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Conservation of birds in fragmented landscapes requires protected areas

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For successful conservation of biodiversity, it is vital to know whether protected areas in increasingly fragmented landscapes effectively safeguard species. However, how large habitat fragments must be, and what level of protection is required to sustain species, remains poorly known. We compiled a global dataset on almost 2000 bird species in 741 forest fragments varying in size and protection status, and show that protection is associated with higher bird occurrence, especially for threatened species. Protection becomes increasingly effective with increasing size of forest fragments. For forest fragments >50 ha our results show that strict protection (International Union for Conservation of Nature [IUCN] categories I–IV) is strongly associated with higher bird occurrence, whereas fragments had to be at least 175 ha for moderate protection (IUCN categories V and VI) to have a positive effect. This meta-analysis quantifies the importance of fragment size, protection status, and their interaction for the conservation of bird species communities, and stresses that protection should not be limited to large pristine areas.

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Home to ~80% of the world's terrestrial biodiversity (World Bank 2004), forest systems are increasingly under threat from a wide range of anthropogenic pressures (Newbold *et al.* 2015). Between 2000 and 2012, 2.3 million km² of forest was lost globally (Hansen *et al.* 2013), and up to 70% of the remaining forest area worldwide is estimated to be within only a single kilometer of forest edges (Haddad *et al.* 2015). Habitat loss and fragmentation are major

drivers of biodiversity loss, with disproportionate species declines in small, isolated fragments (Lees and Peres 2006; Bregman *et al.* 2014; Keinath *et al.* 2017). Protected areas (PAs) are increasingly being implemented as a tool to conserve species and maintain associated ecosystem services. As a result, PA coverage has almost doubled over the past 30 years, from ~8.2% of terrestrial land surfaces in 1990 to 15% in 2020 (UNEP-WCMC and IUCN 2020), although coverage still falls short of the Convention on Biological Diversity's Aichi Biodiversity Target of 17%. However, to what extent PAs are an effective conservation measure in landscapes where natural habitat types have become fragmented and are under growing pressure of human activities (hereafter “fragmented landscapes”) remains unclear.

Several global studies on PA performance have demonstrated the importance of protection status of relatively large and pristine areas for conservation (Geldmann *et al.* 2013; Coetzee *et al.* 2014; Barnes *et al.* 2016; Gray *et al.* 2016). The PAs analyzed in these studies do not reflect the PA characteristics of the many small and isolated PAs embedded within fragmented landscapes. At the same time, PAs across the world are facing increasing isolation, encroachment, and degradation (DeFries *et al.* 2005; Laurance *et al.* 2012). This is a cause for concern given that species richness and population sizes tend to decline with reductions in forest fragment size and increasing fragment isolation (Lees and Peres 2006; Bregman *et al.* 2014; Keinath *et al.* 2017).

PAs are invested with different degrees of protection, which might affect their ability to conserve species in fragmented landscapes. The International Union for Conservation of Nature (IUCN) recognizes six categories of PAs (designated as categories I–VI) that can be grouped into two broad protection

In a nutshell:

- We analyzed the combined effects of size and protection status of isolated forest fragments on bird species occurrence in human-modified landscapes
- Declines in species occurrence across all feeding guilds with decreasing fragment size underscore the importance of large intact forests for conserving avian diversity
- Positive associations between protection and species occurrence suggest that protected areas are effective for maintaining bird species in fragments >50 ha
- Conservation of threatened bird species in fragmented landscapes should preferably focus on strict protection of large forest fragments

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types (WebTable 1). “Strict protection” areas are managed for ecosystem and species conservation (categories I–IV), while “moderate protection” areas encompass culturally modified landscapes (category V) and areas managed primarily for the sustainable use of natural resources (category VI) (Locke and Dearden 2005; Dudley 2008). Much of the recent increase in PA cover consists of PAs under moderate protection (WebFigure 1), which currently account for ~42% of the global area dedicated to PAs with a designated IUCN category (UNEP-WCMC and IUCN 2020). Hence, understanding whether the effectiveness of species conservation in fragmented landscapes differs among protection types and how large fragments should be to minimize species loss and maintain ecosystem functioning is of great importance.

