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RESEARCH ARTICLE

Comparing impacts of fragmentation on bird functional and phylogenetic diversity in primary and secondary rainforests

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Abstract

1. Avian biodiversity in tropical rainforests is threatened by increasing intensity of anthropogenic disturbances. Secondary forest birds can maintain ecosystem services that are otherwise lost with disappearing primary forests. However, the stability of these services can be impeded by area effects reducing bird diversity.
2. We compared the effects of fragmentation on avian ecosystem functions in both primary and secondary forests. We performed point count surveys in both continuous rainforests, as well as isolated forest fragments in lowland Papua New Guinea. We combined taxonomic diversity with functional and phylogenetic indices and patterns of individual functional traits.
3. Bird taxonomic diversity was lower in secondary forests and decreased considerably due to fragmentation. In contrast, functional diversity was not affected by fragmentation but increased in secondary forests. Phylogenetic diversity increased in all human-modified forests.
4. Decreases in taxonomic diversity stemmed from the loss of forest-dependent birds. In contrast, decreases in functional and phylogenetic diversity were prevented by the introduction of open-habitat species. This was demonstrated by shifts in trait composition, as bird phenotypes reliant on forest continuity became less prevalent. Specifically, we recorded a proportional decrease in insectivory and ground foraging, and an increase in nectarivory and dispersal ability. Increased dispersal ability was also observed in secondary forests, where it was associated with shifts towards frugivory and canopy foraging. Increases in phylogenetic diversity were likely amplified by high phylogenetic dispersion of introduced habitat generalists.
5. *Policy implications*. We show that compensatory patterns of species introduction fail to account for the loss of ecosystem functions due to the decline of forest-dependent birds. As such, conservation policies should be targeted towards species that share traits associated with disturbance sensitivity, such as insectivory, ground foraging and low dispersal ability. This could prevent biodiversity

loss in poorly explored tropical landscapes in the early stages of large-scale deforestation.

KEYWORDS
bird diversity, environmental filtering, forest degradation, forest disturbance, forest-dependent birds, functional trait composition, New Guinea

1 | INTRODUCTION

Tropical rainforests are becoming increasingly fragmented due to deforestation, with formerly continuous woodlands replaced by forest patches interspersed by agricultural land (Turubanova et al., 2018). In extensively human-modified landscapes, a range of ecosystem functions associated with forest birds depends on these fragments, which act as habitats for surviving populations (Whelan et al., 2008). Rainforest birds are heavily involved in multitrophic interactions, for example, pollination, seed dispersal and herbivore control (Sodhi et al., 2008). As tropical forest fragmentation severely impacts bird assemblages, ecosystem services performed by birds may be jeopardized (Sodhi et al., 2008). Despite this, there remain gaps in our knowledge of fragmentation effects. In particular, it remains unclear whether fragmentation impacts avian ecosystem functions in the same way in secondary and primary rainforests. In this study, we investigate the connection between forest fragmentation, degradation and avian ecological roles in modified rainforest ecosystems.

Avian ecology can be studied through species functional traits, which determine how birds respond to their abiotic and biotic environment, and how they contribute to ecological processes and ecosystem functions (Schleuning et al., 2023). Functional diversity metrics capture the variability of trait values expressed by biotic assemblages, offering a valuable framework for assessing the integrity of ecosystem services (Suárez-Castro et al., 2020). However, some authors suggest that functional diversity should be complemented by phylogenetic diversity metrics, taking into account species´ evolutionary relationships, in order to predict how cascading extinctions could impact ecological networks (Srivastava et al., 2012).

Combining functional and phylogenetic metrics also allows researchers to discern community assembly mechanisms influencing long-term response to environmental effects (Mouchet et al., 2010). Phylogenetically conserved traits can be filtered by environmental conditions selecting species capable of survival at a given locale, promoting similarity in phenotypes and a decrease in functional and phylogenetic diversity (Dehling et al., 2014). Conversely, competition among similar phenotypes can limit co-occurrence of closely related species, increasing trait dispersion without loss of functional diversity (Grime, 1973). Discerning core patterns of community assembly can help guide conservation approaches. For example, identifying certain bird phenotypes that are filtered by fragmentation can help prioritize conservation of sensitive and evolutionarily distinct taxa, depending on the congruence between traits and phylogeny (Cadotte et al., 2019).

In our study, we use fragmentation to jointly represent the loss of forest on the landscape level, as well as the associated effects of habitat isolation and dispersal limitation stemming from landscape configuration (Fahrig, 2003). Forest fragmentation can function as an environmental filter by disproportionately impacting sedentary birds with poor dispersal ability, leading to the prevalence of similar phenotypes and a resulting loss of functional diversity (Mariano-Neto & Santos, 2023). Others have reported a strong role of competition among similar taxa in restricting species occurrence in forest fragments, causing the disappearance of birds that are functionally redundant (Ulrich et al., 2018). Lastly, forest fragmentation may act as a general threshold leading to species loss regardless of phenotypes (Solé et al., 2004).

