying sizes (300–1200 ha) located within a formerly clear-cut landscape, S1) small-scale (ca. 400 ha) secondary forest area created by subsistence-level slash-and-burn agriculture, surrounded by continuous primary forest, S2) secondary forests regrown after large-scale clear-cutting which occurred circa 50 years ago (Shearman and Bryan 2011). Some secondary sites were located close (min. 4 km) to surveyed primary forest fragments (Fig. 1a). For a list of surveyed study sites, their centroid coordinates, general locations, mean elevations, and survey periods refer to Appendix 1, Table S1.

Fig. 1. (a) Map of our study sites within the Madang province of PNG. Blue circle = P1 forest, blue squares = P2 forests, orange circle = S1 forest, orange squares = S2 forest. Dashed white ovals with names are used to denote general areas where study sites are located, corresponding to random effect in our models. Transparent white overlay represents the extent of primary forest, per Turubanova et al. (2018). (b) Field survey design example: 16 points (black dots) with buffers representing 50 m point-count radius. All maps created using the Basemap service of Arcgis Pro Desktop (ESRI 2024). For further information on study sites, refer to Appendix 1, Table S1.



Bird surveys

We surveyed bird communities using point counts and mist-netting. Each study site was surveyed three times per month of study (respectively January, June, October; Appendix 1, Table S1). At each site, counts were conducted at 16 points semi-regularly (ca. 150 m apart) spaced along a 2250 m transect (Fig. 1b). Transects at each site were directed through representative microhabitats (e.g., ridges, valleys, rivulets, emergent trees, small natural forest gaps, and flat land forest; Sam et al. 2014). For forest fragments, the transects were located within the forest interior (<250 m from edge), to minimize immediate edge effect. Coordinates of each point were marked down. All birds seen or heard within 50 m radius of the point were recorded. We measured distances to bird individuals from the center of the point with a laser rangefinder, with each recorded bird being classified within one of five distance bands (0–10, 11–20, 31–40, 41–50, as per Sam et al. 2014). We started censuses 15 minutes before sunrise (5:45 AM) at a randomly selected starting point, and we then continued counts in a randomly selected direction along a circular route, sampling points in a site. We counted birds for 15 minutes at each point so all 16 points were surveyed before 11:00 AM. To minimize double-counting, we attempted to accurately track movements of birds, and recorded more individuals of the same species only when they called at the same time or from distinctively different directions. The total sampling effort amounted to 160 counting points over 90 days of fieldwork, as each counting point has been surveyed nine times. All surveys were conducted by B. Koane, S. Jeppy, and K. Sam, all of whom had previous experience with bird surveys in Papua New Guinea. Surveys were conducted by a team of two of rotating membership, ensuring equal contribution by each author present in the field.

We mist-netted birds in two blocks of 3 days (Appendix 1, Table S1). At each study site, we mist-netted birds along a 200m-long line of nets (2.5 m high × 1–18 m long each, 16-mm mesh) for 6 days from 05:30 to 17:30, with checks every 20 minutes. During the first 3 days, nets were placed between the first three points of the point-count transect, and then transferred to the last three points of the point-count transect for the next 3 days. We identified all mist-netted birds to species, marked them with color bands, and released them within 10 minutes.

Bird community datasets

We used the bird data collected during the point counts as the basis for all our analyses of the bird community. We used bird records from mist-netting to determine whether we omitted any bird species during point counts, but we did not include mist-netting data in our analyses because they provide an incomplete record of bird community composition, as they primarily catch birds that live in the understory, but fail to detect birds of other forest strata (Mulvaney and Cherry 2020). Prior to data analysis, we excluded all raptors and swift species from our datasets, due to their wide home ranges or aerial lifestyles (Beehler and Pratt 2016).

All observed bird species were categorized into four broad feeding guilds, including insectivores (invertebrates as main food), frugivores (fruit and seed eaters), omnivores (feed on plant material and invertebrates in similar ratios), and nectarivores, based on empirical data by (Sam et al. 2017), supplemented by information obtained from literature (Beehler and Pratt 2016, Billerman et al. 2022). We used the 14.1 version of the IOC world bird list as taxonomical authority (Gill et al. 2024).

Point-count data were used to create two datasets: first, we created a table noting down the presence/absence of each species over all counting points. If a species was recorded at a counting point over any of nine replications in time, we considered it present at this point for further analyses. We used data on bird species presence/absence to calculate the following variables: bird species richness, measured as the number of species present per counting point over all nine visits (for example, if five species of birds were recorded at one visit, and one additional species was recorded at the next visit, the total species richness would be six, et cetera). Using the same approach, we calculated the species richness of insectivore, frugivore, nectarivore, and omnivore birds.

A second dataset was based on the abundance of each species at each point, averaged over all visits. This number was further adjusted using a distance sampling method for each species recorded, in order to provide an unbiased abundance estimate (Buckland et al. 2005). We used the package RDistance (Mcdonald et al. 2019) in R 4.3.2 (R Core Team 2024) to perform these adjustments. Furthermore, we converted the number of individuals per counting point (i.e., 0.78 ha) to the number of individuals per hectare, so that our data represented actual density of bird populations that can be observed during a bird survey. We then used the population density of each bird species averaged over the nine visits to calculate total assemblage density of birds per counting point. The same way we calculated the assemblage density of insectivores, frugivores, nectarivores, and omnivores.

Habitat survey

To characterize the habitats at our study sites, we recorded at each point: canopy height (using the heights of three randomly selected trees within the point-count circle and measured with a laser meter); shrub foliage density (five measurements at randomly selected locations within each point-count circle using scatterplot estimates; Creagh et al. 2004); and percent cover of shrubs, grass, bare ground, and litter (within 1 m^2 at 15 randomly selected locations within each point-count circle). We also measured canopy density (based on three photos taken from a 1.5 m tall tripod at the places where canopy height was also measured and analyzed).

Preliminary analysis of habitat structure

Because most vegetation characteristics are likely to be correlated with each other (Sam et al. 2014), we did not include them as predictors in bird community analyses to avoid the confounding effect of multicollinearity (Alin 2010). Instead, we summarized the variation in the habitat characteristics listed above by performing a principal components analysis (PCA) in the Canoco 5 program (ter Braak and Šmilauer 2012). This analysis allowed us to reduce the dimensionality of the variables while minimizing information loss (Abdi and Williams 2010). For each sample (point where birds were surveyed), we included the values of each habitat characteristic as dependent variables. Each counting point was categorized based on the forest type where it was located: P1 (continuous primary forest); P2 (fragmented primary forest); S1 (secondary forest after subsistence agriculture); and S2 (secondary forest after clear-cutting). Following this, we performed an unconstrained PCA analysis on the vegetation characteristics, and projected forest type categories as supplementary variables in ordination space (Šmilauer and Lepš 2014). This process allowed us to identify which vegetation characteristics were more associated with particular types of forest, and determine whether forest type is an accurate proxy for effects of vegetation structure on birds.

