












Drivers and spatial patterns of avian defaunation in tropical forests

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Abstract

Aim: Wildlife overexploitation, either for food consumption or for the pet trade, is one of the main threats to bird species in tropical forests. Yet, the spatial distribution and intensity of harvesting pressure on tropical birds remain challenging to quantify. Here, we identify the drivers of hunting-induced declines in bird abundance and quantify the magnitude and the spatial extent of avian defaunation at a pantropical scale.

Location: Pantropical.

Methods: We compiled 2968 abundance estimates in hunted and non-hunted sites across the tropics spanning 518 bird species. Using a Bayesian modelling framework, we fitted species' abundance response ratios to a set of drivers of hunting pressure and species traits. Subsequently, we applied our model to quantify the spatial patterns of avian defaunation across tropical forests and to assess avian defaunation across biogeographic realms, and for species captured for the pet trade or for food consumption.

Results: Body mass and its interactions with hunter accessibility and proximity to urban markets were the most important drivers of hunting-induced bird abundance declines. We estimated a mean abundance reduction of 12% across the tropics for all species, and that 43% of the extent of tropical forests harbour defaunated avian communities. Large-bodied species and the Indomalayan realm displayed the greatest abundance declines. Further, moderate to high levels of defaunation extended over

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24% of the pantropical forest area, with distinct spatial patterns for species captured for the pet trade (Brazil, China and Indonesia) and for food consumption (SE Asia and West Africa).

Main Conclusions: Our study emphasizes the role of hunter accessibility and the proximity to urban markets as major drivers of bird abundance declines due to hunting and trapping. We further identified hotspots where overexploitation has detrimental effects on tropical birds, encompassing local extinction events, thus underscoring the urgent need for conservation efforts to address unsustainable exploitation for both subsistence and trade.

KEYWORDS

abundance, bird, bushmeat, defaunation, hunting, overexploitation, pantropical, pet trade, poaching, wild meat

1 | INTRODUCTION

No other terrestrial biome on Earth holds more species than tropical forests, which harbour nearly 50% of terrestrial vertebrate species worldwide (Pillay et al., 2022). Despite this diversity of life forms, these ecosystems face unprecedented rates of biodiversity loss exacerbated by a myriad of human activities such as deforestation, land use changes, fires and fragmentation (Ceballos et al., 2015; Malhi et al., 2014). However, other human pressures such as direct overexploitation entail cryptic impacts which frequently occur under the canopy of apparently undisturbed forests that may otherwise be 'empty' (Redford, 1992) or 'half-empty' (Wilkie et al., 2011) of animal species. 'Empty' forests are mostly the consequence of unsustainable harvest rates of vertebrate species (Corlett, 2007; Peres, 1990; Redford, 1992), which ultimately result in depleted or extirpated populations, a phenomenon coined as defaunation (Dirzo et al., 2014).

Although wildlife overexploitation accounts for the most widespread form of resource extraction in the tropics (Fa et al., 2022), unravelling the total extent of their impacts remains a challenge. Nearly 20% of the current extent of tropical forests worldwide is apparently intact (Potapov et al., 2017). Yet, these estimates rely on remote sensing approaches that, while successful in detecting other drivers of defaunation such as habitat loss, are ill-suited to track hunting activities (Peres et al., 2006). Consequently, wildlife populations inhabiting those seemingly intact forests could be decimated by the cryptic effects of hunting (Benítez-López et al., 2019). This is particularly worrisome as recent evidence suggests that demand for wild meat and wildlife products will increase significantly in the future decades due to the expected human population growth coupled with infrastructure development (i.e. roads) in rural areas of SE Asia, South America and, particularly, Sub-Saharan Africa (Dulac, 2013; Fa et al., 2022; Laurance et al., 2015). These processes will undoubtedly amplify the accessibility of hunters and trappers to isolated places, thus further magnifying and expanding the impact of hunting and wildlife

trade on vertebrate populations (Benítez-López et al., 2017; Fa et al., 2022; Scheffers et al., 2019). Hence, there is a pressing need to develop tools that are able to infer the spatial patterns of contemporary overexploitation on tropical wildlife.

Threat maps can aid in the identification of areas where biodiversity is at risk and have become key tools for the spatial prioritization of locations for conservation (Tulloch et al., 2015). There have been several attempts to map hunting pressure and its impact on mammal populations in Central Africa (Ziegler et al., 2016), in the Neotropics (Bogoni et al., 2020), and at pantropical scale (Benítez-López et al., 2019; Harfoot et al., 2021). Yet, despite the fact that ~43% of all bird species are harvested across the tropics (IUCN, 2022), the magnitude and extent of hunting impacts on tropical bird populations remains unknown, hampering our ability to fully gauge the toll that this threat imposes on tropical biodiversity.

Around 1076 bird species are known to be widely consumed as wild meat, even replacing mammals as the most hunted group for food consumption at sites such as the Caribbean islands, Oceania and SE Asia (Fa et al., 2022; IUCN, 2022; Redmond et al., 2006). A recent study in Madagascar reports that consumption prevalence of wild birds across >1300 households is 75% (Borgerson et al., 2023). In the Neotropics, subsistence hunting of birds is frequent and widespread (Stafford et al., 2017), with birds being an important source of protein and fat (Begazo & Bodmer, 1998; Thiollay, 2005), or are used to produce tools, cultural adornments or for traditional medicine (Mena et al., 2000; Santos-Fita et al., 2012). Further, a large proportion of tropical birds are subject to both illegal and legal trade, particularly as pets (Scheffers et al., 2019). It has been estimated that the annual global commercial exploitation of wild birds for pets is worth €2 mill. (van Uhm, 2016), and that the annual trade volume ranges between 5 and 10 million wild birds (Gilardi, 2006). This high volume of bird trade in tropical regions is clearly exemplified in Southeast Asia, where 1 million birds were exported between 1998 and 2007, and over ~¼ mill. birds were captured from the wild (Nijman, 2010).

In the Neotropics, illegal bird trade has also become prominent in Brazil (Alves et al., 2013; do Nascimento et al., 2015), where 2–5 million live birds are trafficked annually (RENCTAS, 2001). Overall, unsustainable hunting for subsistence or commercial purposes has reduced bird abundance by 58% in hunted sites across the tropics (Benítez-López et al., 2017), and it represents a major contributor to extinction risk for ~22% of hunted tropical bird species (IUCN, 2022).

Harvesting of tropical birds is influenced by a complex interplay between both subsistence and commercial motivation, in which bird traits cater to specific needs and preferences. In the context of subsistence hunting, the choice of large-bodied birds is pragmatic, as they yield larger amounts of meat, which can be crucial for local sustenance (Begazo & Bodmer, 1998; Whytock et al., 2016). Conversely, in the context of the pet trade, besides the obvious aesthetic qualities (e.g. plumage coloration, melodious songs) (Senior et al., 2022), smaller birds are often preferred due to their manageable size and adaptability to captivity (Sodhi et al., 2011; Su et al., 2014). Beyond size and appearance, other traits influence trapping and trade dynamics, including cultural significance (Brooks-Moizer et al., 2008), and rarity, with uncommon species being traded at high prices in both legal and illegal markets (Harris et al., 2017; Sagar et al., 2023). Moreover, bird hunting for subsistence and commerce is also influenced by socio-economic factors. In Africa, wealth is linked to increased wild meat consumption rates in urban areas, while opposite patterns are found in rural areas where economic deprivation is associated with a higher dependence on wild meat (Brashares et al., 2011). In the Neotropics, higher harvest rates of Piciformes (mainly toucans) and Galliformes species for food consumption are linked to poorer areas (Richard-Hansen et al., 2019). Meanwhile, trade is however unequivocally related to greater wealth: higher trade volume and larger numbers of exports are associated with wealthier tropical countries (Liew et al., 2021). However, whether hunting motivations for food consumption or commercialization result in diverging or similar spatial patterns of avian defaunation has not been addressed to date.

