

Colorful birds face heightened extinction risk around the world

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Abstract

Many of the functional traits that mediate extinction risk across the tree life relate indirectly to a species' ability to persist in a changing world. Yet, there are certain traits such as coloration that directly affect human interactions with wildlife. Here, we use an existing dataset of color metrics for 4334 passerine bird species combined with global functional trait data to determine whether two measures of extinction risk covary with the colorfulness i.e., number of color loci for each species. We also control for the potentially confounding effects of three other traits related to a species' size, dispersal ability, and forest dependency. Finally, we assess whether the global relationship between extinction risk and colorfulness varies by 1) biogeographic realm or 2) breeding latitude and human development index. Overall, we find that more colorful passerines are at a greater risk of extinction than more drab species, and this is especially true in Indomalaya and Australasia. We also find that the strength of this relationship is greater at higher breeding latitudes but also in countries with lower human development index. More colorful birds are likely at greater risk of extinction due to the trade in pet birds that favors more attractive species. In stark contrast, there is also a potential bias resulting from the increased public, research, and conservation focus on more charismatic species. More colorful birds should be used as successful conservation emblems if we are to avoid eroding the world's colorfulness.

Introduction

Biodiversity around the world is facing an unprecedented risk of extinction (Barnosky et al. 2011; Ceballos et al. 2015). Habitat loss, climate change, invasive species, and overexploitation interact to filter out vulnerable species and homogenize communities (Clavel et al. 2011; Baiser et al. 2012; Ducatez & Shine 2017). Species vary greatly in their responses to different impacts of global change—with many losers and some winners (McKinney & Lockwood 1999)—and the fate of these trajectories depends in large part on species' functional traits (Blackburn et al. 2009; Chichorro et al. 2022; Hua et al. 2023; Neate-Clegg et al. 2023). Many aspects of a species' morphology, ecology, and life history can increase the risk of extinction (Wang et al. 2018; Kittelberger et al. 2021; Chichorro et al. 2022). For example, species with lower dispersal ability are less likely to persist in fragmented landscapes (de la Fuente et al. 2022; Weeks et al. 2023); species with more specialized diets are more vulnerable to a loss of resources (Şekercioğlu et al. 2004; Clavel et al. 2011; Neate-Clegg et al. 2023); and species with slow life histories are less able to adapt to rapid environmental change (Carmona et al. 2021; Chichorro et al. 2022). Many of the traits implicated in extinction risk typically relate to whether species can persist in human-altered environments (Chichorro et al. 2022; Neate-Clegg et al. 2023; Neate-Clegg 2024), implying an indirect link between humans and wildlife. Yet, humans often interact directly with wildlife (Nyhus 2016) and those interactions, mediated by traits, can directly affect risk (Scheffers et al. 2019). In particular, many charismatic taxa have an aesthetic value to humans that can help or hinder their ability to persist in a changing world (Frynta et al. 2010; Veríssimo et al. 2014; Romero-Vidal et al. 2020).

Aesthetic beauty is one of the clearest ways that humans value wildlife (McCauley 2006; De Pinho et al. 2014; Santangeli et al. 2023). Species that are more colorful are more likely to be rated positively by people (Santangeli et al. 2023), and colorfulness elicits greater popularity and research attention (Schuetz & Johnston 2019; Adamo et al. 2021; Fischer et al. 2025). Colorfulness is thus a functional trait that relates directly with human value. However, colorfulness can potentially have

contrasting effects on extinction risk. At one end of the spectrum, by valuing attractiveness, people are more likely to recognize threat and rally around colorful plants and animals as symbols of conservation (Veríssimo et al. 2009; Frynta et al. 2010; Garnett et al. 2018). For example, colorful species make better conservation flagships, inspiring a commitment to protection that benefits the wider community of less charismatic species (Veríssimo et al. 2014; Bennett et al. 2015). For millennia, humans have valued iconic, beautiful wildlife and sought to protect those symbols (Wills 2017; Sax 2021). However, colorfulness has a dark side. Humans have always coveted shiny, rare things and this is true of wildlife; we have kept beautiful pets for thousands of years, trading them across continents (van Uhm 2016). This pressure to capture beauty has led to an international pet trade currently worth billions of dollars (Scheffers et al. 2019; Senior et al. 2022). Thus, being colorful could be the cause of extinction or conservation success, and the outcome likely depends on the ways that beauty is valued in different socio-cultural systems around the world.