Our primary objective was to assess the interplay between fragment size and protection status in determining species occurrence. We test the hypothesis that protection of forest fragments mitigates declines in bird species occurrence in response to decreasing fragment size (WebPanel 1). We focused on birds because they are highly represented in fragmentation studies and provide important ecosystem services, such as control of phytophagous insects, plant pollination, and seed dispersal (Figure 1). Through a meta-analytical approach, we examined how fragment size and protection status are associated with the probability of occurrence of bird species within 46 fragmented landscapes worldwide. We systematically searched existing literature and compiled a global dataset that draws on 61,716 occurrence records of 1990 bird species across 741 mature forest and savanna woodland fragments ranging in size from ~0.1 ha to over 10,000 ha (WebFigure 2; WebTable 2). Most of these fragments form sharp boundaries with areas of anthropogenic land use.

Methods

Study selection

For our meta-analysis, we followed the procedures described in Moher *et al.* (2009). We searched the Web of Science Core Collection (WoSCC) and Scopus databases (cut-off date: 1 Jul 2020) using the search strings and selection criteria detailed in WebPanel 2. Further records were obtained from the BIOFRAG (Pfeifer *et al.* 2014), PREDICTS (Hudson *et al.*

2014), ATLANTIC BIRDS (Hasui *et al.* 2018), and FragSAD (Chase *et al.* 2019) databases. Due to strict criteria (WebPanel 2), we were able to select a unique set of high-quality data from 44 publications each with a comparable, well-documented sampling design to perform our quantitative analysis (WebPanel 3). A PRISMA flow diagram depicts how articles were selected for inclusion in the meta-analysis (WebFigure 3).

Protection status and matrix type

We established whether fragments fell within designated PAs (fragment size does not necessarily equal PA size) at the time of bird surveys using the World Database on Protected Areas (WDPA) (UNEP-WCMC and IUCN 2020), and classified PA status as strict protection ($n = 154$ fragments), moderate protection ($n = 90$), or no protection ($n = 497$) following the definitions given above and in WebTable 1. In cases where the IUCN category was not reported in the WDPA ($n = 96$), classification was based on other available information (eg management plans, consulting the relevant author).

The retention of species within forest fragments is affected by various factors acting at the landscape scale, notably surrounding land use (matrix) and degree of fragment isolation (Ewers and Didham 2006; Prevedello and Vieira 2010); we therefore also categorized the matrix based on regional and global land-cover maps, along with information obtained from the original publications (WebPanel 2). Due to the number of studies and variability in the applied isolation metrics, we did not consider degree of fragment isolation in our analysis.

Functional traits

We expected bird species to vary in their sensitivity to fragment size depending on their feeding guild (WebPanel 1), and previous studies have shown that several other bird traits predict species' sensitivity to disturbance (Ewers and Didham 2006; Bregman *et al.* 2014). We therefore included trait data on dietary guild, body mass, hand-wing index (HWI, a proxy of dispersal capacity), migratory status, and forest dependence in our analysis (WebPanel 2). Prior to collecting trait data, all taxonomic names were matched to the IUCN Red List of Threatened Species (www.iucnredlist.org). Species classified as vulnerable, endangered, or critically endangered were considered “threatened” in subsequent analyses.



Figure 1. Examples of ecosystem services provided by birds. (a) Seed dispersal by frugivores like the Guianan toucanet (*Selenidera piperivora*); (b) plant pollination by nectarivores, such as the plain-bellied emerald (*Amazilia leucogaster*); and (c) control of phytophagous insects by insectivores, including the Indian cuckoo (*Cuculus micropterus*).

Statistical analysis

We analyzed the relationship between bird probability of occurrence and predictor variables using a generalized linear mixed-effects model (GLMM) with a binomial distribution and logit link (package *lme4*; Bates *et al.* 2015) in R (v3.6.3; R Core Team 2020). Probability of occurrence is a measure of the average likelihood of any bird species within the community being detected in a particular forest fragment. Our main predictor variables of interest were fragment size (ha) and protection status, and their interaction. In addition, matrix type, feeding guild, forest dependence, migration strategy, HWI, and body mass were all added to the model as fixed effects, with interaction terms for fragment size with all other terms except matrix type. The predictors fragment size, HWI, and body mass were log-transformed prior to analysis. Fragments larger than 10,000 ha ($n = 22$) were considered continuous forest and were set to “10,000” for subsequent analysis. To account for inter-study variability, we added study as a random effect and allowed the slope of each study to vary with fragment size. We also included species as a random effect to account for the potential issue of statistical non-independence of our sample data. To test whether threatened species and forest (in-)dependent species respond differently to our fragmentation metrics and protection status, we ran the same models on corresponding subsets of the dataset. Additional statistical analyses were performed to test for multicollinearity, significance, and the validity and generality of our findings (WebPanel 2).