Bird community analyses

As our core method of data analysis, we built mixed-effect linear and generalized linear models (glmms; Dean and Nielsen 2007), using the R packages lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017). Within each of our models, one sample was represented by the sum of bird species richness/assemblage density at one counting point over all visits. After this, we established two categorical variables. First, we created a factor describing the forest type in which a study site was located. This factor had four levels: P1 (continuous primary forest); P2 (fragmented primary forest); S1 (secondary forest after subsistence agriculture); and S2 (secondary forest after clear-cutting). This factor was used as a fixed effect in all models. Following this, we created a factor describing the general area where study sites were located (Fig. 1a). This grouping variable had six levels, each describing the same general area where respective study sites were located, and was used as a random effect predictor to account for various confounding effects, including pseudo-replication, as points from the same/adjacent study sites are not independent observations (Heffner et al. 1996), as well as spatial autocorrelation between observations from the same or closely adjacent study sites (Dormann et al. 2012). All of our models thus used a continuous dependent variable (such as bird species richness), the fixed effect categorical predictor describing forest type for each sample (point), and the random effect predictor describing the study site where the sample was located.

We used the mean-parametrized Conway-Maxwell distribution with the "log" link function (Huang 2017) with correction for overdispersion (Brooks et al. 2017) in glmmTMB for modeling five count variables (total bird species richness, as well as species richness of insectivores, frugivores, nectarivores, and omnivores). We used package lme4 to build linear mixed-effects models for continuous dependent variables (log-transformed total assemblage density, as well as that of insectivores, frugivores, nectarivores, and omnivores). We performed model residual diagnostics in the Dharma package (Hartig 2018), testing for between-site spatial autocorrelation by calculating Moran's I of clustered residuals (Chen 2016). We used the emmeans package (Lenth 2022) to calculate pairwise post hoc tests. We found no indication of spatial autocorrelation in model residuals (Appendix 1, Table S2).

Species-level community composition

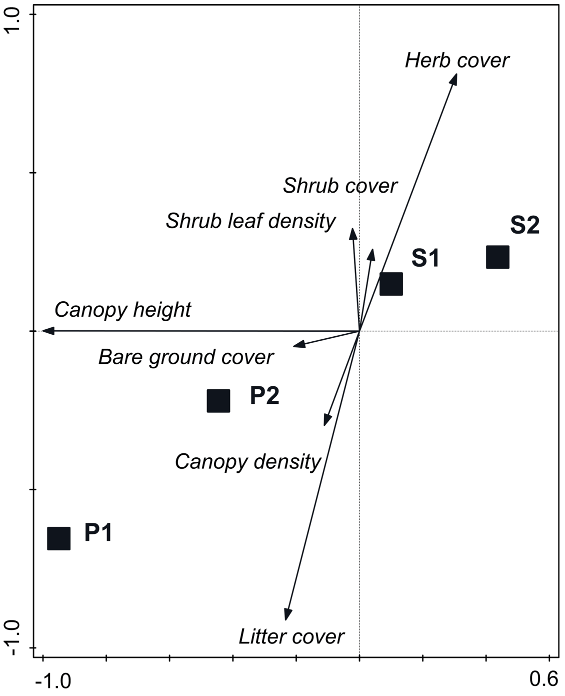
To summarize variation in abundances of individual bird species, we performed unconstrained ordination analyses. Out of the community abundance dataset, we extracted the abundances of 1) insectivores, 2) frugivores, 3) nectarivores, and 4) omnivores. We used these abundances to perform four additional Principal Components Analyses (PCA; Abdi and Williams 2010), with projected supplementary variables describing forest type (P1, P2, S1, S2). The resulting ordination diagram showed which species were associated with each type of forest based on their co-occurrence (Šmilauer and Lepš 2014). These unconstrained ordinations aim to highlight particular species which showed the most pronounced response to habitat modification and to what extent was species composition shared among forest types.

RESULTS

Habitat structure

In our PCA ordination, we found that P1 (continuous primary) and P2 (continuous fragmented) forests were associated with greater cover of bare ground, plant litter, as well as increased canopy density, while S1 (secondary after subsistence agriculture) and S2 forests (secondary after clear-cutting) were associated with increased herb cover, shrub cover, and shrub leaf density. This is visualized by the ordination diagram output of our PCA with projected supplementary variables (Fig. 2, variation explained by supplementary variables: 30.36%, variation explained by first two PCA axes: 99.7%). These results show that primary forests (P1, P2) were in general characterized by greater vertical density and stratification of vegetation, and more consistent canopy coverage, while secondary forests (S1, S2) had a less complex vertical structure of vegetation, and thus denser vegetation grew in the understory. We found that the average daily temperatures ranged from 24.1°C in the early morning to 25.6°C in the late afternoon in the P2 forest and from 24.2°C to 27.8°C in the S2 forest. These results suggest that the secondary forests experienced greater daily temperature fluctuations.

Fig. 2. Ordination diagram, output of unconstrained PCA with displayed relationships among individual variables describing habitat structure (arrows) and projected supplementary variables (squares) describing forest type. Values closer to a given factor level in ordination space occurred more in this forest type compared to other forest types.



Bird community overview

During our survey, we recorded 31,177 bird individuals corresponding to 123 species (Appendix 1, Table S4), of which 113 entered our analyses after carnivorous raptors and strictly aerial insectivores were excluded. The most abundant species was the Mimic Honeyeater (*Meliphaga analoga*, 5.4% of all bird observations), followed by Helmeted Friarbird (*Philemon buceroides*, 5%) and Yellow-bellied Longbill (*Toxorhamphus novaeguineae*, 4.8%). Most species in our study were insectivores (N = 52), followed by frugivores (N = 50), nectarivores (N = 7) and omnivores (N = 5). Insectivores were also the most prevalent guild in terms of assemblage density (46% of individuals), followed by frugivores (35%), nectarivores (13%), and omnivores (6%). Our mist-netting detected only one additional bird species (to point counts), Black-winged Monarch (*Monarcha frater*), caught once.

Variation in bird community metrics

We found significant differences between forest types for overall bird species richness, but not for assemblage density (Table 1). We found that P1 forest had similar species richness (median SR = 59) as S1 forest (SR = 56), but these numbers dropped in P2 forests (SR = 44) and S2 forests (SR = 42, Fig. 3a), showing that connectivity with continuous primary rainforest was important for bird SR.

Insectivores

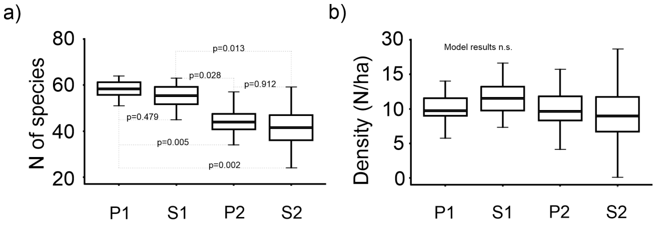
Overall, the most common insectivore species was the Mimic Honeyeater (12% of insectivore observations), followed by Yellow-bellied Longbill (10%), and Northern Variable Pitohui (*Pitohui kirhocephalus*, 8%). We identified insectivores as the bird group most sensitive to rainforest modification. Their species richness dropped from P1 forest to S1 and P2 forest (median SR = 27, 24, 22 respectively), and further in S2 forest (median SR = 18, Fig. 4a). In contrast, insectivore abundances were comparable in P1, S1, and P2 forest (median N/ha = 12, 11, 11), but collapsed in S2 forest (median N/ha = 7, Fig. 4b). Insectivore species

Table 1. Results of models analyzing differences of bird community metrics between types of forest (P1, P2, S1, S2). For each model, forest type is used as a fixed effect. Model significance is determined either by a Type II Wald chi-square test (species richness models, discrete variables, Fox 2015) or a Type III Analysis of Variance with Satterthwaite's method (density models, continuous variables, Chambers and Hastie 2017). For additional information on each model refer to Appendix 1, Table S2.