Avian functional and phylogenetic diversity studies have not considered the potential impacts of fragmentation in tropical secondary forests (Suárez-Castro et al., 2020). This is a crucial knowledge gap, as multiple authors have pointed out that secondary forest birds may be sensitive to fragmentation. For example, Sayer et al. (2017) show that secondary forests can maintain comparable functional diversity to primary forests, but they also present evidence of decreased functional redundancy and a lower stability of avian ecosystem services. As secondary forest birds have already been impacted by a range of environmental stressors (Barlow et al., 2007), this could limit their resilience to fragmentation, amplifying its effects on functional and phylogenetic diversity (Mariano-Neto & Santos, 2023). Compounded effects of forest degradation and habitat isolation reportedly lead to decreases in bird taxonomic diversity in secondary forest fragments (Martin & Blackburn, 2014). The same effects could result in the filtering of forest-dependent birds and pronounced decreases in functional and phylogenetic diversity (Liu et al., 2024).

The effect of forest fragmentation on functional diversity is subject to regional and elevational variation (Santillán et al., 2019). Despite this, aforementioned studies examining this topic are mostly constrained to the neotropics, omitting other hyper-diverse rainforest landscapes. The island of New Guinea contains the planet's third-largest expanse of intact tropical rainforest, which hosts 7% of global biodiversity (Sekhran et al., 1995). Its bird species diversity is reportedly comparable to the Amazon or the Kongo basin (Jetz et al., 2012). In the second half of the 20th century, commercial logging was introduced to New Guinea (Fox, 2011), coupled with a large increase in human population. Rates of deforestation have increased significantly, especially in lowland regions (Shearman & Bryan, 2011), which have the highest avian functional diversity (Korejs, Koane, Jeppy, Jorge, Novotný, & Sam, 2025).

The landscape context of lowland New Guinea makes it possible to study functional diversity of bird assemblages in forests that are primary or secondary, and simultaneously continuous or fragmented. We standardized our functional diversity metrics for species richness to assess the effects of fragmentation on avian ecosystem functions (Kembel et al., 2010). In addition, to detect patterns of community assembly based on congruence of traits and phylogeny, we analysed corresponding phylogenetic diversity metrics (Cadotte et al., 2019). Furthermore, we complemented these analyses by examining trends of specific bird functional traits. This way, we could identify which bird phenotypes are affected by forest fragmentation, and which associated ecosystem services are likely to be impeded in fragmented forests.

According to previous studies on primary forest fragmentation, we predicted two main mechanisms driving bird community response to fragmentation (Figure 1). (a) *Environmental filtering*: Fragmentation has a strong effect on phenotypes that are associated with sensitivity to dispersal limitation (Weeks et al., 2023). This will likely lead to environmental filtering by fragmentation, resulting in an overall decrease of functional and phylogenetic diversity, and decreased dispersion of functional traits. (b) *Functional redundancy*: Limiting similarity (Ulrich et al., 2018) or community-wide thresholds of destruction (Solé et al., 2004) could lead to loss of functionally redundant species without loss of variation in functional traits.

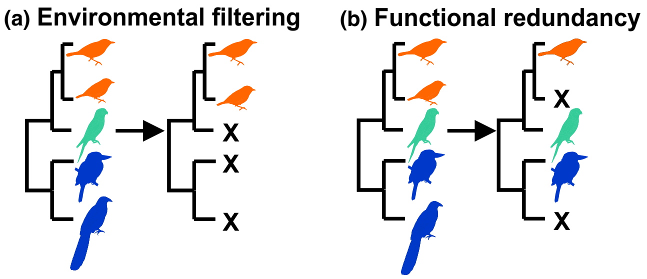

FIGURE 1 Schematic representation of community assembly patterns predicted in this study. Colours represent arbitrary functional categories of species, with phylogenetic relationships displayed. The resulting variation in functional composition of assemblages then roughly corresponds to expected effects on functional diversity. Outlines are based on species illustrations from Billerman et al. (2022).

Functional redundancy of secondary forest bird assemblages is limited by low ecosystem stability (Sayer et al., 2017). As such, *we predict that the compounded effects of fragmentation and forest degradation will selectively filter out forest-dependent birds* (Liu et al., 2024). We predict that the filtered forest-dependent phenotypes will include specialized insectivores (Sekercioglu, 2002), birds inhabiting lower strata of the rainforest (Powell et al., 2015) and birds with low dispersal ability (Matuoka, Benchimol, & Morante-Filho, 2020). This will result in loss of functional and phylogenetic diversity and a corresponding decrease in the provision of ecosystem functions.