Results

Fragment size and protection status

We found that the relationship between fragment size and bird species occurrence depends on the protection status of fragments (Table 1; Figure 2a). A Tukey post-hoc test revealed that the increase in species occurrence was stronger for fragments under moderate protection (slope on logit scale: 0.80 ± 0.09 [mean \pm standard error], z -ratio = -3.59 , $P = 0.001$) and strict protection (0.71 ± 0.08 , z -ratio = -3.00 , $P < 0.01$) than for fragments with no protection (0.56 ± 0.07), whereas no difference was detected between moderate protection and strict protection (z -ratio = 1.36 , $P = 0.36$; WebTable 3). This indicates that for the conservation of birds, protection becomes increasingly effective with increasing size of forest fragments regardless of protection status. Protection was most effective in the largest fragments ($\geq 10,000$ ha), at which size the probability of occurrence was 0.74 (95% confidence interval [CI]: 0.61–0.84), 0.83 (CI: 0.73–0.91), and 0.82 (CI: 0.70–0.89) for no protection, moderate protection, and strict protection, respectively. Tukey post-hoc tests further demonstrated that the difference in probability of occurrence between no protection and strict protection was significant for fragments above ~ 50 ha, whereas fragments under moderate

protection must be at least ~ 175 ha to observe a significant difference.

Threatened species

Differences in species occurrence were much more pronounced when only threatened species were considered (WebTable 3; Figure 2b). With increasing fragment size, the occurrence of threatened species rose most strongly for fragments under strict protection (slope on logit scale: 2.00 ± 0.54 [mean \pm standard error]) compared to moderate protection (0.40 ± 0.37 , z -ratio = -2.89 , $P = 0.01$) and no protection (0.54 ± 0.29 , z -ratio = -2.87 , $P = 0.01$). As with the analysis of the entire bird community, differences among PA types were greatest in the largest fragments. For fragments $\geq 10,000$ ha, the occurrence of threatened species was higher in fragments under strict protection (0.99 [CI: 0.74–1.00]) than in fragments under no protection (0.58 [CI: 0.10–0.95], z -ratio = -3.43 , $P < 0.01$), and marginally higher than in fragments under moderate protection (0.81 [CI: 0.18–0.99], z -ratio = -2.29 , $P = 0.06$). The probability of occurrence under strict protection exceeds that of no protection in fragments larger than ~ 15 ha, and significantly so above ~ 100 ha. Under moderate protection, occurrences

Table 1. Contribution of terms and interactions to the tested models used to explain variation in the probability of species occurrence

Term/interaction	Main model			Threatened species model		
	Δ AIC	χ^2	P	Δ AIC	χ^2	P
Matrix	11	23.2	<0.001	-7	4.7	0.580
Fragment size	131	153.1	<0.001	8	29.6	0.002
Protection status	3	7.3	0.026	6	9.9	0.007
Guild	41	51.4	<0.001	10	20.2	0.001
Forest dependence	6	8.2	0.004	-2	0.5	0.480
Migration status	3	5.1	0.024	-1	0.6	0.420
Hand-wing index (HWI)	30	32.0	<0.001	-2	0.0	0.860
Body mass	23	25.8	<0.001	4	6.4	0.012
Fragment size: protection status	12	16.1	<0.001	6	9.8	0.007
Fragment size:guild	49	59.3	<0.001	5	14.6	0.012
Fragment size: forest dependence	112	114.3	<0.001	0	1.9	0.168
Fragment size: migration status	-2	0.0	0.963	-2	0.0	0.881
Fragment size:HWI	16	18.2	<0.001	-2	0.4	0.509
Fragment size: body mass	-1	1.6	0.199	2	4.4	0.037

Notes: Δ AIC represents the change in model Akaike information criteria (AIC) upon removal of the term/interaction from the model. Chi-square values (χ^2) and P values of likelihood-ratio tests are also provided. Bold values depict statistical significance at the $P < 0.05$ level. Although test statistics for all main effects are shown for reasons of completeness, interpretation of main effects in the presence of significant interactions is not straightforward.

