Title: Traits, threats, and popularity explain extinction risk of birds globally
Running title: Predicting bird extinction risk globally
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Abstract

As the biodiversity crisis deepens, understanding extinction risk is essential for conserving at-risk species and triaging those potentially overlooked. Extinction risk is often estimated with traits (e.g. larger species are more vulnerable) without considering the context of threats or human bias in the listing process (e.g. more popular species are more or less likely to be listed). On the other hand, current global assessments of threats do not include the context of the biological variation of species (e.g. hunting mainly impacts large species). Here, we show that biological traits, threats, and popularity all interact to influence extinction risk for birds globally. We find particularly strong interactions between body mass and hunting (large body mass increases extinction risk for species threatened by hunting), habitat breadth and agriculture (narrow habitat breadth increases extinction risk for species threatened by agriculture), body mass and agriculture (small bodied species have increased extinction risk when threatened by agriculture) and range size and agriculture (for mid range-sized species, agriculture increases extinction risk). Further, we find that extinction risk increases with popularity, likely reflecting the increased chance of popular species having been listed given the same traits and threats. Overall, our results show the importance and necessity of including both biological and human biases, as well as human-posed threats when estimating extinction risk and identifying regions harbouring disproportionally high numbers of vulnerable species.

Introduction

The alarming rate of global biodiversity loss caused by human activities is a major concern for conservationists and policymakers worldwide (Ceballos et al., 2015; De Vos et al., 2015; IPBES, 2019). Preventing the extinction of species is one of the key global 2050 biodiversity goals (Goal A) and 2030 targets (Target 4) defined in the Kunming-Montreal Global Biodiversity Framework (K-M GBF) (CBD COP, 2022). To this end, major efforts are underway globally to assess conservation status of species, with the most comprehensive being the International Union for Conservation of Nature's Red List of Threatened Species (hereafter, IUCN Red List) (IUCN, 2021), including animal, fungi, and plant species (Ceballos et al., 2015).

A better understanding of the factors influencing extinction risk enables us to predict and anticipate potential loss of species (Donaldson et al. 2017). Species declines are linked to human threats (Pimm et al. 2014, Joppa et al. 2016), that have caused current extinction rates to be much higher than the background rate of extinction (Ceballos et al. 2015). Humans have affected species populations historically by hunting (i.e. megafauna extinctions, Sales et al. 2022; Svenning et al. 2024) and habitat modification, which leads to reduced species' ranges (Pimm et al. 2014). The main current threats to biodiversity are loss and conversion of habitat, excessive exploitation and persecution of many species, pollution, invasive species, and climate change (IPBES, 2019), and IUCN has assessed threats globally to most birds, amphibians and mammals (IUCN, 2021). While this work is highly valuable for identifying major threats and regions of concern, it does not typically incorporate a biological basis for why threats impact certain types of species and lacks information on the magnitude of each threat on species.

Biological information is essential to incorporate into threats assessments because a body of literature tells us that intrinsic attributes (life-history and ecological strategies) or traits influence extinction risk (Chichorro et al. 2019). That is because these attributes make species susceptible to particular threats (Purvis et al. 2005). Extinction patterns under human pressures are not random but are linked to demographic responses via specific traits such as body size, habitat specialization, and life history strategies (Richards et al., 2021). This trait-based approach also has the advantage of serving the purpose of inferring extinction risk states (via trait-extinction risk relationships) when the traditional data used for risk assessments are lacking (Chichorro et al., 2022; Richards et al., 2021). And, while this research began in the absence of threats information (Bennett et al. 2005; Purvis et al. 2005), some papers have begun to incorporate threats into trait-based extinction risk models (González-Suárez et al.; 2013, Murray et al., 2014).

The inclusion of both traits and threats into extinction risk modelling has yielded some interesting results (González-Suárez et al.; 2013, Murray et al., 2014). While it has generally been known that larger species are more prone to extinction resulting in trophic downgrading of ecosystems globally (Svenning et al. 2016; 2024), such relationships are likely dependent on the threats impacting species of interest. Larger vertebrates are more vulnerable to hunting than smaller species, but smaller vertebrates may face a relatively higher risk of extinction due to habitat loss (Ripple et al. 2017). Consequently, predicting extinction risk based on species traits can be context-dependent (Murray et al., 2014), and it is likely, though not widely tested, that both traits and threats are essential for predicting species' extinction risk.