2 | METHODS

2.1 | Field surveys

The data collection took place from January 2010 to January 2012 within the Madang province of lowland Papua New Guinea (Figure 2a). The relevant approvals and permits for field work in Papua New Guinea were obtained: Bird sampling was conducted under the animal use permits 1315-20424/2012-30 and research permit 11800056119. We performed surveys in: (1) a primary forest site placed within a >100 km^2 rainforest reserve of Wanang Conservation Area, (2) secondary forest regrown after slash-and-burn agriculture, located within the same continuous forest landscape, (3) mutually isolated primary forest remnants, located in a forest landscape that was fragmented by mass deforestation approximately 50 years prior (Sam et al., 2014) and (4) fragments of

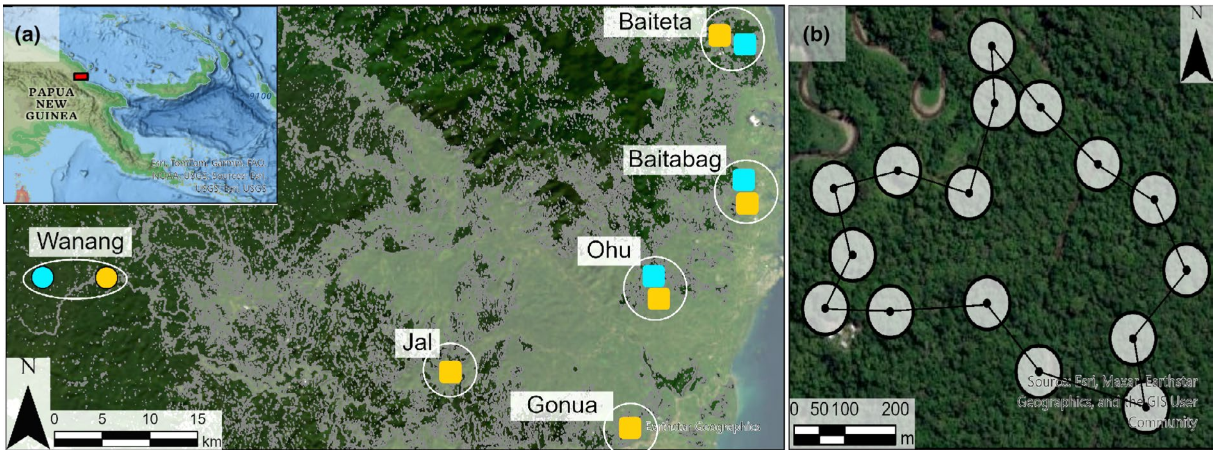

FIGURE 2 Study sites near six villages in the Madang Province of Papua New Guinea. Markers: Blue = primary forests, orange = secondary forests, circles = continuous forest and squares = fragmented forests. Grey overlay represents the extent of primary forest loss, as per Turubanova et al. (2018) (a). Example of a field survey design with 16 points each with a 50-m point count radius. All maps created using the Basemap service of Arcgis Pro Desktop (ESRI, 2024) (b).

regrown secondary forests within the same landscape that are isolated by gardens, roads and deforested village settlements. A list of study sites, coordinates and specific survey periods is in Supporting Informatio Table S1.

To confirm that primary and secondary forests differed in their vegetation structure, we performed a complementary vegetation survey concurrently with bird surveys, and compared varying habitat characteristics between primary and secondary forests. The methodology and results of this survey are available at the end of Supporting Information, in Tables S8, S9, and in Figure S2.

Bird assemblages were surveyed using point counts. We performed nine point counts at 16 points per site, semi-regularly spaced along a circular transect, as illustrated in Figure 2b. The points were arranged to represent the full range of habitat heterogeneity within each studied landscape (see Sam et al., 2014). When located in forest fragments, all point counts were performed more than 250m from the forest edge. Within 50m of each point, we noted down all birds based on auditory and/or visual identification. We quantified how far individual birds were located relative to each surveyed point with a laser rangefinder. Each bird was assigned a distance category (0–10, 11–20, 21–30, 31–40 and 41–50m). We started censuses 15min before sunrise (ca. 5:45AM) at a randomly selected point and continued counts in a randomly selected direction. We counted birds for 15min at each point, so all 16 points were surveyed before 11:00AM. Each transect was surveyed nine times, resulting in 36h of observation along each transect. We used the IOC world bird list version 14.1 as naming authority for bird species in our study (Gill et al., 2024).

We used the average abundance of every bird species per point as a baseline for all our analyses. This average was calculated over the nine visits (= replications in time). To account for imperfect detection, we performed distance sampling in the package *Distance* (Marshall et al., 2024) in R 4.4.1 (R Project & Development Core Team, 2024). The final version of our core dataset was a counting point by species abundance matrix. We calculated the Shannon diversity index to represent the taxonomic diversity of birds on each counting point (Shannon, 1948).