Variable	DF (model)/ DF (residual)	Chisq/F	P
Total SR	3/157	13.557	0.004*
Total assemblage density (N/ha)	3/157	0.882	0.472
Insectivore SR	3/157	24.269	<0.001*
Insectivore N/ha	3/157	14.100	<0.001*
Frugivore SR	3/157	8.021	0.045*
Frugivore N/ha	3/157	2.142	0.090
Nectarivore SR	3/157	21.676	<0.001*
Nectarivore N/ha	3/157	20.401	<0.001*
Omnivore SR	3/157	7.598	0.055
Omnivore N/ha	3/157	4.830	0.019*

* Statistically significant result (P < 0.05).

Fig. 3. Boxplots describe (a) differences in bird species richness and (b) assemblage density. Post hoc test results as pairwise comparisons between all forest types are displayed for significant results. Explanation of x axis labels: P1 = continuous primary forest, S1 = secondary forest after subsistence agriculture, P2 = fragmented primary forest, S2 = secondary forest after clear-cutting. Boxes show 25–75 quartiles, whiskers show non-outlier range. For more details on each respective model, refer to Appendix 1, Table S2.

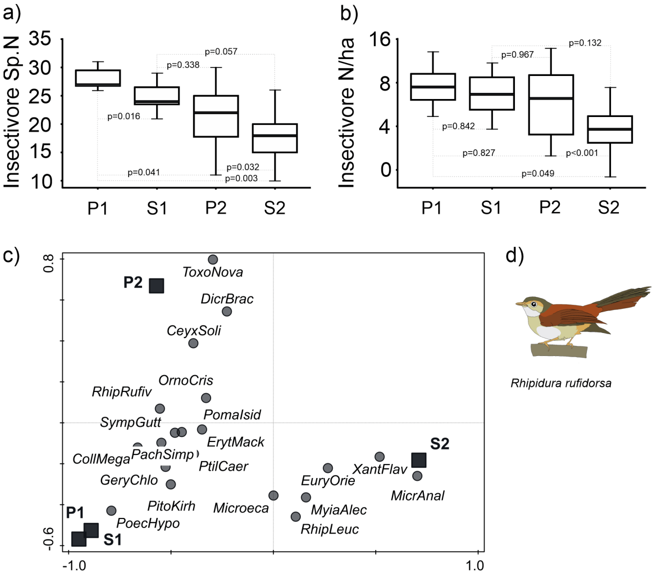


composition changed among forest types, as is shown by our PCA results (Fig. 4c, variation explained by supplementary variables: 24.69%, variation explained by first two PCA axes: 30.35%). P1 and S1 forests were often occupied by the same bird species, such as Northern Variable Pitohui or Black-sided Robin (*Poecilodryas hypoleuca*). In contrast, P2 forest featured a distinct assemblage of birds, including e.g., Yellow-bellied Longbill or Spangled Drongo (*Dicrurus bracteatus*), as did the S2 forest, which was preferred by e.g., Mimic Honeyeater and Tawny-breasted Honeyeater (*Xanthotis flaviventer*).

Frugivores

The most abundant frugivore species was the Metallic Starling (*Aplonis metallica*, 10% of frugivore observations), followed by the Red-capped Flowerpecker (*Dicaeum geelvinkianum*, 7%) and Orange-bellied Fruit Dove (*Ptilinopus iozonus*, 6%). Frugivore assemblages were comparably species rich in P1 and S1 forest (median SR = 23, 24 respectively), but they showed a significant decrease in species richness in P2 and S2 forest (median SR = 17, 16 respectively, Fig. 5a, Table 1). However, mean frugivore abundances only differed marginally between forest types in pairwise post hoc tests. Frugivore species composition also varied between forest types (Fig. 5b, variation explained by supplementary variables: 15.3%, variation explained by first two PCA axes: 35.53%). P1 and S1 forests shared many species, such as Beautiful Fruit Dove (*Ptilinopus pulchellus,* Fig. 5) or Palm Cockatoo (*Probosciger aterrimus*). While some species preferred both P1 and P2 forests, e.g., King Bird-of-paradise (*Cicinnurus regius*) or Black Berrypecker (*Melanocharis nigra*), others strongly preferred P2 forests, such as Lesser Bird-of-paradise (*Paradisaea minor*) or Wompoo Fruit Dove (*Ptilinopus magnificus*). S2 forests were occupied by a distinct assemblage of frugivores not commonly present in other forest types, such as Orange-bellied Fruit Dove, Papuan King Parrot (*Alisterus chloropterus*) or Red-capped Flowerpecker. Despite P2 and S2 forests were comparable in total bird species richness and assemblage density, they were inhabited by different frugivore species, implying that habitat influenced community structure if not diversity.

Fig. 4. Variation in insectivore communities among forest types. Post hoc test results as pairwise comparisons between all forest types are displayed. Boxplots describe differences in (a) insectivore species richness and (b) assemblage densities (abundances per hectare). Displaying median, boxes = 25–75 quartiles, whiskers = non-outlier range. (c) The ordination diagram presents results of our PCA analysis of community composition, based on positions of individual species (grey circles) and projected supplementary variable (forest type, black squares). Species labels are available in Appendix 1, Table S3. (d) Illustration of a typical insectivore species, the Rufous-backed Fantail (*Rhipidura rufidorsa*), drawn by T. Dolejšková based on description from Billerman et al. 2022.



Nectarivores

Nectarivore species richness only differed marginally among forest types, as shown by mostly non-significant post hoc tests (Fig. 6a). However, their density showed a highly positive response to habitat modification (Table 1, Fig. 6b). While P1 and S1 forests contained similar density (median N/ha = 1 and 1 respectively), these numbers increased in P2 forest (median N/ha = 2) and further in S2 (median N/ha = 3). The most abundant nectarivore was the Helmeted Friarbird (40 % of nectarivore observations), followed by the Black Sunbird (*Leptocoma aspasia*, 36%) and Coconut Lorikeet (*Trichoglossus haematodus*, 10%, illustrated in Fig. 5). Individual nectarivore species showed abundance patterns reflected in our model results, increasing in P2 and S2 forest, with the exception of Stella's Lorikeet (*Charmosyna stellae*), which occurred in P1, S1 and P2 forest, but disappeared in S2 forest (Fig. 6c, variation explained by supplementary variables: 16.94%, variation explained by first two PCA axes: 87.55%).