Finally, estimates of extinction risk could be biased by humans. Most bias results from data availability limitations and lag time between detecting impacts and listing the species (Trull et al., 2017). Imperfect sampling and errors in population-level data can also lead to unreliable trends and inaccurate quantification of extinction risk, particularly for lesser-known species (Fox et al., 2019). Finally, certain species may receive more attention and resources for

monitoring and conservation due to their popularity (Ducarme et al., 2013), which can create biases in risk assessments (Böhm et al., 2013, Burkhead et al., 2012, Donaldson et al., 2016).

While this taxonomic bias in research has long been recognized (Clark & May, 2002; Ward, 2014; Troudet et al. 2017), measuring species popularity directly is difficult and resource-intensive, often relying on extensive surveys with many respondents (e.g., Macdonald et al., 2015; Albert et al., 2018; Calaghan et al. 2021). Consequently, such studies are rare, usually focusing on small sets of species at the national or regional level (Berti et al., 2020, Schuetz & Johnston, 2019). Research using indirect measures like internet metrics is scarce and often limited to small geographic areas (e.g., Brambilla et al., 2013; Żmihorski et al., 2013). However, recent studies have relied on proxies for human bias at larger scales (Millard et al. 2021), and this approach could be borrowed for estimating human bias in extinction risk models.

Here, we address the relative and combined roles of these three main factors: traits, threats and bias in estimating species extinction risk (i.e. the probability of being at-risk). For birds globally, we first ask how traits (body mass, habitat breadth, range size, and migration) and human-posed threats influence bird extinction risk and whether the overall influence of traits changes for different threats faced by these species. Second, we ask if popular and data rich species (measured via the number of Google searches on the web and the number of GBIF records) are more or less likely to be listed than unpopular species with similar traits and threats. Finally, we identify regions of the world where our model aligns and deviates from the IUCN extinction risk listings, providing a global overview of species and entire regions that are likely more vulnerable than current indicators suggest.

Methods

Data acquisition and compilation

Traits

We selected relevant traits with high species coverage (n=8394, 77% of birds globally) for estimating extinction risk, including body mass, range size, migration, and habitat breadth (González-Suárez et al., 2013; Ripple et al., 2017; Chichorro et al., 2019; Richards et al., 2021; Chichorro et al. 2022). We used body mass, range size, and migration from AVONET (Tobias et al., 2022). Body mass was available in grams and range size in square kilometers and migration was an index from 1-3, "1" being completely sedentary species, "2" being species of which some populations migrate occasionally, and "3" species in which most of the populations of a species migrate. For our analysis, we aggregated categories to "1" for fully migratory or partially migratory species and "0" for sedentary species for simplicity. We obtained habitat breadth data from Ducatez (2017), who developed metrics of habitat breadth based on the similarity of the habitats where a species is found in terms of species composition. In this metric, a generalist species is a species that occurs in a range of habitat categories (maximum = 14) containing heterogeneous species composition, whereas a specialist species will be found only in habitats that contain a more limited set of other species so that the number of habitats where it occurs in practice is more constrained (minimum = 0).

Threats

We obtained threat information from IUCN for each species using the rredlist R package (Chamberlain, 2020). IUCN structures threat data by categorizing them into various threat types, such as habitat loss, pollution, and climate change, to assess the diverse and multifaceted challenges facing endangered species and ecosystems worldwide. The IUCN Red List Threats

Classification Scheme version 3.3 (IUCN–CMP, 2022) classifies threats into 12 major categories, of which the most prominent and frequent 5 were used here, following Harfoot et al., (2021) and the Living Planet Report (WWF, 2022): agriculture (2), climate change (11), invasive species (8), pollution (9) and resource use (5), from which we further obtained species threatened by hunting (5.1) and logging (5.3).