2.2 | Functional traits

Recorded species were classified into four general guilds: insectivores (primarily consuming invertebrates), frugivores (fruit and seed consumers), omnivores (no dominant food source) and nectarivores, following evidence by Sam et al. (2017), together with information from Beehler and Pratt (2016). We classified each bird species into foraging strata: canopy, midstory-to-understorey and ground-foraging species, according to evidence from ground-to-canopy mist-netting surveys (Chmel et al., 2016), supplemented by Billerman et al. (2022). We used five continuous traits describing the morphology and dispersal ability of each species: body weight, beak length, tarsus length, hand-wing index (HWI, defined as length from the tip of the first secondary feather to the tip of the longest primary, divided by total wing length) and geographical range, based on the AVONET supplementary dataset (Tobias et al., 2022). We constructed a trait dendrogram based on functional distances between species calculated from trait values, determined by the Gower dissimilarity measure using the *mfd* package (Magneville et al., 2022). To see the full list of bird species in our study, as well as their trait values, see Table S2.

2.3 | Phylogeny and trait signals

To construct a phylogenetic representation of the bird community in our study site, we used the global phylogeny of birds as introduced by Jetz et al. (2012). We took a distribution of 10,000 trees from this dataset and performed Bayesian reconstruction of the maximum clade credibility tree using mean node heights in TreeAnnonator v1.10.4 of the BEAST program (Drummond et al., 2012). This tree was then used for all subsequent analyses.

We used the package *picante* (Kembel et al., 2010) to compute phylogenetic signals for body weight, beak length, tarsus length, HWI and geographical range. We used the package *geiger* (Harmon et al., 2023) to estimate the presence of phylogenetic signal for categorical traits (feeding guild and foraging strategy).

2.4 | Functional and phylogenetic diversity

As our main indices of functional and phylogenetic diversity, we used mean pairwise functional distance (MFD) and mean pairwise phylogenetic distance (MPD), as introduced by Kembel et al. (2010). These methodologically analogous indices allow us to include abundance information in our diversity metrics. They are based on a species distance matrix, estimated, respectively, as Gower measure of dissimilarity based on species trait data (Gower, 1971), or a cophenetic distance matrix using our phylogenetic tree. This distance matrix is then combined with our abundance dataset to calculate values of each respective index. Indices of functional and phylogenetic diversity are generally highly correlated with the number of species in an assemblage (Mouchet et al., 2010). To account for this correlation, we generated 999 null communities with the same species number of species by shuffling taxa labels in a species by point matrix. We then calculated standardized effect sizes (Ses) for MFD and MPD by calculating the difference between the observed value and the mean value of null communities, dividing the obtained value by the standard deviation of null communities. We used the *ape* (Paradis & Schliep, 2018) and *picante* packages to calculate our indices and null models.

By performing null model standardization, we can determine whether species distances in functional or phylogenetic space were lower or greater than random expectations. This allows us to assess which processes influenced bird community assembly and their functional trait composition. For example, filtering of certain phenotypes can reduce pairwise functional distance as species will likely be more clustered in functional space, while an increase in functional distance will likely be associated with loss of functionally redundant species due to limiting similarity (Dehling et al., 2014).

We used the species abundance dataset to calculate the community weighted means for each continuous trait, that is, body weight, beak length, tarsus length, HWI, and geographical range for separate bird assemblages (Šmilauer & Lepš, 2014). Categorical trait values for different bird assemblages were based on the proportion of total abundances on counting points, corresponding to each guild (insectivore, frugivore, nectarivore and omnivore) and to each foraging strategy (canopy, understorey-midstory and ground) for each counting point.

2.5 | Statistical methods

For our primary analytical approach, we employed mixed-effects linear and generalized linear models (Table S3), implemented via the *lme4* (Bates et al., 2025) and *glmmTMB* (Brooks et al., 2017) packages. We created two categorical variables describing the forest type (primary vs secondary) and the connectivity of the forest (continuous vs fragmented). We used these variables as fixed effects, and we also tested the effect of their interaction. By using them as fixed effects, we can assess whether functional diversity differed between primary and secondary forests, and between continuous and fragmented forests. The interaction term allows us to assess whether the general effect of fragmentation changed between primary and secondary forests. Following this, we used the sampling site as a random effect.

Linear mixed-effects models were employed to analyse Shannon diversity index, Ses MFD and Ses MPD. We then examined how continuous trait values (log-standardized weighted means of body weight, beak length, tarsus length, HWI and mean geographical range) were affected by forest type and connectivity. To analyse feeding guild composition, we created a model comparing the relative abundance of each feeding guild within bird assemblages, adding guild as a fixed effect to a glmm using the beta distribution with 'logit' link function in *glmmTMB*, as appropriate for analysing proportions (Hardin & Hilbe, 2007). The interaction between feeding guild and forest type, and feeding guild and forest connectivity, then allowed us to determine which variables shape the variation in guild composition. The same approach was used for each foraging strategy. We used the *emmeans* package (Lenth et al., 2025) to calculate pairwise post hoc tests determining which feeding guilds/foraging strategies showed the strongest response to fixed effect variables. We used the *ggplot2* package (Wickham et al., 2024) to visualize our results. We supplemented our information on bird taxonomic diversity by performing detrended correspondence analysis of bird species abundances (Hill & Gauch, 1980), projecting forest type and forest connectivity as supplementary variables in ordination space using the Canoco 5 program (Šmilauer & Lepš, 2014).