Here, we elucidate the drivers of hunting-induced declines in bird abundance and quantify the spatial extent of avian defaunation across the tropics. Specifically, we aim: (1) to assess the relationship between bird abundance declines, species traits and socioeconomic predictors of hunting pressure, (2) to map the spatial patterns of hunting-induced avian defaunation across tropical forests and (3) to quantify the extent of hunting impacts for species captured for subsistence (i.e. food consumption) or commercial (i.e. pet trade) purpose. To this end, we compiled bird abundance estimates at hunted and non-hunted sites across the global distribution of tropical forests, and modelled local abundance as a function of both intrinsic and extrinsic potential predictors of hunting impacts on bird populations (see Benítez-López et al., 2017, 2019). Finally, we project the spatial patterns of contemporary defaunation of bird communities at a pantropical scale, across all species, and for species hunted for subsistence or commercial purposes.

2 | MATERIALS AND METHODS

2.1 | Data collection

We expanded the dataset of hunting impacts on bird populations from Benítez-López et al. (2017) by supplementing additional bird abundance data from local hunting studies through a systematic search of the literature (see details in Methods S1 and S2). Our final dataset comprises 2968 abundance estimates for 518 tropical bird species at both hunted and non-hunted sites (control) based on 60 local hunting studies (Figure S1, Table S1). Studies that report potential confounding effects, such as habitat loss and logging were not included in our analysis. We used all species reported in local hunting studies as long as they were resident or the study location corresponded to their native resident range, according to BirdLife International (2021), except for eight species (14 abundance estimates). Because all sampling data come from pairwise study designs where surveys were conducted within the same period for hunted and unhunted sites, differences in species abundance can be thus attributed to hunting pressure and not migratory behaviour. Changes in abundance due to hunting pressure were subsequently expressed as the response ratio (RR) between the abundance of each bird species (s) in hunted (X_{sh}) and non-hunted (X_{sc}) sites within each study ($RR = X_{sh}/X_{sc}$) (Benítez-López et al., 2017, 2019; Peres & Palacios, 2007). $RR = 0$ then indicates local extinction; $0 < RR < 1$, reduction in abundance; $RR \approx 1$, no changes in abundance and $RR > 1$, increase in abundance.

2.2 | Predictors of hunting pressure

We compiled the following information from each study: the geographic coordinates of hunted and unhunted sites in each study, the hunter's access point to the hunted site (i.e. roads, settlements or rivers) and the motivation for hunting (i.e. subsistence, commercial or both). We further compiled information on different predictors often used as drivers of hunting pressure in the hunting literature and in other correlative models, including the distance to access points, human population density, poverty level and travel time to major cities, as well as information on factors that modulate species responses to hunting pressure, such as net primary productivity or whether hunting activities took place inside or outside protected areas (Benítez-López et al., 2019; Bogoni et al., 2020; Brashares et al., 2011; Peres, 2000; Scabin & Peres, 2021; Whytock et al., 2016). All spatially explicit predictors were calculated within the extent of present-day (sub-)tropical forest ecosystems (i.e. 'forest zone') based on the global tree canopy cover dataset for the year 2000 (Potapov et al., 2017) and resampled at 1×1 km resolution.

Because large-bodied species usually display lower population densities and have slower reproductive rates (Santini et al., 2023; Sibly et al., 2012), we compiled body mass for each bird species from AVONET (Tobias et al., 2022) as a trait related to the inherent

sensitivity of the species to hunting pressure (Redford, 1992). We also categorized tropical bird species as either traded as pets or not (Scheffers et al., 2019), and consumed as food or not (IUCN, 2022), and assessed differences in species' body mass for these two factors (Figure S2).

When reported in the study, we recorded the distance to the nearest hunters' access points (i.e. roads, settlements) for hunted and non-hunted sites. For the rest of the studies, we extracted the distance to the nearest human settlement for hunted and unhunted sites using an updated version of the distance raster map generated by Benítez-López et al. (2019) (see details in Method S3).

Since commercial hunting often involves urban markets and leads to higher harvesting pressure than hunting for subsistence (Brashares et al., 2011; Ojasti, 1996), we used travel time to major cities as a proxy of accessibility to urban markets in tropical countries. We extracted travel time from Nelson (2008) for studies dated before 2000, and Weiss et al. (2018) for studies after 2015. For studies carried out between 2000 and 2015, we interpolated travel times from both of these urban accessibility maps. Additionally, we included human population density as an indicator of wild meat demand and consumption (Fa et al., 2022). We extracted human population density from the Gridded Population of the World map (GPW v4.11, CIESIN, 2018) by matching each human population density raster (available every 5 years between 2000 and 2020) with the period when each study was carried out.

We used the prevalence of stunting among children under 5 years old as a proxy of economic deprivation (FAO, 2003), which is an effective indicator of poverty widely used in the wild meat literature (Benítez-López et al., 2019; Fa et al., 2015). To determine stunting, we used a spatial database on the prevalence of stunting in children under 5 years old (Benítez-López et al., 2019; FAO, 2003) and updated stunting estimates at subnational level for different time periods based on Demographic and Health Surveys (DHS), UNICEF's Multiple Indicator Cluster Surveys (MICS) as well as national surveys (e.g. Health Survey from Indonesia's Central Bureau of Statistics or ESANUT2018 in Ecuador). We used our newly generated poverty map to extract stunting estimates for each study location matching the time periods during which each study and stunting survey were carried out (Table S2).

The intensity of human harvest on wildlife hinges on the total standing and available biomass of the species, and this is influenced by the available primary productivity in different habitats (Alvard & Winarni, 1999; Fa et al., 2022; Peres, 2000; Sodhi et al., 2011). We used the MODIS/Terra Net Primary Production annual rasters from 2001 to 2020 (Running & Zhao, 2021) and matched NPP per study location with the period when each study was carried out. Finally, protected areas play a crucial role in reducing hunting impacts in tropical forests, as hunting activities are regulated or banned within their boundaries (Wright et al., 2001). We retrieved information on the protection status of each hunted site per study using information from the World Database on Protected Areas (WDPA) (UNEP-WCMC, 2022). We retrieved this information as a binary variable

stating if species abundances were estimated within or outside protected areas, regardless of protection levels.

2.3 | Modelling hunting impacts on bird abundance

Before modelling, we assessed the multicollinearity of continuous predictors through Pearson's correlation coefficients (r) and Variance Inflation Factor (VIF), calculated and plotted with 'corrplot' package (Wei et al., 2017) and the 'performance' package (Lüdecke et al., 2021), respectively. We considered highly collinear variables with $r > .7$ and $VIF > 5$ (Figure S3). Subsequently, we fitted a hurdle mixed model using Bayesian inference to simultaneously model the probability of local extinction due to hunting with a binomial distribution, and changes in species abundance with a continuous log-normal distribution (Figure S4). We considered that a given bird species was locally extinct due to hunting pressure when its abundance at the hunted site was zero ($RR=0$). Determining local extinction is challenging and requires substantial effort, hence, we only included studies with sufficient sampling effort (e.g. repeated surveys for line transects, and/or >30 camera trap days per station for camera trap studies, Table S1).