Popularity

To account for popularity, we used the number of Google searches (Google Hits) and the number of Global Biodiversity Information Facility (GBIF) observations for all bird species globally from 2004-2021. From GBIF we calculated the number of observations for each bird species per year, using the R package gbifdb (Boettiger, 2021). One could argue that GBIF is highly correlated with species range size, but that was not the case in this study, as we found only a moderate correlation between the two (r = 0.5). We obtained the number of Google searches per species per year using species' common names (English, Spanish and French) in Google Trends data through the package gtrendsR (Massicotte & Eddelbuettel, 2022). Google Trends provides a comprehensive overview of Google search activity across different geographies over time. Interest over time data shows the relative frequency of searches (0-100) for a given topic compared to all other topics searched (in this case, all other species) over a defined period within a given geographic area. The most searched item gets a 100 score and then the others follow proportionally. In the model, we test the interaction between Google Hits and GBIF number of observations, to see if species that are more looked up online are also the ones with more recorded observations, and we predicted there to be a positive relationship between the two.

Analyses and modelling

For our analyses, we used generalized mixed models (GLMMs) using the glmer function in the lme4 R-package (Bates et al., 2020). We used extinction risk as a binary response with a logit link function, categorizing species as 1 - threatened (VU/EN/CR) or 0 - non-threatened (LC/NT) according to the IUCN Red List. As fixed factors, we used traits (body mass, range size, habitat breadth and migration), threats (agriculture, hunting, climate change, logging, pollution and invasive species) both as main effects and interactions between each trait and threat. We included GBIF and Google Hits numbers both as main effects and as an interaction between the two. We used logged and standardized values for all continuous traits (body mass, range size, habitat breadth, GBIF and Google Hits) and used migration as a binary variable. Threats were binary (0 - not threatened by specific threat, 1 - threatened). To account for potential variations within taxonomic orders and birds that use different habitat types, we included random intercepts for bird order and type of predominant habitat for a given species (both from Tobias et al. 2022) in our models. To obtain predictions and visualize interactions between traits and threats, we used the package ggeffects (Lüdecke, 2018) to plot marginal effects of explanatory variables. We infer that significant trait-threat interactions suggested by our data indicate that the link between extinction risk and a given trait/threat are conditional dependent on the trait of the species and if it is impacted by a given threat. We used the full model with threats and traits interacting to test for individual importance of threats and traits separately and combined, along with GBIF and Google Hits.

Mapping

We used breeding range maps used by Pollock et al. (2017) for 9,993 non-marine birds gridded into 110 km² equal-area grid cells, which were previously validated as the finest justifiable for these data globally without inflating false positives (Jetz et al., 2008). We

identified areas with disproportionately high amounts of vulnerable species in agreement and disagreement between our model and the IUCN Red List, based on species distribution range mentioned above. To do this, we converted the model predictions to binary (threatened or not) for each species based on an optimized threshold using the ROCR package (Sing et al. 2005) to calculate true positive rates (TPR) and false positive rates (FPR) across various threshold values, comparing model predictions with observed data. We then chose an intermediate threshold value (0.25) to maximize TPR and minimize FPR. We matched this information to species distributions to produce a bivariate map of the number of species in each cell that are considered at least vulnerable (VU) by both IUCN and our models, and those areas of vulnerability according to IUCN only or our model only.

Results

We found that the three main factors (traits, threats and popularity) all influenced extinction risk when all other factors were controlled for (Fig. 1). All traits, except habitat breadth, had significant effects with large body, migratory species, small ranges or few GBIF records having the greatest extinction risk. The main effects of the individual threats were also all significant, except for logging. The strongest overall effect was that of agriculture (Fig 1). Other threats (hunting, climate change, pollution, invasive species) also substantially elevate extinction risk with the exception being logging with no significant effect across all species with all other factors considered (Fig. 1). Finally, popularity was also a significant factor, with more popular species more likely to be listed as at-risk given their respective threats and traits (Fig. 1, 3). All results reported here are for the final model fit on all data. Based on 10-fold cross-validation with independent training and testing sets (70:30), models exhibited robust discriminative ability, with an average AUC of 0.9648 (SD = 0.0071).