Omnivores

Omnivores represented only a small portion of bird community. All five species of omnivores were comparable in their occurrence, with Long-Billed honeyeater (*Melilestes megarhynchus*) the most represented (22% of omnivore observations), followed by Rufous-

Fig. 5. Boxplots describe (a) differences in species richness. Diagrams describing the variation in frugivore communities among forest types. Post hoc test results as pairwise comparisons between are displayed. Showing median, boxes = 25–75 quartiles, whiskers = non-outlier range. (b) Ordination diagram presents results of our PCA analysis of community composition, based on positions of individual species (grey circles) and projected supplementary variable (forest type). Species labels are available in Appendix 1, Table S3. A representative illustration of a typical frugivore species is given, the Beautiful Fruit Dove (*Ptilinopus pulchellus*). (c) Illustration of a typical frugivore species, the Beautiful Fruit dove, drawn by T. Dolejšková based on description from Billerman et al. 2022.

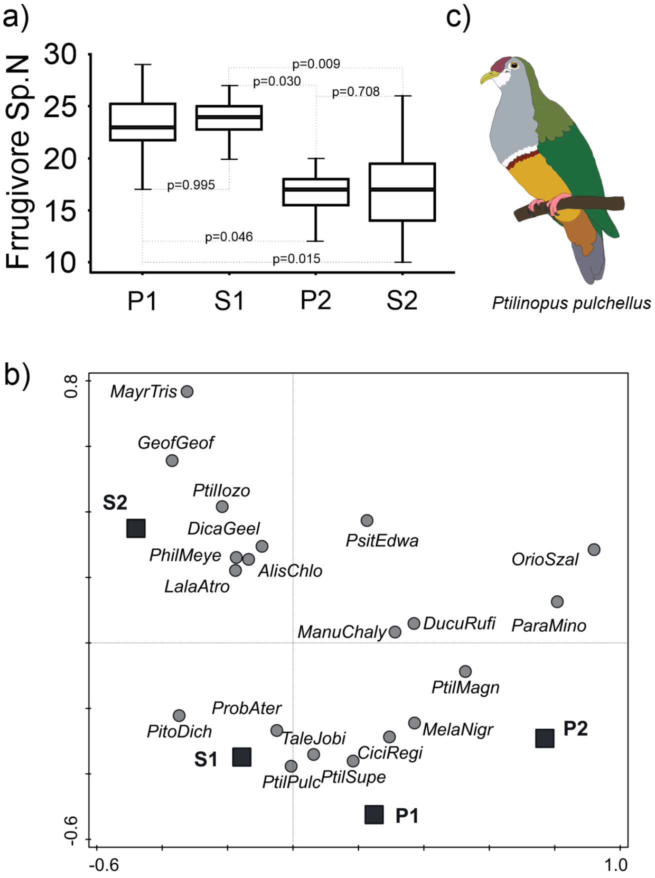
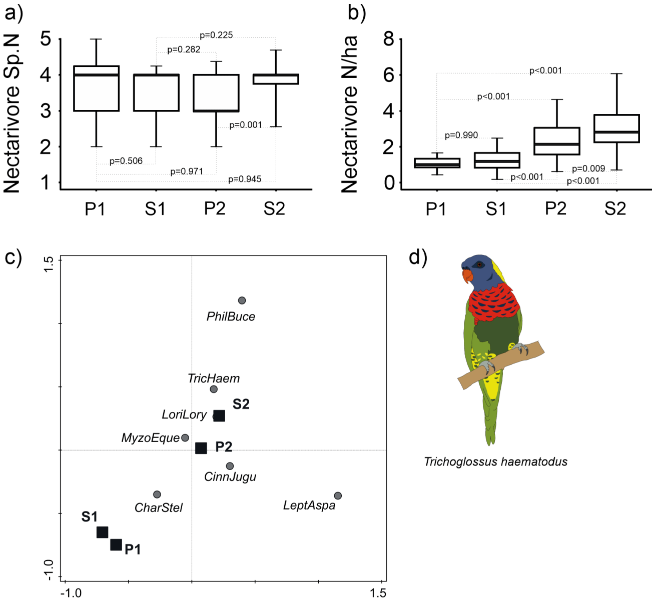


Fig. 6. Diagrams describing the variation in nectarivore communities among forest types. Boxplots describe differences in (a) species richness and (b) densities (abundances per hectare). Post hoc test results as pairwise comparisons between are displayed, with median, boxes = 25–75 quartiles, whiskers = non-outlier range. (c) Ordination diagram presents results of our PCA analysis of community composition, based on positions of individual species (grey circles) and projected supplementary variable (forest type). Species labels are available in Appendix 1, Table S3. (d) Illustration of a typical nectarivore, the Coconut Lorikeet (*Trichoglossus haematodus*), drawn by T. Dolejšková based on description from Billerman et al. 2022.



bellied Kookaburra (*Dacelo gaudichaud*, 21%) and Hooded Butcherbird (*Cracticus cassicus*, 20%). While omnivore species richness was significantly affected by forest type (Table 1), there was only one significant pairwise comparison, marginalizing our results (Fig. S1a). Furthermore, our PCA analysis with supplementary variables showed that most omnivores were not particularly restricted to one forest type, with the exception of Hooded Butcherbird, which preferred S2 forests (Fig. S1).

DISCUSSION

Within our study areas, we show that deforestation leads to impoverished bird communities after decades of forest succession, showing that key forest characteristics for many species are still missing in human-modified forests (Watson et al. 2004). Bird communities in human-modified forests are also strongly influenced by the landscape context. Secondary forests after subsistence agriculture have retained connectivity to continuous primary rainforest, resulting in similar species richness and community structure. Conversely, fragments of primary forests encountered significant loss of species richness and strong changes in community composition due to habitat isolation. The suitability of human-modified forests as habitat for birds is significantly influenced by the adjacent land use systems (Saab 1999, Banks-Leite et al. 2010). As a result, bird biodiversity is shaped by the interplay of local vegetation characteristics and forest connectivity (Powell et al. 2013, Ramos et al. 2020, Salgueiro et al. 2021). This relationship is best explained by deconstructing total species richness and assemblage density into separate functional groups, such as feeding guilds (Sekercioglu 2012, Matuoka et al. 2020).

Insectivores

Insectivores were the dominant bird group in our study, and were the most sensitive to anthropogenic modification. Each modified forest type featured a significant decrease in species richness from the primary forest. Species richness in the S1 forests decreased similarly as in the P2 forest. In S1 forests, there were changes in important habitat characteristics that some insectivores depended on, such as proportion of plant litter and bare groundcover, and decreased canopy height and density (Tvardíková 2010). However, the effects of habitat loss were likely mediated by proximity to primary forest (Mayhew et al. 2019), with disappearance of species prevented by colonization (Bradfer-Lawrence et al. 2018) and community composition influenced by dispersal from the surrounding forest matrix (Johns 1991).

As for the primary forest fragments, our interpretation differs somewhat from Sam et al. (2014). They attributed the loss of insectivore diversity mainly to the decline of important microhabitats. However, our results show that the primary forest fragments were affected by a significant loss of species, although they retained the vegetation structure typical of primary forests. Dispersal limitation is considered by many to be a limiting factor for insectivore occupancy in fragmented forests (Sekercioglu 2002, Moore et al. 2008, Powell et al. 2013). While primary forest fragments are not strictly isolated from other forest habitats, our results showed that the surrounding secondary forest matrix produced by clear-cutting was unable to harbor many insectivore species, likely hindering their dispersal (Stratford and Stouffer 1999, Powell et al. 2015).