3 | RESULTS

3.1 | Bird diversity

We recorded a total of 31,177 bird individuals corresponding to 113 species. Taxonomic diversity decreased significantly in secondary forests ($F = 10.940$, $p = 0.027$), and also decreased due to fragmentation ($F = 8.926$, $p = 0.025$; Table S4; Figure 3a). Our supplementary compositional analysis has shown that some bird species increased their abundance in secondary and primary fragmented forests (Figure S1). Each of the investigated functional traits in our study had a significant phylogenetic signal (Table S5). In contrast to taxonomic metrics, functional diversity represented by Ses MFD increased in secondary forests ($F = 87.176$, $p < 0.001$), but it was not affected by fragmentation (Figure 3b). Mean values of Ses MFD were below −2 in primary forests. Phylogenetic diversity was overall higher in fragmented forests ($F = 4.512$, $p = 0.035$). In addition, there was an interactive effect of forest type and

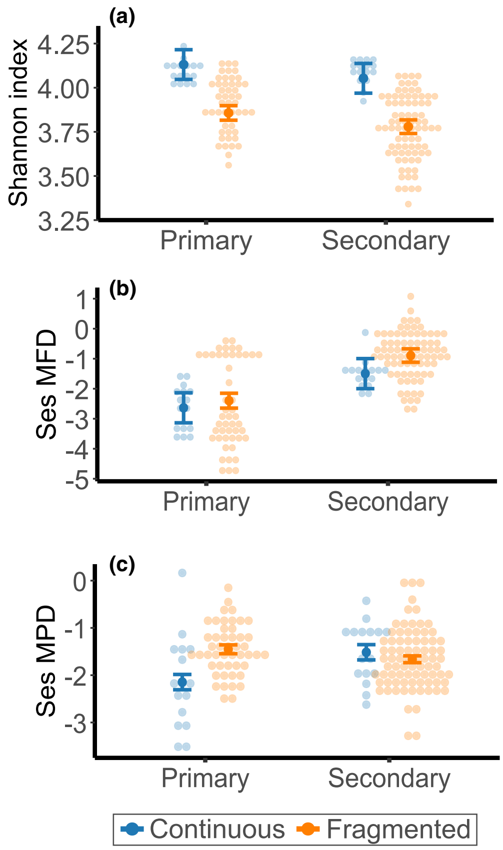

FIGURE 3 Diagrams summarizing the variability in bird taxonomic diversity represented by Shannon diversity index (a), Ses of mean (pairwise) functional distance (MFD) (b) and Ses of mean phylogenetic distance (MPD) (c). Continuous/fragmented refers to the connectivity of the forest landscape. Primary/secondary refers to forest type. Displayed are estimated marginal means extracted from respective models, with whiskers as SE of the means, and projected data points describing individual assemblages detected in point counts. Model summaries are in Table S4.

connectivity that showed an increase of Ses MPD in continuous secondary forest ($F = 10.677$, $p = 0.001$; Figure 3c). Mean values of Ses MPD were below −2 in continuous primary forests. Detailed model summaries are in Tables S3 and S4.

3.2 | Functional trait composition

While there was no decrease in functional or phylogenetic diversity, we found evidence that both forest fragmentation and degradation predominantly affected functional characteristics associated with forest-dependent species. For example, we found that feeding guild composition was impacted both by forest type (effect of Type*Guild on species richness: $\chi^2 = 63.355$, $p < 0.001$) and by forest connectivity (effect of Connectivity*Guild: $\chi^2 = 100.346$, $p < 0.001$). Insectivore proportion decreased from primary to secondary forests, and from continuous to fragmented forests (Figure 4a). In contrast, the proportion of nectarivores increased significantly in response to fragmentation in both primary and secondary forests (Figure 4a). The proportion of frugivores was not affected by fragmentation, but it was overall higher in secondary forests (Figure 4a).