Birds exemplify this conservation conundrum. They are a ubiquitous group, present in every terrestrial ecosystem, where their size and behavior make them very visible to humans. Their feathers display a remarkable complexity of colors, from bright yellow and red pigments, to iridescent structural blues (Stoddard & Prum 2011). In some parts of the world, colorful birds like the Resplendent Quetzal (*Pharomachrus mocinno*) or birds-of-paradise are key flagships for conservation, while in other regions such as Southeast Asia, colorful birds fuel a highly extractive pet trade (Nijman 2010; Bush et al. 2014; Harris et al. 2017; Chan et al. 2021). Colorfulness in birds can thus act as either a risk factor (Vall-Ilosera & Cassey 2017; Romero-Vidal et al. 2020; Senior et al. 2022) or aid in conservation (Frynta et al. 2010; Garnett et al. 2018), depending on the context. It is therefore critical to understand how socio-ecological context mediates the relationship between extinction risk and colorfulness, while also accounting for the fact that colorfulness covaries with other functional traits that mediate extinction risk (Cooney et al.

2022). As birds are so well-studied, we have ample data on their functional traits to test these hypotheses, including direct quantifications of their colorfulness (Cooney et al. 2022).

Here, we test whether colorfulness predicts conservation concern for the world's songbirds. We use an existing dataset of color measurements (Cooney et al. 2022) to define a proxy for colorfulness. We then model extinction risk (as both a binary and ordinal response variable) as a function of colorfulness, while controlling for several other traits that could potentially covary with extinction risk and colorfulness. Critically, we evaluate three geographic variables—biogeographic realm, absolute breeding latitude, and human development index (HDI)—that could putatively mediate the relationship between extinction risk and colorfulness. Using Bayesian hierarchical models, we test three hypotheses: 1) that colorfulness predicts extinction risk, 2) that the relationship between extinction risk and colorfulness varies with biogeographic realm, and that 3) that the relationship between extinction risk and colorfulness is predicted by breeding latitude and HDI. Finally, we map the areas of the world that contain the most threatened and most colorful birds.

Methods

Data gathering

We based our analysis of the extinction risk of colorfulness on a dataset of color across the world's passerine birds (Cooney et al. 2022). In this dataset, Cooney et al. photographed museum specimens from the Natural History Museum (Tring, UK) and quantified whole-body plumage reflectance information for 4527 bird species in the order Passeriformes. For each species, Cooney et al. provided two metrics of colorfulness: the convex hull volume of color space and the number of occupied color loci. Here, we focus on the number of color loci (hereafter “colorfulness”), as we were most interested in the number of distinct colors each species has (but see Supporting Information and Fig. S2 for an analysis

of convex hull volume). Cooney et al. provided these measures for both the visible spectrum and the spectrum including UV reflectance, but we focused on the visible spectrum as we are interested in how birds appear to most humans. Measures of colorfulness were also provided for both males and females of each species, but we choose to focus on males given that they average more colorful (Cooney et al. 2022) and are more likely to be targeted by people (Cooper et al. 2019) (but see Supporting Information and Fig. S3 for an analysis of female color).