The post-clearcut secondary forests were not only species-poor, but also had significantly lower insectivore densities. We hypothesize that the decline in key vegetation features was exacerbated by the loss of connectivity to a contiguous primary forest, leading to a collapse of insectivore assemblages. The reduction in litterfall and bare ground cover was followed by creation of dense herb and shrub overgrowth, making secondary forests unsuitable for terrestrial species such as the Blue Jewel-babbler (*Ptilorrhoa caerulescens*), while the loss of vertical vegetation density impacted flycatchers (e.g., Golden Monarch *Symposiachrus guttula*) and midstory foragers (Sam et al. 2014), such as the Arafura Shrikethrush (*Colluricincla megarhyncha*, Billerman et al. 2022). Furthermore, greater daily temperature fluctuations may have had an additional detrimental effect on sedentary insectivores (Didham and Lawton 1999, Davies-Colley et al. 2000). Observed decrease of insectivore species richness is somewhat contrasting with Indonesia, where secondary forests functioned as suitable alternative habitats (Waltert et al. 2005, Imron et al. 2022). In fact, the loss of species we observed in secondary forests was comparably severe as in Indonesian industrial plantations (Prabowo et al. 2016), highlighting the sensitivity of New Guinean insectivores to severe habitat changes.

Frugivores

Forest connectivity was particularly important for frugivore diversity. Rainforest frugivores are a group that is generally highly affected by large-scale anthropogenic disturbance (Sodhi 2008, Newbold et al. 2013). They are highly sensitive to forest fragmentation (Farwig et al. 2017), as many frugivorous species are unable to survive in smaller forest remnants due to loss of key habitat features and large fruiting trees (Ferger et al. 2014, Mueller et al. 2014). In addition, hunting pressure and nest predation typically increase in fragmented forest landscapes, further increasing the vulnerability of large sedentary species (Riegert et al. 2021). We stress the necessity of focusing on all frugivore taxa, as our results contrast somewhat with Marsden and Pilgrim (2003), who may show slightly misleading results by studying opportunistic species benefiting from disturbances. Findings from Sumatra show a decrease in frugivore occurrence in secondary forests that supports our interpretation (Prabowo et al. 2016).

We report that the species richness of frugivores decreased similarly in primary fragments and clear-cut secondary forests, when compared to continuous primary forest. However, the assemblages of frugivores in secondary forests often contained species that do not prefer the canopy, such as the Papuan King Parrot, or that inhabit forest edges and regrowth vegetation, e.g., Orange-bellied Fruit Dove (Billerman et al. 2022), in contrast to birds in forest fragments, which shared many species with primary forest. These results suggest that while vegetation characteristics influenced the species composition of frugivore groups, overall species richness was determined by the lack of forest connectivity (Moran et al. 2004), possibly associated with hunting or predation (Chmel et al. 2018). The relatively low importance of vegetation complexity for frugivore diversity appears to be region-specific for PNG (Sam et al. 2019), in contrast to other areas where it is a major determinant of frugivore species richness (Morante-Filho et al. 2018). Proximity to primary forest is probably the reason for the high species richness in secondary forests after subsistence agriculture (Mayhew et al. 2019). While these frugivores may show avoidance of large areas of fragmented forests, they are capable of dispersing for large distances within the boundaries of primary forest (Mack and Wright 2005).

Nectarivores

Nectarivores were the only feeding guild that increased in density in fragmented primary and post clear-cut secondary forests. In PNG, obligatory nectarivores form a species-poor assemblage, with their diversity mostly constant in natural forest ecosystems (Sam et al. 2019). However, previous research in PNG showed that both the landscape context and vegetation structure influences nectarivore abundances in human-modified areas (Marsden et al. 2006). We suggest that this is the case for our study. In secondary forests adjacent to forest fragments, the lower canopy density, together with increased shrub and herb cover, likely offered an increased supply of flowering plants (Blake and Loiselle 2001).

Simultaneously, nectarivores often have large home ranges, moving around in search of flowers (e.g., Helmeted Friarbird, Billerman et al. 2022). They can, therefore, disperse more easily and find more food sources in the open secondary forest matrix than in continuous primary forest. In addition, secondary forests are often in the vicinity of small village settlements with home-gardens (Sam et al. 2014), and gardens typically contain a higher density of flowering plants than continuous rainforests (Hagen and Kraemer 2010), suitable for generalist nectarivores. These and other characteristics of human-modified forests likely drive their suitability for nectarivores both in New Guinea and neighboring islands (Imron et al. 2022).

Research and conservation implications

In this study, we give a broad, guild-based overview of bird communities in a human-modified lowland rainforest landscape. While our findings offer valuable insights, they do not cover the regional variability of bird diversity (Sam et al. 2019). In PNG, environmental gradients create a wide range of forest ecosystems, from lowland alluvial rainforests to montane and cloud forests

(Paijmans 1976) to semi-open woodlands and mangroves (Havel 1972). Human pressure on these forests, driven by subsistence-level agriculture and increasingly by large-scale commercial logging (Bryan and Shearman 2015) is significant and varies based on province and historical context (Haberle 2007). To fully understand the impact of human activities on PNG's avian biodiversity, future research should extend toward other areas within this unique landscape.

Guidelines for biodiversity conservation are dependent on baseline knowledge stemming from rigorous case study research (Matuoka et al. 2020, Sodhi 2008). In PNG, this knowledge is almost completely lacking. Our study seeks to address this, by examining birds in human-modified lowland rainforests, which in their natural state host greatest bird diversity across all elevations in PNG (Sam et al. 2019). Within our study areas, we show that large-scale deforestation has strong negative consequences on bird biodiversity. Moreover, we highlight that even large primary forest fragments (up to 1200 ha) only retain slightly greater biodiversity compared to surrounding secondary forests and only for some guilds. Despite this, we agree with Sam et al. (2014), that forest fragments are necessary for future bird conservation. The adjacent secondary forests are subject to regular anthropogenic disturbance that will only increase in magnitude with growing human population, as majority of people in PNG are dependent on home-gardens (Allen and Bourke 2009). Therefore, fragments of primary forest retained by villagers may thus become the only remaining forests in a landscape mostly converted to agricultural use.

Our results also show that the only way to fully protect lowland bird biodiversity is to rigorously maintain connectivity to large reserves of continuous primary forests. Research in other regions has shown that financial incentives for local communities can be the most effective means of preventing disturbance in large-scale forest reserves (Ramsdell et al. 2016). Such incentives may also discourage the sale of large forest areas to predatory logging companies (Novotny 2010). As a developing country, PNG could profit from funding by extra-national organizations for biodiversity conservation and monitoring projects (Turia et al. 2022). However, there remain many issues associated with external funding, such as emphasis on short-term results, poor execution of conservation actions, and corruption (Laurance et al. 2012).