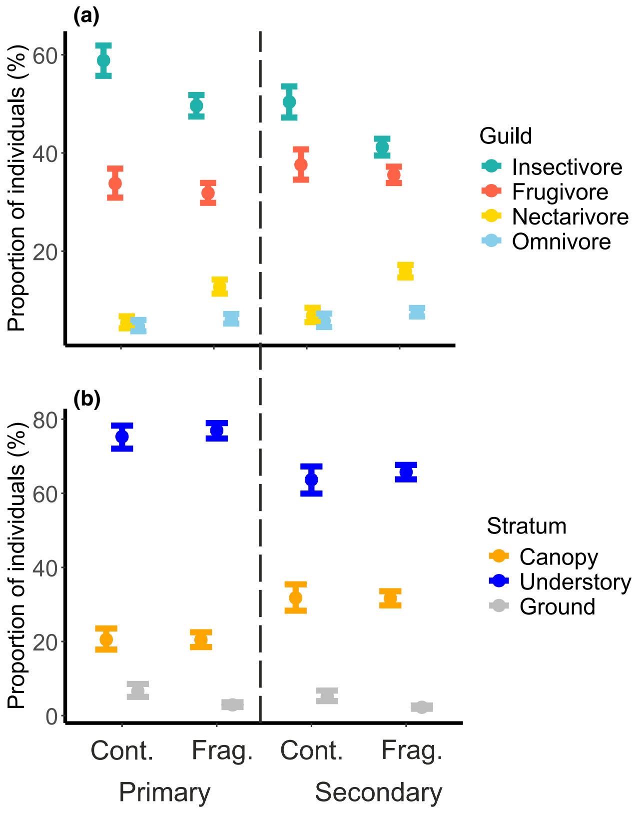

FIGURE 4 Proportion of individual guilds in species abundances (a) and proportion of foraging strategy of birds (b) in continuous and fragmented primary and secondary forests. Estimated marginal means were extracted from respective models (detailed in Table S6), with 95% CI of the means displayed as bars. Model summaries and post hoc test results are in Table S6.

Forest type ($\chi^2 = 130.497$, $p < 0.001$) and forest connectivity ($\chi^2 = 31.798$, $p < 0.001$) also significantly affected the foraging strategy of bird communities, bringing further evidence of loss of forest-dependent phenotypes in response to disturbances. Specifically, the proportion of understorey and midstory foraging strategies decreased in secondary forests, although they were not affected by fragmentation. Conversely, canopy foraging strategy was more prevalent in secondary forests, but independent of fragmentation (Figure 4b). Ground foraging was significantly impacted by fragmentation, but not by forest type (Figure 4b). For details on guild and foraging strategy analyses and associated post hoc tests, see Table S6.

Bird beak length increased in secondary forests ($F = 16.920$, $p < 0.001$), but was highest in continuous secondary forest, as shown in the significant effect of interaction with forest and landscape ($F = 51.301$, $p < 0.001$; Figure 5a). HWI increased in response to fragmentation ($F = 12.377$, $p < 0.001$), and was overall higher in secondary forests ($F = 25.104$, $p < 0.001$; Figure 5b), showing that birds with low dispersal ability were negatively affected by

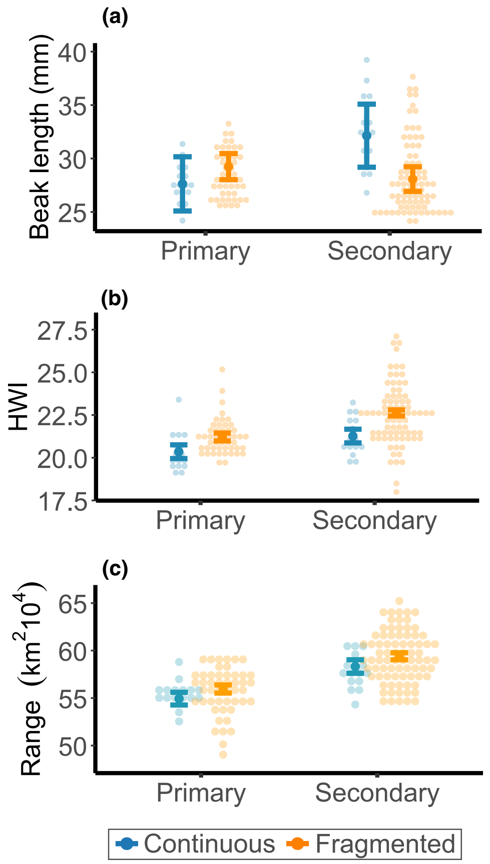

FIGURE 5 Mean beak length (a), mean hand–wing index (HWI) (b) and mean geographical range (in tens of thousands km^2) (c) in assemblages of birds in continuous and fragmented primary and secondary forests. Displayed are estimated marginal means extracted from respective models, with whiskers as SE of the means, and projected data points describing individual assemblages detected in point counts. Model summaries are in Table S7.

disturbances. Furthermore, bird geographical ranges were also greater in secondary than in primary forests ($F=50.166$, $p<0.001$; Figure 5c). Neither body weight nor tarsus length were affected by forest type or forest landscape connectivity. See Table S7 for model summaries.

4 | DISCUSSION

4.1 | Bird diversity response to fragmentation

We found no evidence of changes to functional diversity due to fragmentation. Prevalence of habitat filtering or functional redundancy tends to decrease or increase dispersion of species in functional space, respectively (Mouchet et al., 2010), yet we found neither pattern in pairwise functional distance (Ses MFD). Despite this, we identified directional changes to trait composition. For example, insectivory and ground foraging were strongly negatively affected by fragmentation, corroborating previous findings on species richness (Sam et al., 2014). On the other hand, we saw a significantly higher proportion of nectarivory, as well as increased hand–wing index in fragmented forests, corresponding to higher dispersal ability (Tobias et al., 2022). We also confirmed that some species showed a clear preference for fragmented forests as habitats in our supplementary analysis. This leads us to conclude that while fragmentation acted as a filter of forest-dependent birds, effects on functional diversity were compensated by the introduction of open-habitat species.