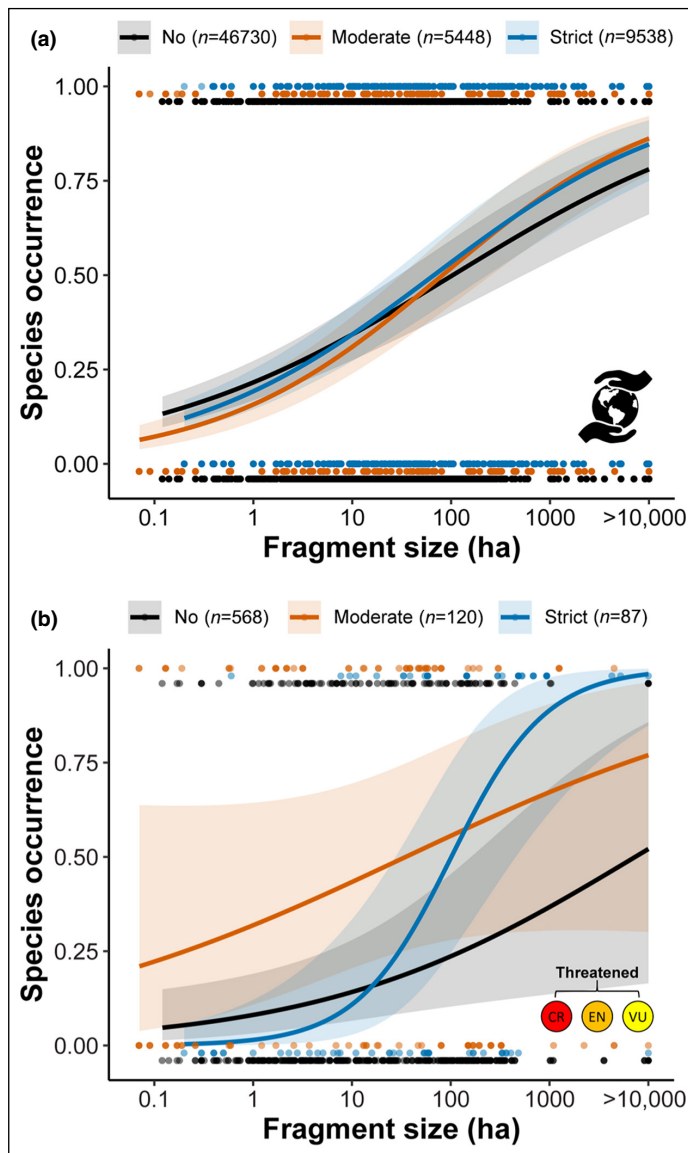


Figure 2. The relationship between the probability of bird species occurrence and forest fragment size and protection status, with probability of occurrence shown for (a) all bird species and (b) only threatened bird species. Sample sizes (n) indicate the number of occurrence records (presence or absence), circles represent the observed data, lines represent predictions from the fitted generalized linear mixed-effects model (GLMM) while controlling for all covariates, and colored bands show the 95% confidence intervals (CIs) based on fixed effects only.

were higher than in fragments under no protection for all fragment sizes, but (due to the large uncertainty) this effect was significant only in fragments smaller than ~225 ha.

Species-specific responses to fragment size

Bird species varied in their sensitivity to fragment size. We found an interactive effect between fragment size and all traits considered, with the exception of body mass and migration status (Table 1). Forest-dependent birds were particularly sensitive to forest fragmentation: their

probability of occurrence declined more strongly with decreasing fragment size, when compared to forest-independent birds (Table 1; WebTable 3). Analyses run for forest-dependent and forest-independent species separately revealed that, although the overall effect of protection was larger for forest-independent species, the distinction between moderate protection and strict protection was more pronounced for forest-dependent species. For forest-independent species, there was no difference in slope (respective slopes: 0.58 [CI: 0.30–0.85] versus 0.60 [CI: 0.36–0.83], z -ratio = -0.2 , $P = 0.98$) or main effect (at mean fragment size: 0.60 [CI: 0.45–0.73] versus 0.59 [CI: 0.45–0.72], z -ratio = 0.12, $P = 0.99$) between moderate protection and strict protection, respectively (Figure 3a). For large fragments (>300 ha), the occurrence of forest-independent species was significantly higher under both types of protection than under no protection, and this difference was greatest in fragments $\geq 10,000$ ha (0.69 [CI: 0.48–0.85] versus 0.57 [CI: 0.37–0.75], z -ratio = -2.58 , $P = 0.03$). For forest-dependent species (Figure 3b), both protection types had similar occurrences in large fragments (at $\geq 10,000$ ha: 0.90 [CI: 0.78–0.96] versus 0.88 [CI: 0.75–0.95], z -ratio = 1.1, $P = 0.52$), but in smaller fragments higher occurrences were observed for fragments under strict protection (at 10 ha: 0.32 [CI: 0.21–0.46] versus 0.40 [CI: 0.28–0.53], z -ratio = -2.3 , $P = 0.06$). For fragments >25 ha, PAs under strict protection had significantly higher species occurrence than PAs with no protection, suggesting that protection of small fragments is of greater importance for forest-dependent than forest-independent birds.