We suggest that additional benefits to particularly avian conservation could be in promotion of citizen science. For example, many other tropical countries already apply the popularity of keystone bird species to foster citizen engagement through banding and bird-watching organizations (Greenwood 2007). PNG is well-regarded for exotic bird-watching prospects, yet amateur ornithology is mostly practiced by foreign visitors (Newsome 2015). Yet local landowners are not opposed to conservation actions, and forest reserves with local fauna are viewed by many as places of cultural significance (Novotny 2010). The main obstacle to citizen science and engagement with amateur ornithology is represented by low standard of living that is joined with increasing criminality and exploitation of native land by foreign agents (Lakhani and Willman 2014). Combating such country-wide issues is mostly beyond the reach of expatriate researchers.

CONCLUSIONS

In response to ongoing deforestation, many tropical regions have seen extensive scientific coverage of human-modified forest ecosystems. There is a need to ensure that other regions, which are at earlier stages of a similar trajectory of forest loss, are not neglected. Furthermore, regional specifics of forest loss progress need to be considered. Our study on bird communities presents one of the few forays into secondary forests in PNG, and highlights the importance of continuous rainforest preservation in the face of increasing deforestation pressure. However, as we focus on only one lowland region of PNG, the elevational and geographical variation in these ecosystems must be investigated for effective countrywide conservation. Bird communities are the ideal study group for monitoring biodiversity in large-scale anthropogenic land use systems replacing natural forests. Therefore, expanding the scope of bird disturbance ecology to other human-modified landscapes in PNG is likely to yield highly valuable information for biodiversity conservation and ecosystem functioning in one of world’s least explored and largest rainforests.

Author Contributions:

Kateřina Sam and Kryštof Korejs are responsible for project conceptualization. Kateřina Sam performed the validation, coordination, and supervision of the work. Kateřina Sam, Bonny Koane, and Legi Sam have designed project methodology. Kateřina Sam, Bonny Koane, Samuel Jeppy, and Legi Sam have performed the investigation (field experiment) of the project. Kateřina Sam and Legi Sam have secured the funding and resources for the project. Kryštof Korejs is responsible for data curation, software code implementation, formal analysis, visualization, and writing of the original draft. Kryštof Korejs and Kateřina Sam have reviewed and edited subsequent versions of the manuscript.

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Data Availability:

The data/code that support the findings of this study are openly available in figshare digital repository at https://doi.org/10.6084/m9.figshare.27169026

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APPENDIX 1

Table S1: Names, locations and geographic coordinates of study sites where our field work was performed. Each study site included 16 counting points where both bird surveys and vegetation surveys were performed. Sites within the same area were assigned the same level of our grouping factor, to account for spatial autocorrelation associated with location and environmental conditions.

ID	Area	Forest type	Description	Elevation (m asl)	Starting point coords (S; E)	Sampling period (months/year)
1	Wanang	P1	Pristine rainforest located within the Wanang conservation area, with little to no disturbance from people occupying the nearby Swire research station.	108	5.23163; 145.181116	January, June, October 2010
2		S1	Secondary forest created by highly spatially restricted small-scale agriculture near the Wanang village, at the border of the Wanang conservational area, and surrounded by continuous primary forest.	113	5.22733; 145.080583	January, June, October 2010
3	Baitabag	P1	Primary forest fragment located near the Baitabag village	80	5.14010; 145.775262	June, October 2010, January 2011
4		S2	Secondary forest after large-scale deforestation, closely adjacent to the Baitabag forest fragment	82	5.14323; 145.773868	June, October 2011, January 2012
5	Baiteta	P1	Primary forest fragment located near the Baiteta village	75	4.99825; 145.7522	June, October 2010, January 2011
6		S2	Secondary forest after large-scale deforestation, closely adjacent to the Baiteta forest fragment	66	5.008; 145.770366	June, October 2011, January 2012

7	Ohu	P1	Primary forest fragment located near the Ohu village	125	5.23081; 145.677786	June, October 2010, January 2011
8		S2	Secondary forest after large-scale deforestation, closely adjacent to the Ohu forest fragment	122	5.23976; 145.689013	June, October 2011, January 2012
9	Gonua	S2	Secondary forest after large-scale deforestation, within 1.5 km of primary forest fragment that was not surveyed	72	5.364; 145.6629	June, October 2011, January 2012
10	Yal	S2	Secondary forest after large-scale deforestation, within 1.5 km of primary forest fragment that was not surveyed	118	5.31558; 145.4897	June, October 2011, January 2012

Table S2: Model parameters for each of our linear mixed-effects (LMM)/ generalized linear mixed-effect models (GLMM). For each model, the dependent variable and model family with the link function are displayed, as well as model parameters and spatial autocorrelation tests. Package lme4 (Bates et al., 2015) was used to fit LMMs, package GLMMTMB (Brooks et al., 2017) was used to fit GLMMs, package Dharma was used for model diagnostics and spatial autocorrelation tests (Hartig, 2018).

Dependent variable	Model type	Model family	Link function	AIC	BIC	loglik	deviance	Moran´s I	P value Moran Test
Total Bird species richness	GLMM	Conway-Maxwell Poisson	log	1031.4	1071.3	-502.7	1005.4	-0.227	0.787
Total Bird abundance	LMM	Gaussian	identity	-40.5	-22.1	26.3	-52.5	-0.199	0.995
Insectivore species richness	GLMM	Conway-Maxwell Poisson	log	873	906.8	-425.5	851	-0.121	0.409
Frugivore species richness	GLMM	Conway-Maxwell Poisson	log	850.4	890.4	-412.2	824.4	-0.238	0.683
Nectarivore species richness	GLMM	Conway-Maxwell Poisson	log	385.8	404.2	-186.9	373.8	-0.218	0.853

Omnivore species richness	GLMM	Conway-Maxwell Poisson	log	401.5	420	-194.8	389.5	-0.252	0.448
Insectivore density	LMM	Gaussian	identity	2.7	21.2	4.6	-9.3	-0.323	0.099
Frugivore density	LMM	Gaussian	identity	163.4	181.9	-75.7	151.4	-0.081	0.205
Nectarivore density	LMM	Gaussian	identity	209.6	228	-98.8	197.6	-0.312	0.234
Omnivore density	LMM	Gaussian	identity	234.5	253	-111.3	222.5	-0.277	0.370

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Table S3: List of all bird species in our study that entered analyses. We used the 14.1 version of the IOC world bird list as taxonomical authority (Gil et al., 2024), meaning we are displaying all species in this table in the same order as they are in the IOC master list, and we are using the newest IOC nomenclature for both English and scientific names. The code column refers to the species codes displayed in our multivariate analyses. Information on relevant functional traits was taken from sources described in methods section the main document of this paper.