We defined the fixed and random structure of our models based on a priori hypotheses between our response variables and our set of predictors (Table S3). The random structure consisted of two random intercepts: *Country* to account for the possible differences between hunting policies, taboos and culture among tropical countries; and *Species* to account for pseudo-replicates since we incorporated multiple response ratios for each species in our database. We included a variance-covariance matrix based on the phylogenetic relatedness between bird species to account for phylogenetic non-independence in our data. To this end, we obtained a consensus phylogenetic tree derived from the phylogeny in Jetz et al. (2012) by calculating the maximum clade credibility tree topology and branch lengths from 10,000 trees downloaded from www.birdtree.org (Stewart et al., 2022). Subsequently, we used this consensus tree to build the phylogenetic variance-covariance matrix with the 'ape' package (Paradis & Schliep, 2019).

Bayesian regression models were fitted employing the 'brms' package (Bürkner, 2021) in R v.4.2.2 statistical software (R Core Team, 2023). All continuous predictors were scaled and centred around zero with an SD equal to 1 before model fitting. We ran the hurdle mixed model with 4 MCMC chains with 4000 iterations each, applying a warm up of 2000. We specified weakly informative priors using a normal distribution $N(0,10)$ for the intercept and $N(0,1)$ for slope coefficients following Lemoine (2019). Chain convergence was checked by the R-hat diagnostic ($R\text{-hat} \approx 1$). Spatial and phylogenetic autocorrelation in model residuals was tested by calculating Moran's I and Pagel's Λ with 'DHARMA' and 'phytool' packages, respectively (Hartig & Hartig, 2017; Revell, 2012). Finally, marginal effects were plotted using the 'sjPlot' and 'ggplot2' packages (Lüdecke, 2022; Wickham, 2016).

Further, we used the 'bayestestR' package to estimate the Probability of Direction (PD) as a measure of the presence of an effect for each predictor (Makowski et al., 2019). PD ranges from 50% to 100% and represents the level of confidence with which an effect is observed to occur in a specific direction (Makowski et al., 2019). We further assessed the magnitude and uncertainty of effects using the estimates and CI reported by the hurdle model, considering them as credible effects when the lower and upper CI values do not overlap with zero. Additionally, we assessed the relative importance of each predictor with a variance partitioning approach (see Method S4).

2.4 | Model predictive performance

We assessed the accuracy of model predictions using a cross-validation approach with taxonomically independent and spatially independent datasets (Roberts et al., 2017). We ran model cross-validation iteratively using the 'loo' package to establish both phylogenetic and spatial blocks (Vehtari et al., 2021). For the taxonomically independent samples, we tested the model against separate orders, families, and species. To achieve this, we divided the dataset into 10-folds, with each fold containing different taxonomic orders, families or species. The model was trained on nine folds (training dataset) and then used to predict the remaining fold (test dataset). To obtain spatially independent samples, we divided the dataset into 10×10 -degree spatial blocks which were then allocated into 10-folds, and the validation process was repeated. Subsequently, we estimated and averaged the Root Mean Square Error (RMSE) across all 10-folds to evaluate model performance. To assess the accuracy of our model in predicting defaunation hotspots as well as areas with low hunting impacts, we categorized our predictions into four levels of hunting-induced abundance responses: high abundance reduction ($RR \leq 0.3$), moderate reduction ($0.3 < RR \leq 0.7$), low reduction ($0.7 < RR \leq 1$) and increase ($RR > 1$). We calculated sensitivity, specificity, and balanced accuracy (BA) metrics for each category using the 'caret' package (Kuhn, 2008). Finally, we conducted a multivariate environmental similarity surface (MESS) analysis using the 'dismo' package (Hijmans et al., 2017) to identify geographical regions that fall beyond the scope of the spatial socioeconomic and environmental predictors in our dataset, and where our predicted defaunation estimates should be treated with caution.

2.5 | Mapping hunting-induced declines in bird abundance

We used Area of Habitat (AOH) maps from Lumbierres et al. (2022) for all bird species with distributions overlapping the tropical forest zone as defined by Potapov et al. (2017) ($n = 8600$ bird species, 3682 of which are harvested and 4918 are non-harvested species) (IUCN, 2022). AOH maps represent potential occupancy by

subtracting areas that are deemed unsuitable for the species based on their habitat and elevation preferences, thereby minimizing commission errors associated with unqualified geographic ranges (BirdLife International & Handbook of the Birds of the World, 2021). For those species defined as migratory, we only employed the raster layer depicting the resident range according to the distribution of the species. AOH maps were resampled at 1×1 km resolution to align with our spatial predictor raster map.

Subsequently, we used our model to project hunting-induced declines in species abundance for each tropical bird species based on the most updated (e.g. prevalence of stunting) or average (e.g. NPP) raster maps of our spatial predictors (see *Predictors of hunting pressure*) and the body mass of bird species. For the 4918 non-hunted species we assigned $RR = 1$ across their AOH. We reversed our predicted RR to produce a defaunation intensity index per species (DI_s), expressed as $DI_s = 1 - RR_s$ (Benítez-López et al., 2019). We then aggregated the species-specific defaunation maps to create a composite map of hunting-induced defaunation by averaging the DI values across all species per grid cell, $DI = \sum (1 - DI_s) / S$, with S being the number of species in a given grid cell. Our maps thus depict an avian defaunation gradient ranging from 0 (not defaunated) to 1 (fully defaunated). Since hunting and trapping activities may result in different abundance responses for species of different body size and diverse reproductive rates, we also generated separate defaunation maps for small (≤ 70 g, e.g. *Euphonia* spp., *Tangara* spp., *Cotinga* spp.), medium (70–600 g, e.g. *Amazona* spp., *Tockus* spp. or *Geotrygon* spp.), and large (≥ 600 g, e.g. *Penelope* spp., *Buceros* spp. or *Crax* spp.) bird species. Trapping and subsistence hunting tend to be mutually exclusive (i.e. if a given bird is captured for the pet trade, it is not hunted for sustenance and vice versa) and only ~15% (553 out of 3682 harvested species) of all tropical bird species are captured for both purposes (IUCN, 2022). Hence, we further generated separate defaunation maps for either bird species only trapped for the pet trade market or only hunted for food consumption to map and assess differences in the spatial patterns of their impacts. Subsequently, for the pantropical forest zone and for the three main tropical realms: Neotropical, Afrotropical and Indomalayan, we estimated the total extent (in mill. km²) that falls within different levels of defaunation, with $DI \leq 0.1$ depicting faunally intact areas, and DI values between 0.1 and 0.3, 0.3 and 0.7, and ≥ 0.7 indicating low, moderate and high defaunation (i.e. defaunation hotspots), respectively.

3 | RESULTS

3.1 | Model diagnostics

R-hat convergence diagnostic showed values equal to 1 for all coefficients, indicating successful convergence of the MCMC chains (Table S4). Model posterior predictive checks closely matched the observed response ratios to hunting pressure, indicating a good fit to the data (Figure S5). Model residuals did not exhibit any spatial autocorrelation (observed Moran $I = -0.007$, expected Moran $I = -0.009$,

p -value=.974) nor phylogenetic signal (Pagels' Lambda<0.001, p -value=1).

3.2 | Drivers of hunting pressure

Our model explained 22% of the variance in changes in bird abundance as a function of drivers of hunting pressure. Most of this variance was captured by the random 'Species' (37.7%) and 'Country' (21.1%) intercepts. Among fixed effects, species body mass (13.0%) and travel time to cities (13.1%) were the most important predictors, followed by distance to hunters' access points (7.0%). Other less relevant predictors were human population density (5.8%), prevalence of stunting (1.3%), net primary productivity (1.3%) and, finally, protection status, which did not capture any variance (0.0%) (Figure 1a).