Full migrant species were as sensitive to fragment size as non-migrating species (Table 1). Regardless of fragment size, full migrants had lower probabilities of occurrence ($\chi^2 = 5.1$, $P = 0.02$; WebTable 3). Among feeding guilds (Figure 4), nectarivores were least responsive to fragment size (slope on logit scale: 0.52 ± 0.10 [mean \pm standard error]), followed by granivores (0.59 ± 0.08), omnivores (0.61 ± 0.08), frugivores (0.76 ± 0.08), insectivores (0.82 ± 0.07), and carnivores (0.82 ± 0.10). Irrespective of fragment size, frugivores had higher probabilities of occurrence (at mean log-fragment size: 0.50 [CI: 0.40–0.60]), followed by omnivores (0.47 [CI: 0.37–0.56]), nectarivores (0.40 [CI: 0.29–0.53]), granivores (0.38 [CI: 0.29–0.48]), insectivores (0.38 [CI: 0.30–0.46]), and carnivores (0.32 [CI: 0.23–0.43]), the latter being the rarest of all species encountered.

We also found that the probability of occurrence of a bird species was strongly dependent on body mass, with larger species being less likely to occur overall (Table 1; WebTable 3), yet there was no evidence that large species respond more strongly to fragment size ($\chi^2 = 1.6$, $P = 0.20$). Finally, a strong interaction was detected between HWI and fragment size, whereby birds with a greater HWI were more sensitive to changes in fragment size ($\chi^2 = 18.5$, $P < 0.001$; Figure 5).

Effect of surrounding land use

Our analysis confirmed that landscape matrix type also contributes to species occurrence within forest patches ($\chi^2 = 23.2$, $P < 0.001$; Table 1). Species were more likely to be present in fragments in a matrix dominated by native forest than in patches embedded in either a semi-developed (z -ratio = -3.75 , $P < 0.01$) or shrubland (z -ratio = 3.97 , $P < 0.01$) matrix.

Discussion

Importance of fragment size and protection

Our meta-analysis shows how strongly bird occurrence in forest fragments declines with decreasing fragment size. Although present across all species groups, declines were especially prominent for forest-dependent species, insectivores, carnivores, and more dispersive species (as indicated by a large HWI). Notably, a significant interaction was detected between protection status and the association between bird occurrence and fragment size. Rather than mitigating fragment size-related declines in bird species occurrence as we had anticipated, we found that protection was associated with higher occurrence in medium to large forest fragments (>50 ha for strict protection, >175 ha for moderate protection), suggesting that in fragmented landscapes, protection of medium to large fragments is essential for bird conservation. This result complements the findings of previous research on PA performance in very large fragments and continuous forest (Coetzee *et al.* 2014; Barnes *et al.* 2016; Gray *et al.* 2016). These studies demonstrated the critical importance of large PAs (in Coetzee *et al.* [2014], approximately 75% of PAs were $\geq 10,000$ ha; in Gray *et al.* [2016], small PAs were considered <40,000 ha) for species conservation through comparisons with unprotected areas, but found no evidence that PAs under strict protection perform better than PAs under less stringent management.

Protection may benefit species through management that either reduces direct human threats (for example, hunting and trapping) or maintains and restores certain habitat types. According to our results, large PAs apparently are more successful in achieving these goals than small PAs, for which we propose several explanations. First, in small fragments, there is an increase in the proportion of species that are unlikely to be sensitive to protection of forest habitat, due to an influx of habitat generalists and non-forest specialists from the surrounding matrix (Lees and Peres 2006; Rutt *et al.* 2019). This was corroborated by our finding that strict protection of small fragments is effective when only forest-dependent species are considered. Second, the negative effects related to small patch size may outweigh the benefits of protection. For instance, competition for resources and breeding habitat in small fragments limits carrying capacity, which may only be resolved by increasing forest area. Simultaneously, greater edge exposure implies that small fragments are more susceptible to changes in microclimate,