Threat vulnerability given traits

We found interactions between traits and threats, namely: body mass with climate change, pollution, hunting and invasive species; range size with agriculture and climate change; habitat breadth with agriculture; and, lastly, migration with logging and agriculture (Fig 1b-e).

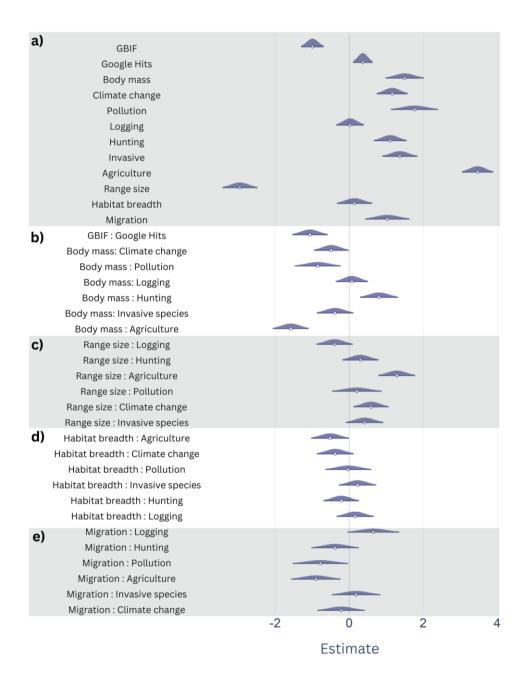


Figure 1: Log-odds of extinction risk for traits and threats represented with standardized regression coefficients (GLMMs), with 95% confidence intervals for all bird species. Confidence intervals not overlapping with 0 indicate a smaller than 5 % probability that the slope of the relationship is zero. The model included habitat

type and bird order as random effects in addition to the main-level parameters and interactions between traits and threats. Positive values indicate a positive relationship between the variable and extinction risk and vice-versa (a). Interactions with coefficients different from zero indicate significant interactions between variables (b-e).

Body mass

Overall, the effect of body mass on extinction risk was positive, as larger species are more at risk than smaller ones given all other effects are controlled by holding them at their mean value (Fig. 1). A particularly strong interaction was found for body mass and hunting, where large species that are threatened by hunting have up to 75% of probability of extinction risk, while large species that are not threatened by hunting have only about 20% risk (Fig. 2a). Unlike hunting, the interaction between body mass and agriculture is negative meaning smaller species are disproportionately at risk from agriculture relative to larger species, whose risk is better explained by hunting (Fig. 1, Fig 2b). Similarly, invasive species and climate change threaten large species less (and smaller more) than expected based on the overall heightened risk of larger species (interaction effects in Fig 1, Fig 2d). Essentially, small species tend to be at low risk unless they are threatened by climate change, pollution or agriculture.

Range size

Small range size was the strongest explanatory variable for extinction risk amongst traits (Fig. 1), and we found significant interactions between range size and agriculture, and range size and climate change (Fig. 2e and f). While all narrow-ranged species have a very high risk of being listed, species of intermediate ranges had the largest difference between those threatened with agriculture and those not threatened by agriculture, whereas wide-ranging species have low extinction risk regardless (Fig. 2e). The same happens with climate change (Fig. 2f), even though the difference in risk for intermediate-ranged species is much smaller than for those threatened with agriculture.

Habitat breadth

While habitat breadth was not a significant main effect, there was significant negative interaction with agriculture (Fig. 1) with most habitat specialists (habitat breadth=1) being substantially at higher risk if threatened by agriculture, going from ~5% to ~25% or a 5-fold increase in extinction risk (Fig. 2g).

Migration

Overall, migratory birds had a higher extinction risk than their sedentary counterparts (Fig. 1). Particularly, we found that migratory birds threatened by pollution (Fig. 2h) and agriculture (Fig. 2i) had higher extinction risk when compared to sedentary ones, even though the presence of threats had an effect of increasing risk even for sedentary species for both. threats.