We found presence of effects on changes in abundance being related to distance to hunters' access points, travel time to major cities, net primary productivity and body mass (probability of direction: PD > 90) (Table S4). Overall, we found that the interactions between body mass with distance to hunters' access point (β = .09, 95% CI = 0, 0.18) and travel time to major cities (β = -.14, 95% CI = -.024, -.05), were major predictors of changes in bird abundance (Figure 1b). Our results indicate that small-bodied species decreased in abundance

in areas closer to urban markets but increased in highly accessible sites from hunter's settlements. Conversely, the abundance of large-bodied species markedly decreased near hunters' settlements, and in areas distant to major cities. We found also an effect of the interaction between net primary productivity and distance to hunters access points (β = -.08; 95% CI = -.016, 0): sites with high NPP displayed higher abundances in the proximity of hunters' access points, whereas no clear relationship was found with a low to moderate NPP (Figure 1a and Figure S6).

Regarding the probability of local extinction due to hunting, we found presence of effects of distance to hunters' access points, travel time to major cities, prevalence of stunting, human population density, net primary productivity and body mass (PD > 90) (Table S4). Overall, our model indicates that the probability of local extinction increased with human population density (β = .65; 95% CI = 0.15, 1.17). We found credible effects of the interaction between body mass and the distance to hunter's settlements (β = -.48; 95% CI = -.086, 0.12) and travel time to major cities (β = .43; 95% CI = 0.11, 0.75). Yet, distance to hunters access points (β = -.22; 95% CI = -.056, 0.12), body mass (β = .12; 95% CI = -.035, 0.60) and travel time (β = -.35; 95% CI = -.074, 0.03) had uncertain effects by themselves on the probability of extinction (Table S4). The probability of extinction of large body-bodied species was considerably higher in the proximity of hunters' access points (Figure 1b), but unrelated to

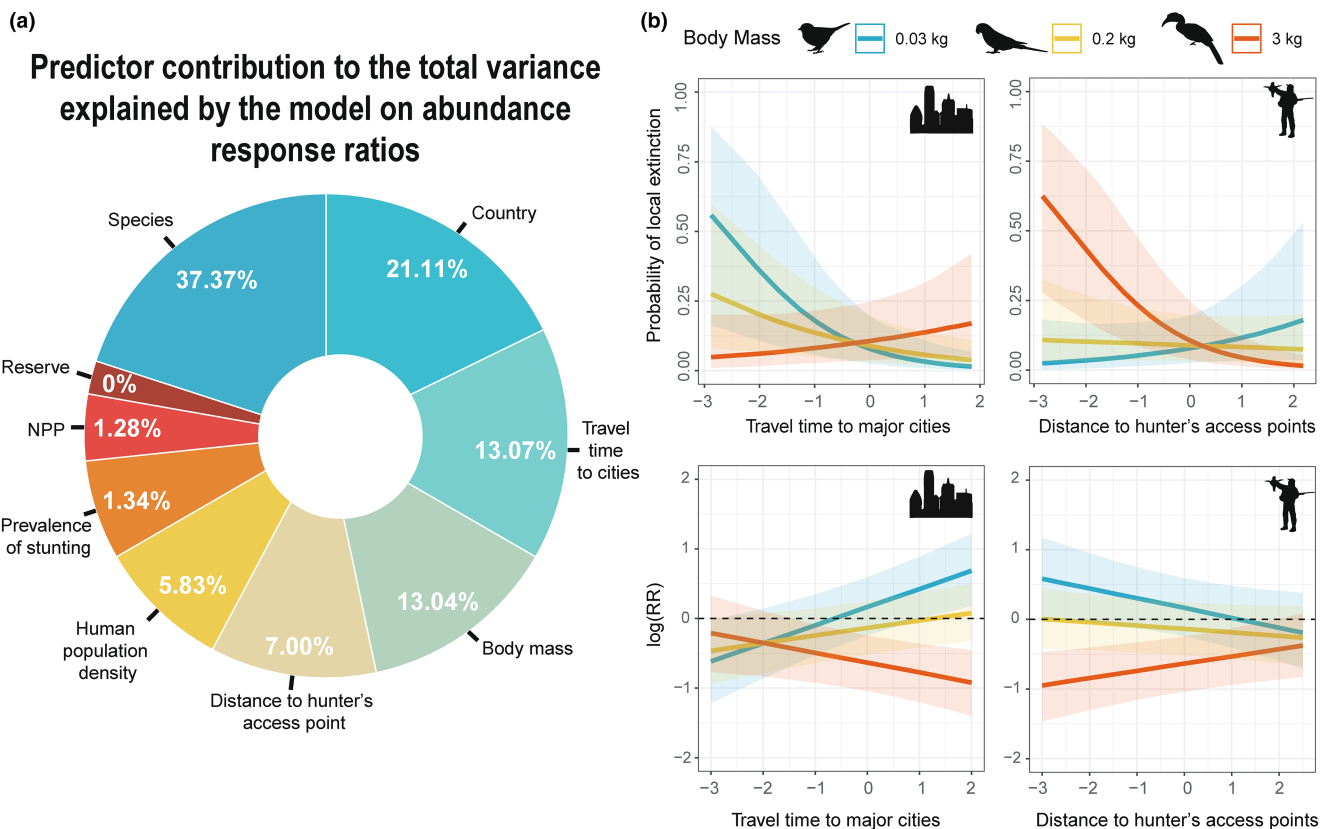


FIGURE 1 (a) Ranked predictor contribution to the total variance explained by our hurdle model in the changes in abundance and probability of extirpation of bird species. (b) Marginal effects of the interaction between body mass and travel time to major cities and distance to hunter's access points on the probability of local extinction and pairwise changes in local bird abundance. Shaded regions along each line denote the corresponding 95% confidence intervals.

the prevalence of stunting. Conversely, for small-bodied species, the probability of extinction drastically increased near urban markets and in areas with a low prevalence of stunting (Figure 1b). We also found a credible effect of the interaction between NPP and accessibility to hunter's settlements ($\beta = -0.41$; 95% CI = $-0.77, -0.06$). The probability of local extinction increased in sites near to hunters' settlements with high net primary productivity, with no clear effects in sites with moderate to low with low primary productivity (Figure S7). Medium-bodied species showed intermediate responses between small- and large-bodied species, for both changes in abundance and probability of extinction.

3.3 | Model predictive performance

RMSE for different blocks (spatial and phylogenetic blocks) showed similar mean and standard deviation values for the 10-folds (RMSE ca. 0.8), suggesting that the model performance is consistent across different parts of the dataset (Figure S8A). Mean sensitivity and specificity values for 10-folds across blocks were similar within different categories of hunting impacts (Figure S8B). Sensitivity was high (ca. 0.75) for large reductions in abundance ($RR \leq 0.3$), and medium to low for the other categories. Specificity values were consistently high across all categories of hunting impacts (ca. 0.75–0.8) (Figure S8B). Overall, the balanced accuracy (BA) of the model was >0.75 for high reductions in abundance, ca. 0.5 for moderate to low reductions in abundance, and >0.6 for increases in abundance across all blocks and folds (Figure S8B).