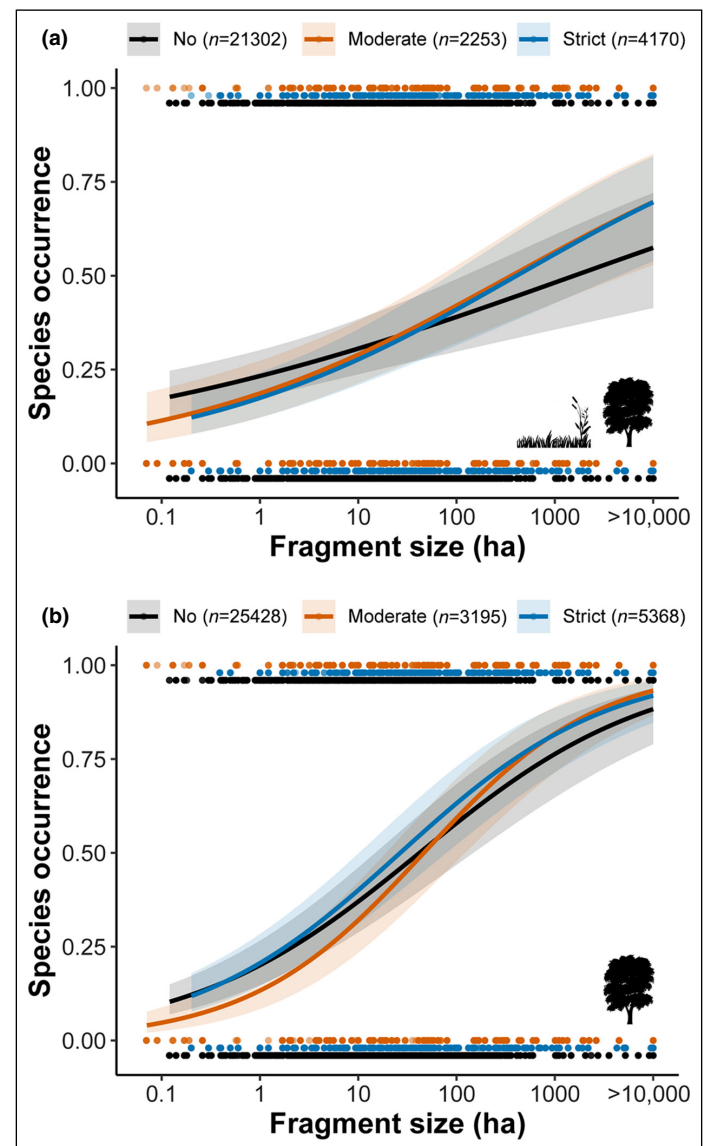


Figure 3. The response of (a) forest-independent and (b) forest-dependent bird species to fragment size and protection status. Sample sizes (n) indicate the number of occurrence records (presence or absence), circles represent the observed data, lines represent predictions from the fitted GLMM while controlling for all covariates, and colored bands show the 95% CIs based on fixed effects only.

forest structure, and species interactions (Laurance *et al.* 2002). Furthermore, areas bordering PAs often act as population sinks for wildlife because of human-wildlife conflicts and hunting (Woodroffe and Ginsberg 1998), and anthropogenic threats may even encroach into PAs, especially if fragments are small and have high edge-interior ratios. Such pressures may offset the potential benefits of protection in small forest fragments.

Threatened species

Protection status was even more strongly associated with bird occurrence for threatened species, and differences between

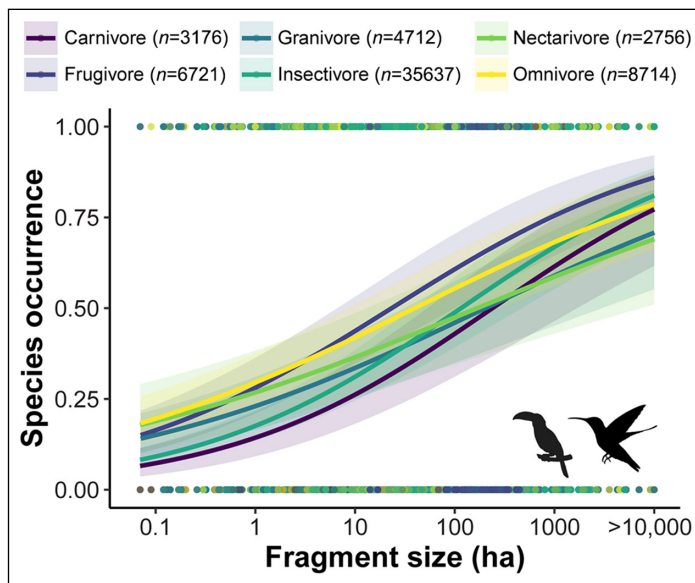


Figure 4. Feeding guild-specific responses to fragment size. Sample sizes (n) indicate the number of occurrence records (presence or absence), circles represent the observed data, lines represent predictions from the fitted GLMM while controlling for all covariates, and colored bands show the 95% CIs based on fixed effects only.