The dataset provided by Cooney et al. was based on the BirdTree.org taxonomy (Jetz et al. 2012). We therefore aligned the taxonomy in this dataset with the most recent taxonomy of BirdLife International: version 9 of the Handbook of the Birds of the World and BirdLife International Digital Checklist of the Birds of the World (Birdlife International 2025). We acknowledge that there has been a lot of taxonomic change in the intervening years (Neate-Clegg et al. 2021a), but taxonomic splits (and lumps) typically involve species that look very similar to one another (but see Supporting Information and Fig. S4 for an analysis including “missing” species). We then extracted the most recent Red List category from the BirdLife checklist. Species recognized by BirdTree.org that are no longer recognized by BirdLife were filtered from the dataset, as were species not determined as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), or Critically Endangered (CR). The resulting dataset contained 4487 species. For this dataset, we derived two numerical metrics of extinction risk: 1) “conservation concern”, a binary variable of whether a species was LC (0) or otherwise (NT, VU, EN, CR) (1); 2) “threat level”, an ordinal variable from 0 (LC) to 4 (CR) (Kittelberger et al. 2021) (see Supporting Information and Fig. S5 for analysis of an alternate binary metric based on threat status).

While we were primarily interested in whether more colorful birds were more threatened, it was important to account for other traits that may confound the signal. Importantly, we note that we are not trying to determine every trait that predicts conservation concern, nor are we trying to explain the most variation possible in our model. Instead, we included traits that 1) are available for all species and 2)

have the potential to covary with both colorfulness and conservation concern. From the Cooney et al. dataset we extracted data on forest dependency and diet. Forest dependency is known to be associated with both colorfulness (Cooney et al. 2022) and extinction risk (Kittelberger et al. 2021). This was originally codified based on species that do not use forest at all (0), vs those that use forest at least to some degree (1). However, there were gaps in this variable, which we filled using information on the BirdLife Datazone species accounts (Birdlife International 2025). Specifically, species with forest as a potential Level 1 habitat received a 1 (and a 0 otherwise). For diet we used a binary variable indicating whether a species was a frugivore/nectarivore (1) or not (0). This variable is positively associated with colorfulness (Cooney et al. 2022) and is putatively linked to extinction risk given the complex relationships between diet and threat (Şekercioglu et al. 2004; Atwood et al. 2020; Benedetti & Morelli 2024). However, we were not able to reproduce the methods used by Cooney et al. to determine diet and fill gaps, and we found no effect of diet on conservation concern for the species that had data. We therefore did not include diet in our final analysis.

From AVONET (Tobias et al. 2022), a global avian trait dataset, we selected two morphological traits: body mass and hand-wing index (HWI). Body mass is known to both predict extinction risk (Kittelberger et al. 2021; Chichorro et al. 2022) and colorfulness (Cooney et al. 2022), and is a suitable proxy for many aspects of life history (Jetz et al. 2008; Bird et al. 2020). HWI, a proxy for dispersal ability (Sheard et al. 2020), is often associated with various anthropogenic threats including habitat loss, urbanization, and climate change (Neate-Clegg et al. 2021b, 2023; Weeks et al. 2023). As an additional measure of life-history strategy, we considered using maximum longevity estimates from (Bird et al. 2020), but we excluded it because we found the values to be strongly correlated with body mass (Pearson's $r = 0.63$).

In addition to our included traits, we wanted to assess whether the relationship between colorfulness and extinction risk varied around the world. To test this, we included three variables that

pertained to the geography of each species' range. The first was absolute breeding latitude—i.e., the mean latitude of occupied cells in a species' breeding range—as a predictor of many biogeographical factors, and available for each species in (Cooney et al. 2022). The second variable we assessed was the mean Human Development Index (HDI) of a species' range as a measure of socio-economic stability (UNDP 2023). Finally, we included biogeographic realm, as human attitudes towards colorful birds are likely to vary predictably around the world based on culture and the available avifauna. This factor also indirectly gets at other possible differences in colorfulness due to biogeography. Critically, all geographic variables interacted with colorfulness in the models (see below), allowing the relationship between colorfulness and extinction risk to vary geographically. We note that, while latitude pertains to the centroid of where species breed, both HDI and realm take into account the entire species range. Thus, a Nearctic-Neotropical migrant has a breeding latitude in the temperate north but an HDI that represents all of the socio-economic landscapes experienced over the annual cycle, and these variables test different hypotheses.