English name	Scientific name	Code	Feeding guild
Northern Cassowary	*Casuarius unappendiculatus*	CasuUnap	Fr
Collared Brushturkey	*Talegalla jobiensis*	TaleJobi	Fr
New Guinea Scrubfowl	*Megapodius decollatus*	MegaDeco	In
Barred Owlet-nightjar	*Aegotheles bennettii*	AegoBenn	In
Moustached Treeswift	*Hemiprocne mystacea*	HemiMyst	In
Ivory-billed Coucal	*Centropus menbeki*	CentMenb	Om

Pheasant Coucal	*Centropus phasianinus*	CentPhas	In
Asian Koel	*Eudynamys scolopaceus*	EudyScol	Fr
Little Bronze Cuckoo	*Chrysococcyx minutillus*	ChryMinu	In
White-crowned Cuckoo	*Cacomantis leucolophus*	CacoLeuc	In
Chestnut-breasted Cuckoo	*Cacomantis castaneiventris*	CacoCast	In
Brush Cuckoo	*Cacomantis variolosus*	CacoVari	In
Amboyna Cuckoo-Dove	*Macropygia amboinensis*	MacrAmbo	Fr
Great Cuckoo-Dove	*Reinwardtoena reinwardti*	ReinRein	Fr
Stephan's Emerald Dove	*Chalcophaps stephani*	ChalStep	Fr
Cinnamon Ground Dove	*Gallicolumba rufigula*	GallRufi	Fr
Victoria Crowned Pigeon	*Goura victoria*	GourVict	Fr
Wompoo Fruit Dove	*Ptilinopus magnificus*	PtilMagn	Fr
Pink-spotted Fruit Dove	*Ptilinopus perlatus*	PtilPerl	Fr
Superb Fruit Dove	*Ptilinopus superbus*	PtilSupe	Fr
Coroneted Fruit Dove	*Ptilinopus coronulatus*	PtilCoro	Fr
Beautiful Fruit Dove	*Ptilinopus pulchellus*	PtilPulc	Fr
Yellow-bibbed Fruit Dove	*Ptilinopus solomonensis*	PtilSolo	Fr
Orange-bellied Fruit Dove	*Ptilinopus iozonus*	PtilIozo	Fr
Purple-tailed Imperial Pigeon	*Ducula rufigaster*	DucuRufi	Fr
Pinon's Imperial Pigeon	*Ducula pinon*	DucuPino	Fr
Zoe's Imperial Pigeon	*Ducula zoeae*	DucuZoea	Fr
Long-tailed Honey Buzzard	*Henicopernis longicauda*	HeniLong	In
Blyth's Hornbill	*Rhyticeros plicatus*	RhytPlic	Fr
Oriental Dollarbird	*Eurystomus orientalis*	EuryOrie	In
Hook-billed Kingfisher	*Melidora macrorrhina*	MeliMacr	In
Common Paradise Kingfisher	*Tanysiptera galatea*	TanyGala	In
Rufous-bellied Kookaburra	*Dacelo gaudichaud*	DaceGaud	Om
Yellow-billed Kingfisher	*Syma torotoro*	SymaToro	In
Papuan Dwarf Kingfisher	*Ceyx solitarius*	CeyxSoli	In
Azure Kingfisher	*Ceyx azureus*	CeyxAzur	In
Palm Cockatoo	*Probosciger aterrimus*	ProbAter	Fr
Sulphur-crested Cockatoo	*Cacatua galerita*	CacaGale	Fr

Buff-faced Pygmy Parrot	*Micropsitta pusio*	MicrPusi	Fr
Papuan King Parrot	*Alisterus chloropterus*	AlisChlo	Fr
Moluccan Eclectus	*Eclectus roratus*	EcleRora	Fr
Red-cheeked Parrot	*Geoffroyus geoffroyi*	GeofGeof	Fr
Blue-collared Parrot	*Geoffroyus simplex*	GeofSimp	Fr
Stella´s Lorikeet	*Charmosyna stellae*	CharStel	Ne
Black-capped Lory	*Lorius lory*	LoriLory	Ne
Dusky Lory	*Pseudeos fuscata*	PseuFusc	Fr
Coconut Lorikeet	*Trichoglossus haematodus*	TricHaem	Ne
Large Fig Parrot	*Psittaculirostris desmarestii*	PsitDesm	Fr
Edwards's Fig Parrot	*Psittaculirostris edwardsii*	PsitEdwa	Fr
Double-eyed Fig Parrot	*Cyclopsitta diophthalma*	CyclDiop	Fr
Papuan Pitta	*Erythropitta macklotii*	ErytMack	In
Hooded Pitta	*Pitta sordida*	PittSord	In
White-eared Catbird	*Ailuroedus buccoides*	AiluBucc	Fr
Long-billed Honeyeater	*Melilestes megarhynchus*	MeliMega	Om
Ruby-throated Myzomela	*Myzomela eques*	MyzoEque	Ne
Meyer's Friarbird	*Philemon meyeri*	PhilMeye	Fr
Helmeted Friarbird	*Philemon buceroides*	PhilBuce	Ne
Tawny-breasted Honeyeater	*Xanthotis flaviventer*	XantFlav	In
Mimic Honeyeater	*Microptilotis analogus*	MicrAnal	In
Rusty Mouse-warbler	*Origma murina*	OrigMuri	In
Pale-billed Scrubwren	*Aethomyias spilodera*	AethSpil	In
Yellow-bellied Gerygone	*Gerygone chrysogaster*	GeryChry	In
Green-backed Gerygone	*Gerygone chloronota*	GeryChlo	In
Fairy Gerygone	*Gerygone palpebrosa*	GeryPalp	In
Papuan Babbler	*Garritornis isidorei*	GarrIsid	In
Black Berrypecker	*Melanocharis nigra*	MelaNigr	Fr
Yellow-bellied Longbill	*Toxorhamphus novaeguineae*	ToxoNova	In
Spotted Jewel-babbler	*Ptilorrhoa leucosticta*	PtilLeuc	In
Blue Jewel-babbler	*Ptilorrhoa caerulescens*	PtilCaer	In
Yellow-breasted Boatbill	*Machaerirhynchus flaviventer*	MachFlav	In

Black-breasted Boatbill	*Machaerirhynchus nigripectus*	MachNigr	Fr
Lowland Peltops	*Peltops blainvillii*	PeltBlai	In
Black Butcherbird	*Melloria quoyi*	MellQuoy	Om
Hooded Butcherbird	*Cracticus cassicus*	CracCass	Om
Boyer's Cuckooshrike	*Coracina boyeri*	CoraBoye	Fr
White-bellied Cuckooshrike	*Coracina papuensis*	CoraPapu	In
Common Cicadabird	*Edolisoma tenuirostre*	EdolTenu	Fr
Black Cicadabird	*Edolisoma melas*	EdolMela	In
Black-browed Triller	*Lalage atrovirens*	LalaAtro	Fr
Piping Bellbird	*Ornorectes cristatus*	OrnoCris	In
Rusty Whistler	*Pachycephala hyperythra*	PachHype	In
Grey Whistler	*Pachycephala simplex*	PachSimp	In
Rusty Pitohui	*Pseudorectes ferrugineus*	PseuFerr	In
Arafura Shrikethrush	*Colluricincla megarhyncha*	CollMega	In
Northern Variable Pitohui	*Pitohui kirhocephalus*	PitoKirh	In
Hooded Pitohui	*Pitohui dichrous*	PitoDich	Fr
Brown Oriole	*Oriolus szalayi*	OrioSzal	Fr
Spangled Drongo	*Dicrurus bracteatus*	DicrBrac	In
Northern Fantail	*Rhipidura rufiventris*	RhipRufiv	In
Sooty Thicket Fantail	*Rhipidura threnothorax*	RhipThre	In
Black Thicket Fantail	*Rhipidura maculipectus*	RhipMacu	In
White-bellied Thicket Fantail	*Rhipidura leucothorax*	RhipLeuc	In
Rufous-backed Fantail	*Rhipidura rufidorsa*	RhipRufi	In
Drongo Fantail	*Chaetorhynchus papuensis*	ChaePapu	In
Spot-winged Monarch	*Symposiachrus guttula*	SympGutt	In
Hooded Monarch	*Symposiachrus manadensis*	SympMana	In
Black-winged Monarch	*Monarcha frater*	MonaFrat	In
Golden Monarch	*Carterornis chrysomela*	CartChry	In
Ochre-collared Monarch	*Arses insularis*	ArseInsu	In
Shining Flycatcher	*Myiagra alecto*	MyiaAlec	In
Grey Crow	*Corvus tristis*	CorvTris	Fr
Crinkle-collared Manucode	*Manucodia chalybatus*	ManuChal	Fr