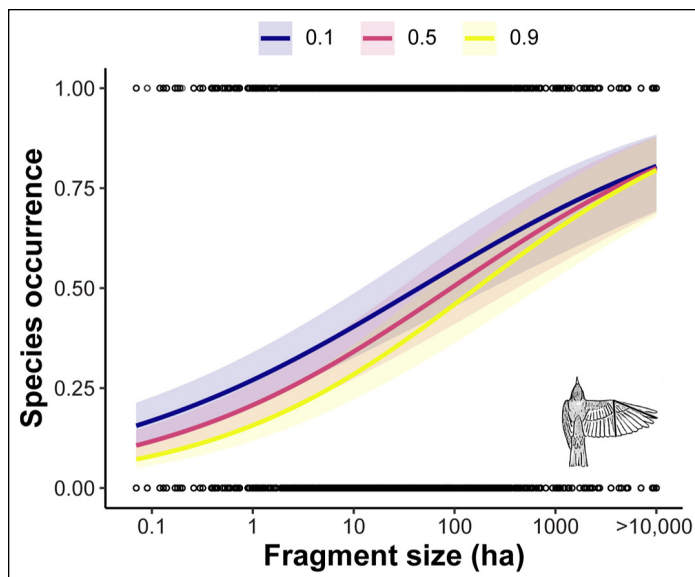


Figure 5. Hand-wing index (HWI) was negatively correlated with species occurrence. Colored lines and legend values represent the 0.1, 0.5, and 0.9 quantiles, obtained from the fitted GLMM while controlling for all covariates; and colored bands show the 95% CIs based on fixed effects only.

strict protection and moderate protection became apparent. In fragments >100 ha, strict protection was associated with the highest occurrence of threatened species. To a lesser extent, moderate protection also led to increased occurrence of threatened birds in medium to large fragments, although this did not differ significantly from fragments under no protection. However, this effect was significant for fragments smaller than

225 ha, suggesting that even small forest fragments have conservation value for threatened birds (as found for forest-dependent species) when under protection.

The strong response of threatened species to fragment size and their low occurrence in small fragments indicate that protection of threatened species should focus on larger areas, where occurrence was higher under both protection types than in unprotected patches. This finding is promising, as it suggests that species most in need of conservation are indeed benefiting from protection. The threatened species in our analysis included many iconic species, such as the yellow-headed Amazon (*Amazona oratrix*), brown-cheeked hornbill (*Bycanistes cylindricus*) and black-fronted piping guan (*Pipile jacutinga*). Over half of the threatened species (23/42) included in our analysis are under threat from hunting and trapping (IUCN 2020), activities that are likely to be less common in large and adequately managed PAs. At the same time, however, one could also argue that PAs under strict protection are more likely to have been established in order to protect particular threatened species, which may indeed be the case for individual sites. However, our dataset also contains many occurrences of threatened bird species in areas under no protection (59% of observations); in addition, threatened birds were no more likely to occur in areas under strict protection than in areas with no protection (30 versus 93 fragments, ratio: 0.32) when compared to all other bird species (152 versus 497 fragments, ratio: 0.31). Moreover, it is questionable whether in practice assigning higher PA status to fragments with threatened species would be fragment size-specific. Thus, we expect that the association we observed is more likely to be causal, with protection successfully conserving threatened birds in medium to large fragments, but this remains to be evaluated under more controlled conditions.

Fragmentation-induced community shifts and implications

Several bird traits were found to be important predictors of high sensitivity to fragment size, most notably forest dependence, HWI, and dietary preference. As fragment size decreased, forest-dependent species underwent a much stronger decline than forest-independent species. However, our results also suggest that even small fragments (>25 ha) are worth protecting under a strict IUCN category in order to maintain forest-dependent species.