For the latter two variables we made use of shapefiles for the ranges of each species (Birdlife International 2025). We processed and consolidated the range maps for each species using the R package *sf* (Pebesma 2018), focusing only on extant ranges and including breeding and non-breeding ranges. We were not able to validate/consolidate the range maps of 153 species, so these were dropped from the analysis. We then downloaded natural earth world country polygons using the *rnaturalearth* package (<https://docs.roppensci.org/rnaturalearth>). For each species, we calculated the percentage of its range that intersects every country or territory. We then sourced HDI values for the countries of the world (UNDP 2023), and calculated the mean HDI of every species' range, weighted by the percent of its range in each country. For example, if a species was 50% in the US and 50% in Canada its HDI would be the average of the two countries. For biogeographic realm, we assigned every country/territory to one of seven realms: Nearctic, Neotropics, Palearctic, Afrotropics, Indomalaya, Australasia, and Oceania (Fig.

S1). We then assigned the corresponding realm to any species with $\geq 80\%$ of its range in that realm. For the remaining species, we then created higher-order groupings with an increasing number of realms, applying the same 80% cut-off: Americas (Nearctic + Neotropics), Afro-Palearctic (Afrotropics + Palearctic), Indo-Palearctic (Indomalaya + Palearctic), and Austronesia (Indomalaya + Australasia + Oceania). Following this protocol, only 23 species were not assigned a realm. To these species we assigned the realm/grouping with the highest percentage. We also decided to list all Hawaiian endemic songbirds as Oceania rather than Nearctic. The Neotropics was the realm with the most species (1306) and Oceania had the fewest (47).

Modeling

We modeled extinction risk in a Bayesian hierarchical framework using the program JAGS (Plummer 2003) via the R package *R2jags* (Su & Yajima 2021), visualized via *MCMCvis* (Youngflesh 2018). We modeled as response variables both conservation concern (binary) and threat level (ordinal) and for each response variable we ran two models, one where the effect of colorfulness varied by realm, and one where the effect of colorfulness varied by breeding latitude and HDI. We used this two-model approach because realm is so correlated with both latitude and HDI that to model all three simultaneously would be to overparameterize the model. Instead, we used a model with realm to test for biogeographic variation in the importance of color (hypothesis 2), and a model with latitude and HDI to test geographic predictors (hypothesis 3).

In the first model,

$$CC_i \sim \text{Bernoulli}(p_i) \tag{1}$$

$$\text{logit}(p_i) = \alpha_i + \theta_i \cdot \text{color} + \beta_2 \cdot \text{mass} + \beta_3 \cdot \text{HWI} + \beta_4 \cdot \text{FD}, \tag{2}$$

conservation concern, CC_i , of a species in realm i is drawn from a Bernoulli distribution with probability p_i . In turn, $\text{logit}(p_i)$ is modeled as a linear function of an intercept, α_i , and four covariate coefficients. For both the intercept and the effect of colorfulness, θ_i , realm is treated as a random effect in that these parameters are realm-specific and drawn hierarchically from normal distributions:

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha) \quad (3)$$

$$\theta_i \sim \text{Normal}(\beta_1, \sigma_\theta). \quad (4)$$

Importantly, θ_i is drawn from a distribution with mean β_1 so that the fixed effect of colorfulness can be compared alongside β_{2-4} . The coefficients β_{2-3} represent the effects of two other numerical traits on extinction risk— $\log(\text{body mass})$ and $\log(\text{HWI})$ —while β_4 represents the binary effect of being a forest-dependent bird.

In the second model, eqn. 2 is replaced with

$$\begin{aligned} \text{logit}(p) = & \alpha + \beta_1 \cdot \text{color} + \beta_2 \cdot \text{mass} + \beta_3 \cdot \text{HWI} + \beta_4 \cdot \text{FD} + \\ & \beta_5 \cdot \text{lat} + \beta_5 \cdot \text{color} \cdot \text{lat} + \beta_7 \cdot \text{HDI} + \beta_8 \cdot \text{color} \cdot \text{HDI}, \end{aligned} \quad (5)$$

with a single intercept and covariate coefficient for colorfulness. The coefficients β_5 and β_7 represent the effects of two geographic variables, absolute breeding latitude and mean HDI, on extinction risk, while β_6 and β_8 represent the interactions between colorfulness and latitude/HDI.