3.4 | Spatial patterns of avian defaunation

Our Multivariate Environmental Similarity Surface analysis (MESS) indicated that our model projections display limited extrapolation beyond the environmental domain of the predictors in our training dataset (Figure S9). We estimated an average DI of 0.12 ± 0.14 (mean \pm SD) across the pantropical forest zone (Figure 2a, Table S5). These values were slightly higher for large-bodied species, with an average DI of 0.16 ± 0.16 , followed by medium-bodied species (0.14 ± 0.16) and small-bodied species (0.11 ± 0.14). At a pantropical scale, we estimate that 56.9% of all tropical forests (~ 18.8 million km^2) are faunally intact ($DI \leq 0.1$) and that 24.4% of the overall pantropical forest area is under moderate to high risk of hunting-induced defaunation, respectively (Table S6). However, the extent and spatial patterns of avian defaunation differed among realms and species depending on their body mass (Figures 2 and 3, Tables S5 and S6).

We found that hotspots of hunting-induced defaunation ($DI \geq 0.7$) are concentrated in the Indomalayan realm (0.2 mill. km^2 , 2.6% of the forest extent), mostly in China and Indonesia (Figures 2a and 3). Indomalayan forests showed higher average DI values (0.22 ± 0.18) than Afrotropical (0.08 ± 0.09) and Neotropical forests (0.09 ± 0.1) (Table S5). Overall, populations of small-sized, medium-sized and

large-sized birds were moderately to highly defaunated across 47%–62% of the Indomalayan forest extent (Figure 3, Table S6). Additionally, we identified hotspots of avian defaunation for large-bodied species in West Africa (10,592 km^2 , 1.41%), and to a lesser extent, for medium-sized species (2005 km^2 , 0.59%) (Figure 2c,d). We further identified hotspots of defaunation for medium-bodied species in the Brazilian Atlantic Forest (10,312 km^2 , 0.26%) and Paraguay (1502 km^2 , 0.18%), particularly in the humid Chaco (Figure 2c).

When considering only bird species trapped for pet trade, we estimate an average DI of 0.19 ± 0.2 , with ca. 14.3 mill. km^2 intact tropical forests worldwide ($\sim 47\%$). We further estimate that 7.7 (25.3%), 7.9 ($\sim 26\%$) and 0.46 mill. of km^2 (1.5%) are under low, moderate and high defaunation, respectively. We identified hotspots of defaunation in SE Brazil (61,924 km^2 , 0.82%), China (90,504 km^2 , 2.7%) and Indonesia (130,034 km^2 , 3.9%) (Figure 4a). We further identified Central and South American countries (Costa Rica, Colombia, Venezuela, El Salvador and Nicaragua), West Africa (Nigeria, Benin, Togo, Ghana and Ivory Coast) and Caribbean islands as regions with high defaunation levels of traded species (Figure 4a). Further, almost all the forest extent of insular nations was under moderate to high defaunation due to pet trade. Examples include Jamaica (percent forest: 99.8%; 10,490 km^2), Trinidad and Tobago (99.8%; 3861 km^2), Puerto Rico (99.5%; 5242 km^2) and Taiwan (99.1%; 24,851 km^2) (Figure 4b, Table S7).

In the case of bird species hunted for food consumption, we estimated an average DI of 0.17 ± 0.18 for all tropical forests. We estimated a total extension of intact forest of ~ 14.1 mill. km^2 (46.8%) and 9.5 (31.4%), 6.3 (20.8%) and 0.3 mill. km^2 ($\sim 1\%$) under low, moderate and high defaunation, respectively. We identified areas of high defaunation in China (96,373 km^2 , ca. 2.9%), Indonesia (99,332 km^2 , 5.8%) and West Africa (13,316 km^2 , 5.7%) (Figure 5a). We further identified India (22,943 km^2 , $\sim 4\%$) and Mesoamerica (6827 km^2 , 0.54%) as areas with hotspots of defaunation for bird species hunted for food consumption. Yet, our model projections indicate that islands fared the worst, with Jamaica (99.5%; 10,453 km^2), Taiwan (99.3%; 24,900 km^2) and Puerto Rico (98.8%; 5203 km^2) having most of their relative extent of forest under moderate to high defaunation ($\geq 30\%$ abundance decline) due to subsistence hunting (Figure 5b, Table S7).

4 | DISCUSSION

In this study, we present a comprehensive analysis of the far-reaching impacts of overharvesting on tropical bird populations, shedding light on the main drivers of hunting pressure on bird species and the underlying spatial patterns at a pantropical scale. Our findings suggest that human accessibility, in both rural and urban settings, plays a role as a general predictor of avian defaunation, with species responses modulated by body mass. Our modelling framework also allowed us to reveal hitherto obscure patterns of hunting-induced bird defaunation and identify the key hotspots, unravelling the impacts of this cryptic yet pervasive threat across the tropics.

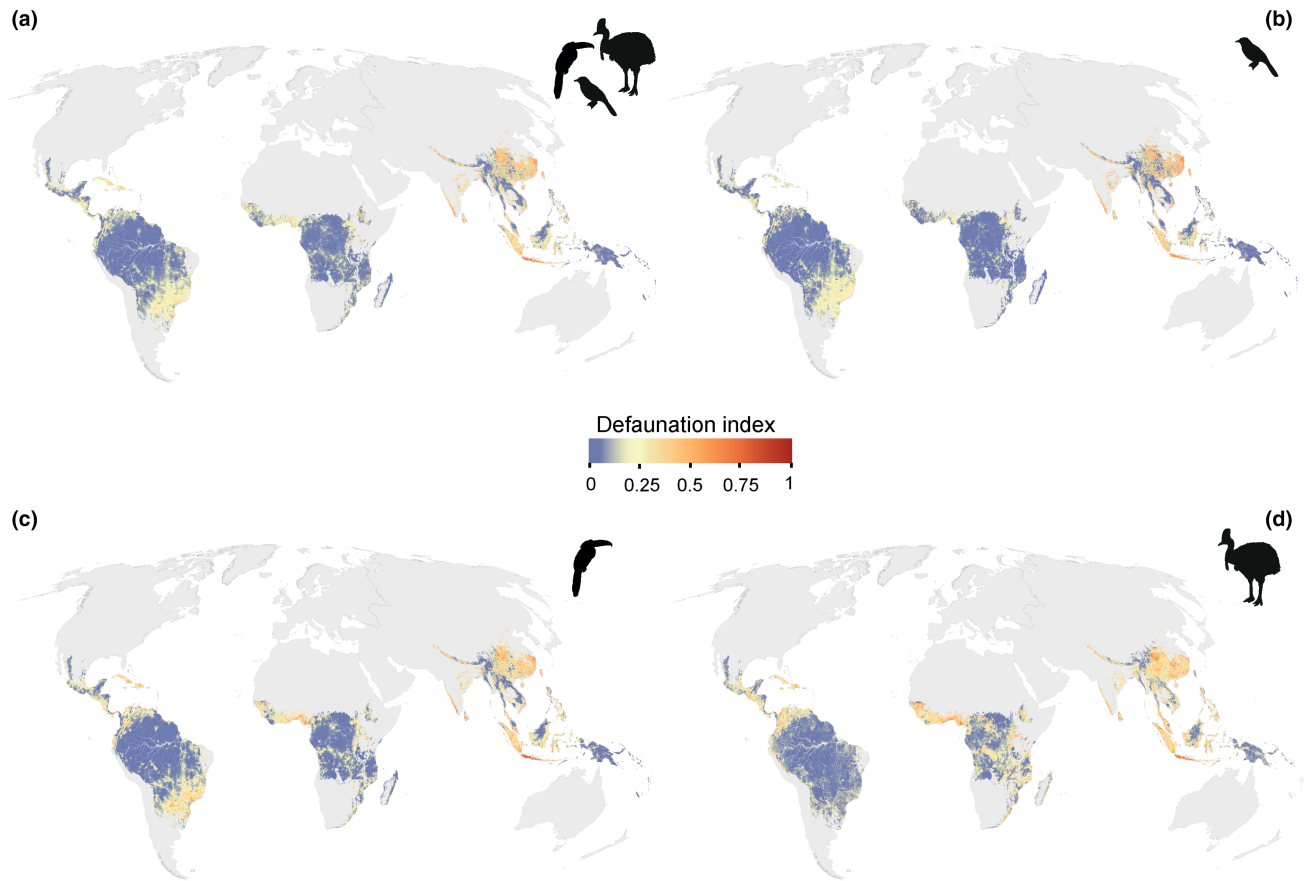


FIGURE 2 Predicted spatial patterns of hunting-induced defaunation of bird communities (a) for all tropical bird species ($n=8600$), (b) for small-bodied ($n=5942$), (c) medium-bodied ($n=2140$) and (d) large-bodied ($n=518$) bird species.