Species with higher HWI were more sensitive to variation in fragment size. Bovo *et al.* (2018) also found that within frugivorous bird communities, species at the upper extreme (>90 th percentile) of HWI variation responded more strongly to fragment size reductions. By ranging widely, these species are more susceptible to adverse effects of unsuitable habitat surrounding forest patches (Woodroffe and Ginsberg 1998). In addition, dispersive birds are capable of relocating to larger, more suitable areas, whereas less dispersive gap-avoiding birds remain in small forest fragments (Van Houtan *et al.* 2007). Loss of dispersive bird species from small fragments could further isolate such fragments in terms of plant

dispersal and subsequently impact meta-community dynamics (Cordeiro and Howe 2001; Emer *et al.* 2018).

The strong response of carnivorous birds to fragment size and their overall low occurrence make these species particularly vulnerable to local extinction in small fragments. Past research on mammals often demonstrated the sensitivity of apex predators to disturbance (eg Cardillo *et al.* 2005; Dirzo *et al.* 2014). This finding in mammalian apex predators has been attributed to several characteristics, including their position at the top of the food chain, which places energetic limits to their population sizes; their need of large territories for foraging; their low reproductive rates; and their being subject to increased hunting pressure – all of which equally apply to the avian (predominantly apex) predators included in our analysis. The effect of fragment size on insectivorous birds was equally strong, adding to the growing amount of evidence that insectivores are sensitive to fragmentation (Şekercioğlu *et al.* 2002; Bregman *et al.* 2014).

Notably, body mass was identified as an important predictor of fragmentation sensitivity for threatened species but not for the bird community as a whole (Table 1). We suspect this is due to a correlation between body mass and hunting pressure, as all of the large threatened species in our analysis were impacted by hunting and trapping, whereas most of the smaller threatened species were not.

Limitations

Our meta-analysis was based on observational studies, which restricted our ability to draw causal inferences on the effects of PA status and fragment size. Our results, along with those of others (Coetzee *et al.* 2014; Barnes *et al.* 2016; Gray *et al.* 2016), indicate that PA effectiveness varies greatly among PAs, species, and regions. Local PA context is determined by many elements, including socioeconomic context, local human pressures, and PA management. Budgetary constraints have consistently been identified as a key driver of PA performance (Barnes *et al.* 2017). Although this suite of drivers affecting PA effectiveness obscures the interactions between bird occurrence and the variables included in our analysis, we detected several strong associations that provide a basis for conservation management until causal relationships are further explored in experimental settings.

It is important to note that we could not control for sampling effort in our main analyses due to the variety of applied survey methods, and therefore the consistent effects of fragment size shown here may be partially driven by unequal sampling effort across fragment sizes. However, using a subset of the data we demonstrated that the effect of sampling effort on species occurrence is relatively small and that fragment size remains the strongest predictor, probably due to contrasting relationships of fragment size with absolute and relative sampling effort (WebPanel 4; WebFigure 7).

Finally, our response variable – probability of occurrence – also reflects probability of detection (Kellner and Swihart

2014). Species detectability may vary among fragments depending on numerous factors, including observer error (Nichols *et al.* 2000) and environmental conditions (Gu and Swihart 2004). As detection may be more difficult in older, larger, and better protected forest fragments (WebPanel 5), our results are likely to be conservative in regard to the impacts of fragment size and protection status.

Conclusions

In this global meta-analysis, we show that bird occurrence was significantly associated with fragment size, protection status, and matrix type. The impact of fragment size was larger than that of any other factor, highlighting the critical importance of large forest areas for conserving bird diversity. We also found evidence that protection can be an effective strategy for preserving diversity in fragmented landscapes. For forest fragments >50 ha, strict protection (IUCN categories I–IV) positively contributes to maintaining bird species. For forest-dependent species, even smaller fragments (>25 ha) are worth strict protection. Under moderate protection, fragments must be >175 ha for protection to have a positive effect. The benefits of protection are especially evident for threatened species, for which strict protection of sufficiently large forest patches appears to be crucial. Other avian species that benefit from the conservation of large forest fragments include insectivores, carnivores, and dispersive birds. In light of the ongoing debate about the conservation values of disturbed versus intact forests (Gibson *et al.* 2011; Watson *et al.* 2018; Wintle *et al.* 2019), the results of our analysis provide additional support for the following position: the value of forest fragments should not be underestimated, but protection is required to slow or stop declines in bird species populations in fragmented forest landscapes.

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Data Availability Statement

Data are available on Dryad (doi.org/10.5061/dryad.wpzgmsbn9). No novel code was used for this submission.

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