In models 3 and 4, threat level was modeled using a Poisson distribution with linear equations identical to models 1 and 2, respectively (but with a log-link). In all models, numerical covariates (besides forest dependency) were scaled to have a mean 0 and standard deviation 1. We used vague priors ($\text{Gamma}(1,1)$ for standard deviations, $\text{Normal}(0,100)$ otherwise), and ran the model over 40,000 iterations with three chains, a burn-in of 10,000, and 30-fold thinning. For every parameter we extracted the mean of the posteriors, the 95% credible interval, and the percentage of posteriors $>$ (or $<$) 0, as a

measure of the strength of evidence. We considered a parameter estimate to have “strong evidence” when $(\Pr(\theta_i > / < 0) > 95\%)$ and moderate evidence when $(\Pr(\theta_i > / < 0) > 75\%)$.

Finally, we also performed sensitivity analyses to test the robustness of our results (Supporting Information). These analyses included: 1) a model using an alternate metric of colorfulness based on the convex hull volume of color space (Cooney et al. 2022); 2) a model based on female colorfulness; 3) a model with a binary response variable based on whether species were threatened (VU, EN, or CR) or not (LC, NT); 4) a model that included species missing color data; 5) phylogenetic generalized linear models.

Results

Our analysis of conservation concern included 4334 species representing 133 passerine families, i.e., 65% of extant passerines. Our results were robust to the choice of color metric (Fig. S2), the choice of analyzing male color (Fig. S3), species missing color data (Fig. S4), the choice of response variable (Fig. S5), and potential phylogenetic non-independence (Fig. S6).

In our model of all traits and geographical covariates, all four traits were important predictors of conservation concern (Fig. 1A). Most notably, there was strong evidence of a positive relationship between conservation concern and colorfulness ($\beta_1 = 0.137$, 95% Bayesian credible interval [CrI]: 0.033, 0.241; $\Pr(\beta_1 > 0) = 99.5\%$), such that more colorful birds were more likely to be of conservation concern (Fig. 2A). In addition, there was a positive relationship with body mass ($\beta_2 = 0.278$, CrI: 0.178, 0.373; $\Pr(\beta_2 > 0) = 100\%$), and negative relationships with both HWI ($\beta_3 = -0.123$, CrI: -0.225, -0.018; $\Pr(\beta_3 < 0) = 98.9\%$) and forest dependency ($\beta_4 = -0.242$, CrI: -0.492, 0.023; $\Pr(\beta_4 < 0) = 96.23\%$), where species were more likely to be of conservation concern if they were larger with lower dispersal ability and no forest association (Fig. 2B-C). All four traits were also strong predictors of threat level (Fig. 1B, 2D-F).

In our models of biogeographic realm, we found strong evidence of a positive relationship between conservation concern and colorfulness in two realms (Fig. 1C, 3A): Indomalaya ($\theta_{Indomalaya} = 0.180$, CrI: 0.023, 0.339; $\Pr(\theta_{Indomalaya} > 0) = 98.7\%$) and Australasia ($\theta_{Australasia} = 0.271$, CrI: 0.005, 0.584; $\Pr(\theta_{Australasia} > 0) = 97.7\%$). There was also moderate evidence of a positive relationship for the Nearctic (75.7%) Palearctic (93.2%), Afrotropics (82.3%), Oceania (83.7%), Afro-Palearctic (84.1%), and Indo-Palearctic (81.8%). Similar patterns were found for threat level (Fig. 1D, 3C), with the notable difference of much stronger evidence of a positive relationship in the Palearctic ($\theta_{Palearctic} = 0.464$, CrI: 0.109, 0.891; $\Pr(\theta_{Palearctic} > 0) = 99.9\%$).