Our study provides valuable insights into the complex dynamics and drivers of exploitation pressure on tropical bird populations, and particularly, the interplay between commercial and subsistence exploitation, including their asymmetrical effects on bird species as a function of body size. The strong relationships between bird abundance and distance to hunter's access points and travel time to major cities pinpoint the significant role of accessibility in shaping bird abundance and wildlife communities (Abrahams et al., 2017; Benítez-López et al., 2017, 2019; Harris et al., 2017; Peres & Lake, 2003; Sagar et al., 2023). Interestingly, these predictors showed uncertain effects in the changes in the abundance (e.g. travel time) and probability of local extinction (e.g. distance to hunters access point), but clear and strong effects when considering its interaction with the body mass of the bird species, thus indicating different functional responses of bird species under similar hunting pressure.

Large-bodied species' vulnerability in highly accessible sites suggests that hunting pressure near rural settlements can have severe consequences for the persistence of this size class. Rural communities rely on hunting for sustenance, and large game birds often provide a vital protein source for these populations. Hence, subsistence hunters tend to preferentially target large-bodied game species, likely due to their greater nutritional returns per unit effort (Begazo & Bodmer, 1998; Borgerson et al., 2023; Jerzolimski & Peres, 2003; Whytock et al., 2016). However, large-bodied species tend to have

slower life histories than small-bodied birds (Cooke et al., 2019) and are thus able to sustain lower levels of hunting pressure. The increased vulnerability of large-bodied species in rural areas and near to human settlements suggests that hunting practices need to be better managed to ensure their sustainable use. Implementing community-based conservation and sustainable hunting practices can help strike a balance between meeting food security of local communities and conserving harvest-sensitive species (Campos-Silva et al., 2017; dos Reis & Benchimol, 2023; Muench & Martínez-Ramos, 2016) particularly large-bodied species, most of which (491 of 526 species; 93.3%) are harvested (IUCN, 2022).

On the other hand, an increase in small-bodied bird abundance at highly accessible sites from hunter's settlements may indicate potential ecological release from competition and predation when the larger competitors are extirpated or reduced in numbers due to hunting. These results align well with previous studies exploring changes in community composition for mammals in hunted versus unhunted sites (Benítez-López et al., 2019; Peres & Dolman, 2000; Peres & Palacios, 2007; Scabin & Peres, 2021). Yet, we found contrasting impacts of hunting between small- and large-bodied bird species in relation to proximity to urban markets, reflecting preference dynamics in both commercial and subsistence hunting scenarios. Our results suggest that the vicinity of urban markets are significant hotspots for the extraction of small- and medium-sized bird species where high

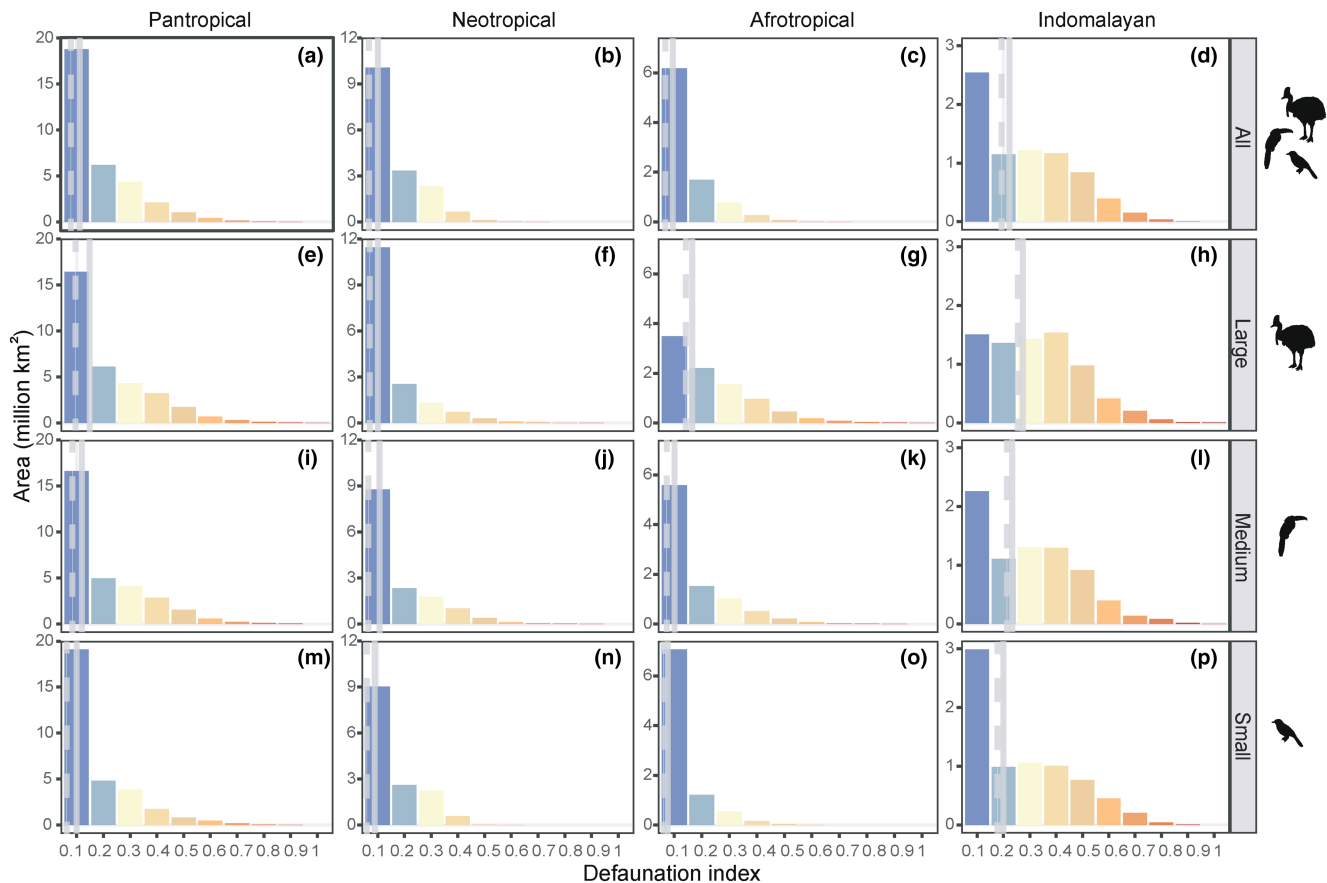


FIGURE 3 Overall distribution of tropical forest area ($\times 10^6$ km²) for each geographic realm (Neotropical, Afrotropical and Indomalayan) and body size class. The first column indicates a pantropical assessment including all three realms. Rows, from upper to lower, indicate the differential degree of avian defaunation for all, large-, medium- and small-bodied species, respectively. Vertical lines in each plot show mean (solid) and median (dashed) values of defaunation.