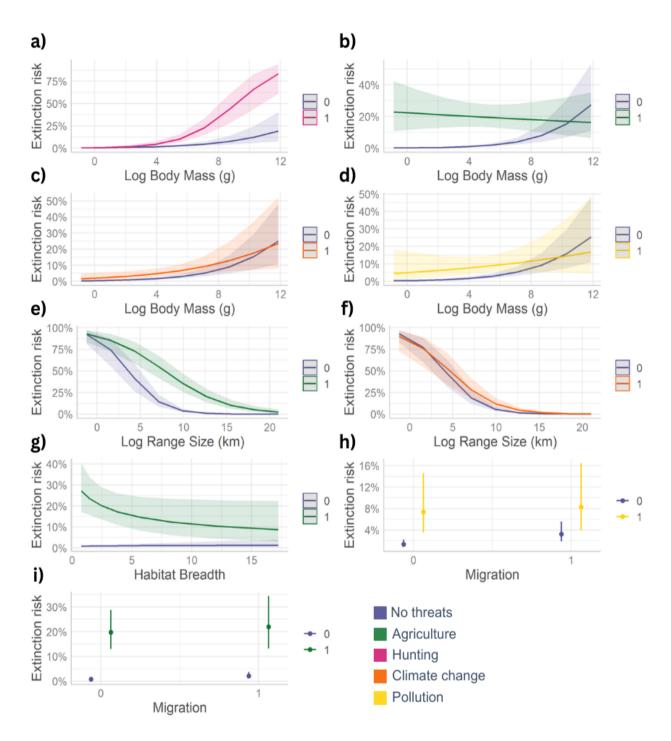


Figure 2: Extinction risk explained by interactions of traits and threats (partial effects). Predicted extinction risk for bird species a) threatened (pink) and not threatened by hunting (deep blue), b) agriculture (green), c) climate change (orange), d) pollution (yellow), given their body mass. Predicted extinction risk given range size for birds threatened by e) agriculture and f) climate change. Predicted extinction risk given habitat breadth for birds threatened by g) agriculture. Predicted extinction risk for 1 - migratory and 0 - sedentary birds threatened by h) pollution and i) agriculture.

Extinction risk and popularity metrics

Overall, popularity was a significant factor to predict extinction risk, with more popular species (more Google Hits) being more likely to be listed as at-risk given their respective threats and traits, especially species with more google hits coupled with fewer GBIF records indicated by the interaction between google hits and GBIF (Fig. 1, 3). Examples of these are as the pink pigeon (*Nesoenas mayeri*), the blue duck (*Hymenolaimus malacorhynchus*), endemic respectively to Mauritius and New Zealand and the hyacinth macaw (*Anodorhynchus hyacinthinus*), from South America.



Figure 3: Predicted extinction risk for species given Google Hits and GBIF number of observations derived from model. Google Hits is relative to the most searched terms (0-100). GBIF numbers of observations were logged (log10).

Spatial predictions

In most areas, our model identified more species at high risk than those listed by IUCN (Fig 4, in blue). These areas comprise large areas of Southeastern South America, sub-Saharan Africa, the Mediterranean, Central and Southeast Asia, the Andes, and Indonesia, to

name a few large regions. Our model also predicted moderately high numbers of species to be at risk in North America and large portions of Asia and Oceania (in lighter blue). On the other hand, some regions had greater portions of species listed by IUCN than the model predicted based on threats, traits and popularity. These tended to be high latitudes of the Northern Hemisphere, namely Canada, Alaska and Russia. Finally, some areas had high numbers of vulnerable species according to both listings and the model. These include some regions of the Amazon and Central Andes and South America (in purple), with moderate numbers of species in large portions of the Amazon, Northeastern United States, Northern Europe and Asia (in lighter purple).