Magnificent Riflebird	*Ptiloris magnificus*	PtilrMagn	Fr
King Bird-of-paradise	*Cicinnurus regius*	CiciRegi	Fr
Lesser Bird-of-paradise	*Paradisaea minor*	ParaMino	Fr
Black-sided Robin	*Poecilodryas hypoleuca*	PoecHypo	In
Olive Flyrobin	*Kempiella flavovirescens*	KempFlav	In
Metallic Starling	*Aplonis metallica*	AploMeta	Fr
Singing Starling	*Aplonis cantoroides*	AploCant	Fr
Yellow-faced Myna	*Mino dumontii*	MinoDumo	Fr
Golden Myna	*Mino anais*	MinoAnai	Fr
Red-capped Flowerpecker	*Dicaeum geelvinkianum*	DicaGeel	Fr
Black Sunbird	*Leptocoma aspasia*	LeptAspa	Ne
Olive-backed Sunbird	*Cinnyris jugularis*	CinnJugu	Ne
Streak-headed Mannikin	*Mayrimunia tristissima*	MayrTris	Fr

Table reference

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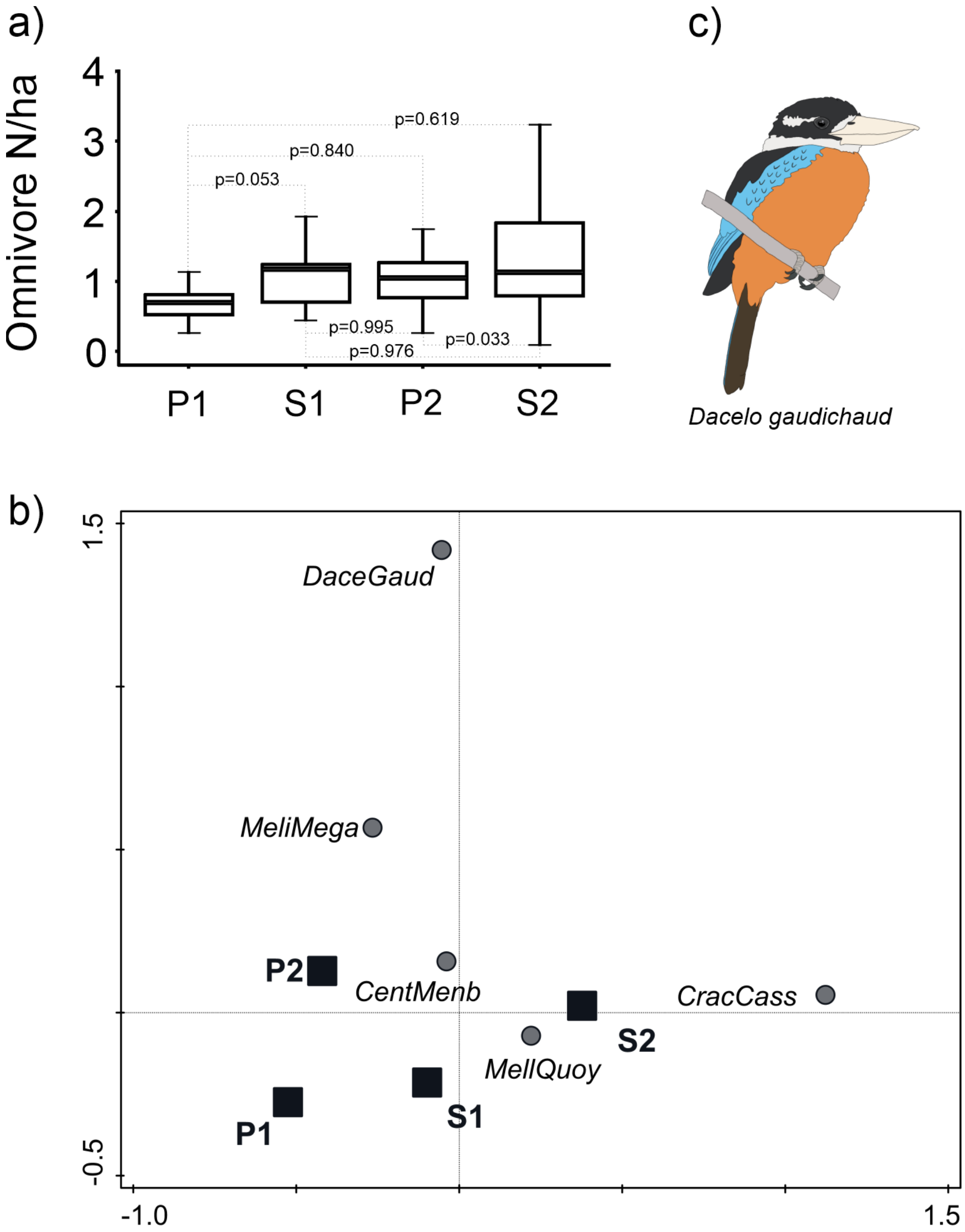
Figure S1: Diagrams describing the variation in omnivore communities among forest types. Post-hoc test results as pairwise comparisons between all types are displayed. Boxplots describe differences in **a)** omnivore density (abundance/ha) Displaying median, boxes = 25 – 75 quartiles, whiskers = non-outlier range**. b)** Results of unconstrained ordination analysis of omnivore community composition using the CANOCO 5 programme (Braak & Smilauer, 2012). Into this PCA ordination, forest type is projected as a supplementary variable (Šmilauer & Lepš, 2014). The first and second ordination axes explained together 84% of all variation, and supplementary variables account for 13 %. Species codes correspond to those listed in Supplementary material, Table S3. Explanation of forest type labels: P1 = continuous primary forest, S1 = secondary forest after subsistence agriculture, P2 = fragmented primary forest, S2 = secondary forest after clear-cutting. **c)** Illustration of a typical omnivore, the Rufous-Bellied Kookaburra (*Dacelo gaudichaud*), as drawn by Anonymized.

Figure references

Šmilauer, P. and J. Lepš. 2014. Multivariate Analysis of Ecological Data using CANOCO 5. Cambridge University Press.


a)
Omnivore N/ha
0
1
2
3
4
p=0.619
p=0.840
p=0.053
p=0.995
p=0.033
p=0.976
P1
S1
P2
S2
c)
Dacelo gaudichaud
b)
1.5
-0.5
-1.0
1.5
DaceGaud
MeliMega
P2
CentMenb
CracCass
S2
MellQuoy
S1
P1