accessibility to urban centres facilitates the cost–benefit equation to pursue those populations (Harris et al., 2017; Sagar et al., 2023). This preference for smaller and medium-bodied species (e.g. parrots) for commercial exploitation may be driven by the ease of transport and the lower overhead costs associated with handling and trading these birds (Sodhi et al., 2011; Su et al., 2014). Our findings are consistent with these size-biased patterns of selectivity, showing that commercial trapping for the pet trade disproportionately affects small-bodied species, particularly in wealthier sites with high accessibility to urban markets. The influence of human population density on the probability of local extinction suggests that increasing human presence can exacerbate harvesting pressure, not least because of larger demand for wild meat (Fa et al., 2022; Ingram et al., 2021) and birds for the life wildlife trade (Ribeiro et al., 2019), thus underscoring the need for targeted conservation efforts in tropical forest areas experiencing rapid human population growth. Furthermore, it is noteworthy that protection status did not show reliable effects on changes in abundance and probability of local extinction. This may indicate potential gaps in the implementation of otherwise underfunded and ineffective protected areas (Bruner et al., 2001; Geldmann et al., 2019) or the establishment of protection status in the aftermath of overharvesting (Harrison, 2011).

Moreover, we found credible effects of the interaction between distance to hunter access points and NPP, but not when considering the effect of NPP solely. We found a weak buffer effect of NPP on hunting pressure which potentially indicates that areas with low net primary productivity may experience more pronounced hunting-induced population depletion (Peres & Dolman, 2000). However, we found contrasting responses on the probability of extinction, where highly productive sites were associated with a higher probability of local extinction due to hunting. Net primary productivity is indicative of standing game biomass in tropical forests (Fa et al., 2022). Additionally, hunters tend to target and capture more abundant species in larger numbers, a phenomenon known as ‘harvesting bias’ (Alvard & Winarni, 1999; Borgerson et al., 2023; Redmond et al., 2006; Sodhi et al., 2011). This preference can be attributed to maximizing their harvest to meet their resource needs, and abundant species provide a more readily available source of individuals to catch (Alvard & Winarni, 1999; Borgerson et al., 2023). Under this premise, highly productive sites may experience higher levels of hunting pressure due to spatial selectivity targeting higher available biomass. Yet, further research is needed to validate and better understand the relationship between net primary productivity and hunting-induced defaunation of tropical vertebrate populations.

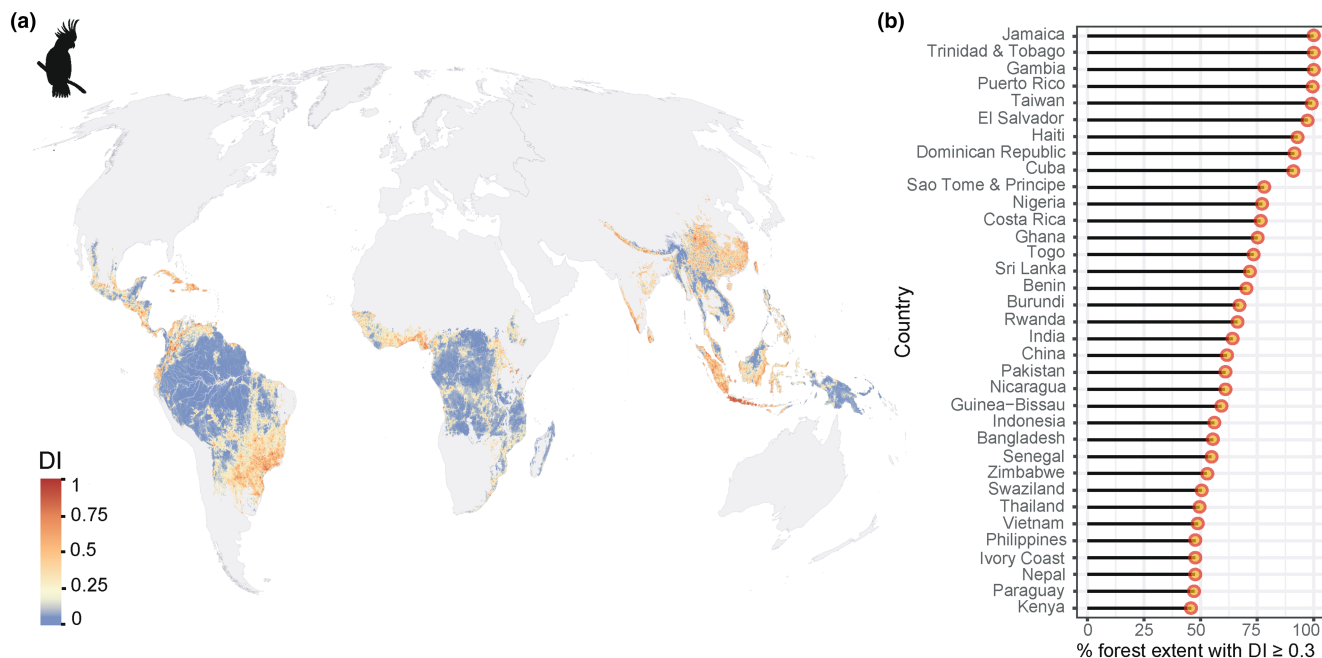


FIGURE 4 (a) Map of hunting-induced defaunation for bird species exploited for the pet trade ($n=2200$ species). (b) Ranking of 35 tropical countries with the greatest relative extent of forest area with a $DI \geq 0.3$ (estimated abundance declines $\geq 30\%$ for bird species traded as pets).

On the basis of the estimated relationships with drivers of hunting pressure, we predicted that the impacts of subsistence hunting for bird species are mostly allocated within SE Asia and Caribbean Islands, which are congruent with previous studies reporting the preference of birds as wild meat in those sites (Redmond et al., 2006). Consequently, this spatial pattern aligns well with the spatial pattern of hunting-induced defaunation for large bird species at a pantropical scale, where we estimated that ca. 50% of Indomalayan realm is severely defaunated due to hunting. The local extinction and drastic reductions in abundance of large-bodied species can have severe consequences on ecosystem functionality due to the pivotal and non-redundant role in processes related to seed dispersal and forest regeneration (Naniwadekar et al., 2019; Peres et al., 2016). Under this premise, we estimated that 4.62, 3.28 and 2.47 mill. km² in the Indomalayan, Afrotropical and Neotropical tropical humid forests respectively can be threatened by the cryptic impacts of hunting, triggering shifts in ecological functioning by impairing seed dispersal and predation rates, as well as predation processes (top-down and bottom-up regulation) (Benítez-López et al., 2019; Ripple et al., 2014, 2015).