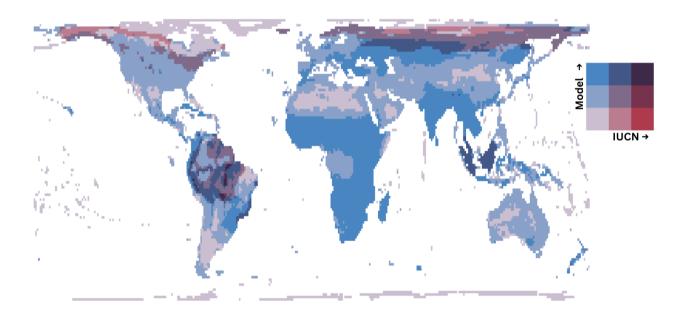


Figure 4. Bivariate map showing the number of species at risk given the model (maximum 38 species, in blue) and IUCN Red List (maximum 12 species, in red). Species that are considered at risk by both model and IUCN are in purple.

Discussion

We asked how well traits, threats, and popularity explain global extinction risk of birds, and found that all three were important factors, but often context dependent – threats impact species differently depending on their traits. Specifically we found that: 1) threats, especially agriculture, climate change, hunting and pollution, strongly explained extinction risk, 2) traits, especially, range-size, body mass, and migration, were also strong predictors and more certain than threats, 3) some trait-threat interactions were notable including the disproportionate impact of hunting on large species and agriculture on small and migratory species, 4) popular species are more likely to be listed than their threats and traits indicate, particularly when limited GBIF data were available, and 5) several regions of the world potentially have many more vulnerable species than the IUCN Red List indicates. This paper demonstrates how the integration of biologically relevant attributes, threat information and human bias together can help the understanding and prediction of species extinction risk.

Threat information needs a biological context

Risk, generally speaking, is some combination of the likelihood of an event happening and the impact if it does. For species risk or vulnerability assessments, the equation often includes sensitivity, adaptive capacity, and exposure, with traits being used to explain sensitivity and adaptive capacity and threats being the exposure (e.g. Foden et al. 2013). This risk calculation is based on assumptions that traits and threats lead to increased risk, so our results generally support these methods. Our results lend more support to recent work showing that the major threats to biodiversity (IPBES 2019), are not uniformly impacting species, but exert a somewhat predictable influence based on relatively simple biological traits of species (González-Suárez et al. 2013, Chichorro et al. 2019, Richards et al. 2021). We discuss some examples below.

Body mass especially important for species threatened by hunting

Our results corroborate literature showing that larger-bodied birds are inherently more prone to extinction (Ripple et al., 2017; Chichorro et al., 2022; González-Suárez et al., 2013 for mammals). Large-bodied species typically exhibit lower reproductive rates, smaller annual fecundity, and clutch sizes, factors associated with increased vulnerability to stochastic events (Bennett et al., 2005). However, we did not find a significant interaction between body size and other threats for birds, unlike observations in mammals, where smaller body size predicts vulnerability to habitat-related effects like agriculture and logging (González-Suárez et al., 2013). We did find that large species are particularly more threatened by hunting, in alignment with the literature, e. g. Benítez-López et al. (2017) that showed hunters typically go longer distances for larger-bodied mammal and bird species.

Range size (still) a consistent predictor of extinction risk

Range size is directly tied to the listing process, specifically for criteria B (IUCN, 2012), and has had consistent results in predicting extinction risk (Harris & Pimm, 2011; Henry et al. 2023; Ripple et al., 2017;), including in the present study (Fig. 1). We additionally found that small-ranged species are even more vulnerable if they are exposed to agriculture or climate change. That was expected for threats that modify habitat (indirect threats, see González-Suárez et al. 2013), such as agriculture and climate change. This can be exemplified by a study by Rushing et al. (2020), who found a contracting latitudinal distribution of Neotropical birds due to climate change.

Migration increases extinction risk of birds

We found that migratory birds have greater extinction risk than sedentary species given their traits and threats, which is supported by a body of research on the myriads of challenges facing these seasonal nomads. Migratory species are at high risk due to factors like climateinduced phenological mismatches, reliance on multiple habitats, and increased competition in temperate regions (Amano and Yamaura, 2007; Jiguet et al., 2010; Thaxter et al., 2010; Flousek et al., 2015). Interestingly, migratory and sedentary birds tended to be similarly threatened by agriculture and pollution. This corroborates the literature, since, as tropical forests undergo clearance, an increasing number of migratory birds inhabit agricultural and disturbed habitats during the wintering season, and if these habitats prove to be of lower quality compared to natural forests, the conversion of tropical land could contribute to population declines (Johnson et al. 2006). Additionally, it is documented that air pollution and light pollution negatively affect migration, the latter especially in birds who migrate at night (Cabrera-Cruz et al. 2018).