Examining the relationship between colorfulness and geography (Fig. 1A), there was fairly strong evidence (i.e., $\Pr(\beta > 0) > 90\%$) of a positive interaction with absolute breeding latitude ($\beta_6 = 0.088$, CrI: -0.037, 0.219; $\Pr(\beta_6 > 0) = 91.5\%$), such that the positive effect of colorfulness became stronger for species breeding closer to the poles (Fig. 3B), with an even stronger interaction in the model of threat level ($\Pr(\beta_6 > 0) = 99.0\%$; Fig. 1B, 3E). While in general there was a strong positive relationship between extinction risk and HDI (Fig. 1A-B), there was only moderate evidence of a negative interaction with colorfulness ($\beta_8 = -0.054$, CrI: -0.167, 0.063; $\Pr(\beta_8 < 0) = 82.9\%$), whereby the positive relationship between conservation concern and colorfulness became stronger for species found in countries with low HDI (Fig. 3C), and this pattern was similar for threat level (Fig. 3D).

Overall, countries with both high average colorfulness and high percentage of species at risk of extinction were concentrated in Southeast Asia, particularly Indonesia, Malaysia, Thailand, Myanmar, and the Philippines (Fig. 4). Elsewhere in the world, this relationship was also present in Tanzania and Mozambique, countries in West Africa (Guinea, Sierra Leone, Liberia, and Côte d'Ivoire), and Caribbean nations such as Haiti, the Dominican Republic, and Saint Lucia. Countries with a high percentage of imperiled species but low levels of colorfulness were clustered around North Africa, while countries with

more colorful but fewer imperiled birds were mostly distributed throughout sub-Saharan Africa. These spatial patterns were also consistent for the average threat level of each country (Fig. S7).

Discussion

There is mounting evidence of the functional traits that place species at greater risk of extinction in a changing world (Wang et al. 2018; Chichorro et al. 2019, 2022; Kittelberger et al. 2021; Hua et al. 2023), but few of these traits are also associated with human perception and valuation of those species. Using a coloration dataset for >4000 songbird species, we demonstrate that more colorful songbirds are more likely to be species of conservation concern (Fig. 2). This finding corroborates another study of coloration in songbirds which found that color uniqueness was associated with threat status (Senior et al. 2022). However, when evaluating the drivers of extinction risk, it is critical to simultaneously assess other functional traits that could covary with both extinction risk and colorfulness. In addition to colorfulness, we show that body mass, dispersal ability (as represented by hand-wing index), and forest dependency, are also important predictors of extinction risk for the world's songbirds, supporting other studies that have implicated these traits (Chichorro et al. 2019; Rosenberg et al. 2019; Kittelberger et al. 2021; Neate-Clegg et al. 2023; Weeks et al. 2023).

The most likely explanation for the high extinction risk of more colorful birds is the pet trade. Almost a third of the world's birds are traded for various reasons (Scheffers et al. 2019) and it has been shown that more colorful birds are more likely to be traded (Romero-Vidal et al. 2020; Senior et al. 2022) and fetch a higher price at market (Vall-Ilosera & Cassey 2017). In particular, we found a strong positive relationship with colorfulness for both conservation concern (as a binary variable) and threat status in the biogeographic realms of Indomalaya and Australasia. Southeast Asia has a thriving bird trade (Nijman 2010; Harris et al. 2017; Scheffers et al. 2019), with dozens of species being trapped across the islands of

Indonesia and mainland Indochina and traded both internally and farther afield such as Taiwan (Su et al. 2014, 2015) and Australia (Vall-Ilosera & Cassey 2017). The relationship between rarity, colorfulness, and trade is further complicated by feedbacks: aesthetic value might be an important predictor of being traded but if trade then drives population declines (Harris et al. 2017), being threatened itself adds value to desirable species (Courchamp et al. 2006; Su et al. 2015; Vall-Ilosera & Cassey 2017; Senior et al. 2022). If the illegal pet trade continues unabated, targeting more colorful and endangered species, the result could be a less colorful world overall (Senior et al. 2022).