Our model projections across traded species indicated that China, Indonesia, Taiwan, Brazil and the Caribbean islands are the regions with the highest trade-based avian defaunation levels. Our results are consistent with other studies that have highlighted the high volume and lucrative commerce of wild birds involved in both the legal and illegal pet trade in countries such as China, Taiwan, Vietnam, Malaysia, Indonesia and Brazil (Alves et al., 2013; Harris et al., 2017; Nijman, 2010; Sagar et al., 2023; Su et al., 2014). For example, it is worth mentioning the estimated defaunation of Java

island (0.8 ± 0.08), with a total predicted extent of 0 km² of intact forests and 73,201 km² (~88.4% of its tropical forest extent) with decimated populations ($DI \geq 0.7$) for bird species subjected to pet trade. Recent surveys estimated that ca. 66–84 million cage birds are kept by one-third of Java's 36 mill. households (Marshall et al., 2020). Well-known examples of this vast impact on the island are the cases of *Pycnonotus zeylanicus*, *Acridotheres melanopterus* or *Nisaetus bartelsi* which were decimated due to the detrimental impacts of live-trapping (Eaton et al., 2015). Currently, ~60% of all harvested bird species (2200 of 3682) across the tropics are traded as pets (IUCN, 2022). Yet, non-traded species may also be threatened in the near future by the growing demand for products and/or pets. With the decline in the availability of a targeted species, trade targets promptly transition to non-traded conspecifics (Scheffers et al., 2019), thereby exacerbating the wariness of the yet-to-come declines of non-traded species in the defaunation hotspots that we identified. Hence, we further emphasize the need for increased law enforcement and public awareness campaigns to curb market demand for vulnerable bird species in tropical countries where the legal or illegal trade is expected to grow in the incoming decades (Harris et al., 2017; Ribeiro et al., 2019).

While our study provides valuable insights into the cryptic impacts of overhunting, it is important to note that, in many cases, hunting practices are compounded by the synergistic effects of other drivers of defaunation such as habitat loss, degradation or, in the future, climate change (Bogoni et al., 2022; Gallego-Zamorano et al., 2020; Mancini et al., 2023; Romero-Muñoz et al., 2020). Hence, our results are particularly useful for quantifying hunting impacts in continuous, undisturbed forests, but less so in forest

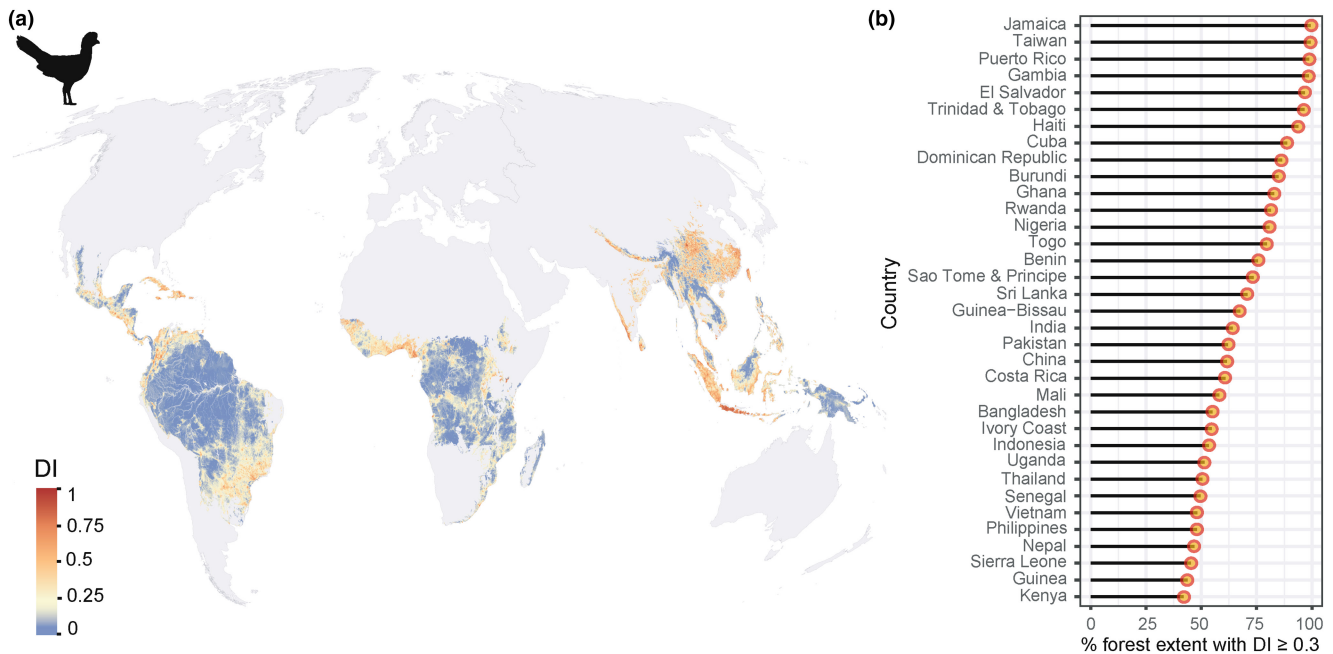


FIGURE 5 (a) Map of hunting-induced defaunation for bird species hunted for food consumption ($n = 1076$). (b) Ranking of 35 tropical countries with the greatest relative extent of forest area with a $DI \geq 0.3$ (estimated abundance decline $\geq 30\%$ for bird species hunted for food consumption).

frontiers and fragmented landscapes, where they should be combined with other modelling approaches and quantitative data capturing species habitat preferences, tolerance to degradation and human presence, and dispersal ability. It is worth noting, however, that while our model elucidates the drivers of hunting-induced declines in bird abundance and local extinctions, its predictive capacity is limited. Therefore, the maps generated are not intended to be prescriptive of where populations have gone extinct, but rather provide a representation of the expected spatial gradient of hunting impacts, acknowledging the inherent uncertainty at the pixel level. Additionally, our modelling approach can be conservative when estimating hunting impacts as we are assuming that abundance estimates from hunted and non-hunted sites come from populations at equilibrium with local hunting pressure, thereby ignoring delayed impacts on bird abundance. Also, hunting pressure may persist over time, with hunters shifting to more remote areas once medium- and large-bodied bird species are depleted (Coad et al., 2013; Peres & Lake, 2003). Dynamic spatially explicit population models that include the spatial distribution of hunting effort in relation to prey availability, the frequency of hunts, settlement population size and kill efficiency (e.g. Levi et al., 2011; Peres et al., 2016) could be scaled up to larger scales to better reflect population dynamics of species subject to hunting pressure across space and time.

5 | CONCLUSIONS

Our analysis highlights the potential of macroecological models to provide valuable insights into the large-scale spatial patterns of

hunting-induced defaunation and identify the drivers of overexploitation pressure worldwide. The large-scale dataset we used uncovered significant relationships between the physical accessibility to hunted sites and urban markets, and projected declines in bird populations at a pantropical scale. Our findings underscore the urgent need for conservation efforts that address the root causes of unsustainable hunting and trapping practices worldwide for bird species across their size spectrum. Furthermore, identifying key drivers of hunting pressure provides crucial guidance for targeted interventions and policy measures aimed to mitigate the detrimental effects of direct overexploitation on biodiversity in the identified defaunation hotspots (e.g. SE Asia, West Africa, South Brazil or Caribbean islands). Our study emphasizes the importance of understanding the complex interactions between harvesting offtake and wildlife populations to inform effective conservation strategies and foster a more sustainable coexistence between humans and tropical wildlife.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13855>.

DATA AVAILABILITY STATEMENT

Data and R codes used in this study are deposited in Dryad (<https://doi.org/10.5061/dryad.2z34tmpsw>).

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BIOSKETCH

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Author contributions: ABL conceived the original idea. IFA and ABL performed the literature review and compiled abundance data from ecological studies. HSCS, CRH, EG, PMF, MVK, ABS and CP provided field data on bird abundance in hunted and non-hunted sites. IFA led the modelling, writing of the manuscript and design of figures. LS and ABL coordinated the modelling approach. All authors contributed to the writing and reviewing of the manuscript.

SUPPORTING INFORMATION

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

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