Narrow habitat breadth predicts vulnerability to different threats in different directions

Previous work has focused on the increased risk of specialists (species with narrow habitat breadth), showing habitat breadth to be one of the few consistent predictors of extinction risk for vertebrates, invertebrates and plants (Chichorro et al. 2022). Our results differ slightly in that, in our model formulation, we only found a context-dependent effect of habitat breadth (habitat specialists have greater vulnerability to agriculture). This provides evidence supporting the hypothesis that traits may not directly affect extinction risk but rather influence vulnerability to specific threats (González-Suárez et al., 2013; Murray et al., 2014).

The potential human bias in the listing process

Our finding that popular species (on average, but especially those that are rare) are more likely to be listed than their traits and threats suggest is an interesting finding and likely reflects some element of human bias. It could be explained by: 1) species are advertised as at-risk and that makes people more interested in them (especially those that are critical), or 2) more popular species are also more studied, and so we have more data to consider them to be threatened, or 3) more popular species have more conservation attention and are more likely to have been listed in the first place.

While 'Google Hits' is increasingly used as a proxy for popularity, there are a number of other useful metrics (Schuetz & Johnston et al. 2019; 2021; Holmes et al. 2024), such as Wikipedia page views as the species awareness index (Millard et al. 2021) or directly measuring people's preferences using pictures of species (Shaw et al. 2024). While we explored the effect of GBIF as helping to define popularity, and it has been used in the past to indicate taxonomic bias in biodiversity occurrence data (Troudet et al. 2017), GBIF more likely reflects commonness, rather than range size (other important and more direct correlates of extinction risk, but that has also been incorporated purposefully in the model). Our findings that range size and GBIF have a similar effect on extinction risk (both small-ranged and low GBIF species increase extinction risk) support this. Our work also shows the complementary but unique aspects of using both range size and GBIF observations to explain extinction risk. A low number of observations of a species in GBIF can indicate species that have few individuals left in nature and tend to be less recorded than more abundant ones, or that fewer people are looking for and recording them. The use of Google Hits plus the interaction between Google hits and GBIF records seemed like a useful approximation of popularity as Google hits increases extinction risk (or the likelihood of being listed given traits), but specially for species with low or medium GBIF observations. Future work is needed to develop robust metrics of popularity,

but our results suggest that popularity is likely an important factor when estimating extinction risk and bias in the listing process.

Spatial patterns of extinction risk

Our work also adds to the recent work mapping out threats (Harfoot et al. 2021) by showing how the risk to biodiversity could be substantially under-estimated in most regions of the world. This suggests that many species in those regions tend to have characteristic traits (large body size, small range size and migration) and threats that would typically render them at-risk. The areas where both the model and IUCN agree many species are under threat, such as the Amazon basin, the Andes and Southeastern Canada (in deep purple and light purple) are not surprising, but yet more evidence that these places are critically important in terms of monitoring, threat mitigation and area protection.

Conclusions

Our study demonstrates that extinction risk is predictable but nuanced and likely remains biased, even for well-studied groups such as birds. Potential human and spatial biases would likely be even more important for other taxonomic groups, since most have been assessed recently and are fairly well studied (Donaldson et al., 2016), despite differences amongst groups (Ducatez & Lefebvre, 2014). There is a strong need to identify both the areas and the species under most threat with species that potentially have heightened risk in different taxa, to facilitate conservation action for a wider range of taxonomic groups, particularly megadiverse and highly endemic regions such as South America, Africa and Southeast Asia. Understanding these complexities is crucial for more accurate and robust extinction risk assessments and conservation efforts.

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Conflict of Interest Statement

The authors declare no conflict of interest.

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