Compensatory patterns of species introduction stem from the relatively high proportion of habitat generalists in partially deforested landscapes (Morante-Filho et al., 2018). They tend to be functionally distinct from more forest-dependent birds, exhibiting in particular higher dispersal ability, which results in increased variation of functional traits, impacting functional and phylogenetic diversity (Matuoka, Benchimol, & Morante-Filho, 2020). The degree to which functional compensation mediates functional diversity varies, as it can still be outweighed by loss of range-sensitive birds (Jones et al., 2021). However, the masking of negative effects of fragmentation on overall functional diversity may nevertheless jeopardize our ability to assess the intactness of forest-dependent ecosystem functions (Matuoka, Benchimol, de Almeida-Rocha, et al., 2020).

Phylogenetic diversity increased in secondary forests both fragmented and continuous, showing a similar response as functional diversity. Yet, it also increased in fragmented primary forests, while functional diversity did not. Even in assemblages where functional traits are conserved within the phylogeny, there remains variation between functional and phylogenetic metrics that confirms their complementary function (Cadotte et al., 2019). Similar to our study, Morante-Filho et al. (2018) report that phylogenetic diversity can be enriched by the introduction of open-habitat birds. In addition, the species pool of open-habitat birds in more fragmented landscapes tends to be more phylogenetically dispersed (Prescott et al., 2016). As a result, phylogenetic metrics may show a more pronounced response to species introduction. Therefore, phylogenetic diversity should be treated as an imperfect proxy for functional diversity (Chapman et al., 2018).

4.2 | Variation in trait composition

Our results on trait variation show that particular ecosystem services tied to forest-dependent birds were negatively affected by fragmentation. For example, the observed decrease in insectivore phenotypes may reduce herbivore control and lead to a greater influx of disease-carrying insects (Sekercioglu, 2002). These issues could be compounded by the introduction of invasive species, as they may lack natural predators in fragmented forests (Kenis et al., 2009). Ground-foraging birds may only represent up to 10% of abundances in our study, but they nevertheless perform important ecosystem functions, ranging from the dispersal of herb layer seeds to food web interactions with litter invertebrates (Whelan et al., 2008).

On the other hand, other functional traits, such as nectarivory and frugivory, were well represented in fragmented forests. A previous study from this region shows that nectarivores respond positively to fragmentation in their abundances, likely resulting in increased provision of pollination (Korejs, Koane, Jeppy, Sam, & Sam, 2025). Despite frugivory remaining widespread, some larger species were likely negatively affected, as evidenced by our results on beak length, which decreased in secondary forests in response to fragmentation. In addition, seed dispersal may still be impeded by frugivore turnover eroding the mutualistic relationships between birds and feeder plants (Siegel et al., 2024).

Secondary forests showed increased avian functional diversity compared to primary forests. Moreover, fragmented secondary forests had overall the lowest proportions of insectivores and ground species, together with the highest values of dispersal traits, such as HWI and geographical range. This suggests that the effect of functional compensation increased additively with changes to vegetation structure and forest connectivity (Matuoka, Benchimol, & Morante-Filho, 2020). While functional diversity may be increased by open-habitat species, the stability of ecosystem function was likely endangered by forest degradation. Observed changes to foraging strategy could already translate to loss of niche space for understorey and midstory species (Sekercioglu, 2002). As the bulk of insectivore diversity can be found in these intermediate forest strata (Chmel et al., 2016), this could weaken the provision of ecosystem services tied to this functional group. Moreover, increases of pairwise functional distance (Ses MFD) point towards the loss of functionally redundant species and lower ecosystem stability in secondary forests (Sayer et al., 2017).

4.3 | Study limitations

Functional diversity studies tend to be constrained by their selection of functional traits. Especially among tropical birds in poorly explored landscapes, there is little information on species life history, apart from rare experimental studies (Chmel et al., 2016; Sam et al., 2017). However, our trait dataset was based on listed empirical data and joined together with morphological traits sourced from measurements of bird individuals caught in mainland New Guinea (Tobias et al., 2022). This makes our functional trait selection as robust as currently achievable.

4.4 | Conservation implications

Our study demonstrates that an effective method for assessing ecosystem service integrity is to complement functional diversity variation with information on individual trait patterns (Korejs, Koane, Jeppy, Jorge, Novotný, & Sam, 2025). This way we avoid overlooking effects of functional compensation due to only evaluating functional diversity for the whole assemblage. In addition, we demonstrate that the loss of taxonomic diversity and ecosystem function integrity is not compensated by the presence of open-area species, underscoring the critical need to conserve forest-dependent birds. There is a large number of conservation strategies that successfully protect threatened rainforest birds with declining populations (Cazalis et al., 2020). However, in data-deficient regions like New Guinea, alternative measures of species vulnerability may be particularly valuable, as limited knowledge of avian population status can hinder the establishment of effective conservation priorities (Sodhi et al., 2008).

We specify functional characteristics that are associated with disturbance sensitivity, which are in agreement with other pioneer studies (Weeks et al., 2023). There exist ongoing policies targeting birds with these ecological traits: For example, understorey insectivores as listed by Powell et al. (2015); ground-dwelling birds (Clout & Craig, 1995) or birds with geographically restricted ranges (Donald et al., 2019). These could be used as templates for protecting targeted species in regions where conservationists lack accurate data on population status. Doing so can help guide pre-emptive conservation in developing countries such as Papua New Guinea, which are at relatively early stages of widespread forest loss (Shearman & Bryan, 2011). This way, species-level conservation may help maintain ecosystem functions, as well as crucial components of avian biodiversity that are most threatened by forest fragmentation and degradation.

AUTHOR CONTRIBUTIONS

Vojtech Novotny, Katerina Sam and Krystof Korejs conceived the study and designed the methodology. Bonny Koane, Samuel Jeppy, Legi Sam and Katerina Sam have performed investigation and data curation. Formal analysis, validation, and visualization were performed by Krystof Korejs and Leonardo Ré Jorge. Krystof Korejs wrote the original draft. Review and editing were performed by Krystof Korejs, Leonardo Ré Jorge, Vojtech Novotny and Katerina Sam. Funding was acquired by Legi Sam, Vojtech Novotny and Katerina Sam. The project was supervised by Katerina Sam. All authors read and approved the final draft of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Figshare digital repository, https://doi.org/10.6084/m9.figshare.27993584 (Korejs, Koane, Jeppy, Sam, Novotný, & Sam, 2025).

STATEMENT ON INCLUSION

This research has been fostered by the cooperation of researchers native to the study region, expatriate authors who visited the study region and local stakeholders. The funding of this project has contributed to the well-being of the indigenous population by employing local services and assistance, and fostering cooperation with native scientists. The paper includes contributions of local researchers, whose works were cited when possible.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Names, locations and geographical 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. All study sites have a humid climate with a mild dry season from July to September; average annual rainfall is 3600 mm (McAlpine et al. 1983).

Table S2: 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 (Gill 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 IOC nomenclature for both English and scientific names. Information on relevant functional traits was taken from sources described in the main document of this paper.

Table S3: 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 and package *Dharma* was used for model diagnostics and spatial autocorrelation tests (Hartig, 2018). Factor levels with effects that were not significant based on *F*-tests for LMMs or chi-square tests for GLMMS were dropped from the final models.

Table S4: Results of bird diversity and assemblage structure models, represented by overall significance levels of factors. Factor levels/interactions with effects that were not significant based on *F*-tests for LMMs or chi-square tests for GLMMS are not reported.

Table S5: Phylogenetic signals of different bird traits in our dataset, calculated using the picante package (Kembel et al., 2010). A significant *p*-value means that a trait had a significant phylogenetic signal. Our results for discrete traits were based comparisons of two fitted macroevolutionary models using discrete traits in the *geiger* package (Harmon et al., 2015). A null model was fitted that assumed no relationship between species phylogeny and trait values, while a second model was fitted based on our maximum clade credibility tree. A log-likelihood test then determined whether model fit was significantly better for our phylogeny than for the null model, and simultaneously whether there was a phylogenetic signal for a given trait (i.e. whether there is a high likelihood that related species exhibit similar trait values).

Table S6: Results of trait-level community composition models regarding categorical traits, represented by overall significance levels of factors, and by pairwise post hoc tests using the emmeans function. Post hoc tests are displayed for individual guilds and strata for each combination of forest type (primary: P, secondary: S), and forest landscape connectivity (continuous: C, fragmented: F).

Table S7: Results of trait-level community composition models regarding continuous traits, represented by overall significance levels of factors.

Table S8: Model parameters for each of our linear mixed-effects (LMM)/generalized linear mixed-effect models analysing vegetation characteristics (GLMM).

Table S9: Results of vegetation structure models, represented by overall significance levels of factors, which were Forest type (Primary/Secondary) and forest landscape connectivity (Continuous/Fragmented).

Figure S1: DCA analysis (Hill & Gauch, 1980) of bird community composition performed in the Canoco 5 program (Šmilaurer & Lepš, 2014). Species occurrences at points (0/1) were used as response variables. Forest type (primary/secondary) and forest landscape connectivity (continuous/fragmented) are projected as supplementary variables. First and second axis explained together 23.62% of variation. Supplementary variables accounted for 15.68% of all variation.

Figure S2: Boxplot diagrams created by the *ggplot2* package (Wickham et al., 2016) describing the differences in vegetation characteristics.

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