Despite the clear importance of the pet bird trade in driving the relationship between color and extinction risk, it alone cannot explain all of our observed results. For example, we found that the positive relationship between threat level and colorfulness was stronger for species breeding closer to the poles, with the relationship very weak overall for species breeding near the equator (Fig. 3E). Looking to other regions of the tropics such as the Afrotropics and Neotropics, there is little-to-no relationship between threat level and colorfulness (Figs. 1D,3D). Latin America and sub-Saharan Africa may experience less trade in songbirds overall: while these regions do see hotspots of diversity in traded bird species (Scheffers et al. 2019), many of the traded groups may not be songbirds and instead be species from other groups such as pigeons (Columbidae), hummingbirds (Trochilidae), and parrots (Psittacidae). It could also be the case that the colorful songbirds of these regions are either not particularly endangered or not targeted by the pet trade. In the Neotropics and Afrotropics, many of the more colorful groups of songbirds are often common and disturbance tolerant, including sunbirds (Nectariniidae), starlings (Sturnidae), New World orioles (Icteridae), and tanagers (Thraupidae). Some of these groups may also be harder to trap or may not do well in captivity. By contrast, many other families in these regions are rich in drab, range-restricted forest specialists, such as akalats/alethes (Muscicapidae), antpittas (Grallariidae), and tapaculos (Rhinocryptidae). For these latter groups, their

extinction risk derives not from their attractiveness (or not) to humans but primarily from habitat loss (Ducatez & Shine 2017; Henry et al. 2024).

In addition to the stronger positive relationship for species breeding closer to the poles, we saw a strong positive relationship between threat level and colorfulness in the Palearctic (Figs. 1D,3D). This pattern could be explained by a bias in research toward temperate bird species, which could mean a higher likelihood of species being evaluated as at risk of extinction (Ducatez & Lefebvre 2014; Titley et al. 2017; Chichorro et al. 2019). Among temperate birds, research and public perception is biased towards more colorful species (Schuetz & Johnston 2019; Santangeli et al. 2023; Fischer et al. 2025). For example, all but one (Sillems's Rosefinch, *Carpodacus sillemi*) of the 19 Data Deficient songbird species are found in the tropics (Birdlife International 2025). More colorful and charismatic species are more often chosen as conservation flagship species, meaning they receive more conservation attention and funding in general (Veríssimo et al. 2009; Frynta et al. 2010; Garnett et al. 2018). Thus, given that temperate regions have fewer species overall, and fewer colorful species (Cooney et al. 2022), the conservation spotlight will be felt most on imperiled, colorful birds. In addition to these biases in the Palearctic realm, there are also a handful of more colorful and imperiled species which are located on Japan's islands—e.g., Amami Jay (*Garrulus lidthi*), Izu Thrush (*Turdus celaenops*), and Ryukyu Robin (*Larvivora komadori*)—where they suffer from typical island conservation issues (invasive species, habitat loss). On the mainland, a notable colorful and critically endangered bird, the Yellow-breasted Bunting (*Emberiza aureola*), suffers little threat during the breeding season, spending the summer in pristine breeding grounds, but this species is widely trapped on its wintering grounds in China (Birdlife International 2025).

In addition to breeding latitude, we found moderate evidence of a stronger positive relationship between extinction risk and colorfulness for species whose range covered a lower human development index (HDI). This is despite the fact that, on average, species had a higher risk of extinction if they lived in countries with higher HDI. Combining these two facts together (Fig. 3C,F), our results suggest that, for a

given breeding latitude, more colorful birds have a more similar risk of extinction regardless of whether they are found in countries with low or high HDI, whereas drabber birds have a higher risk of extinction if they are found in countries with higher HDI. The reason for this disparity could be that countries with higher HDI have greater resources to evaluate extinction risk for both drab and colorful birds alike (Chichorro et al. 2019). Or it could be that threats that disproportionately affect colorful birds, like trapping, are more prevalent in countries with lower HDI (Scheffers et al. 2019). Although the country with the highest HDI is Switzerland (0.967), the species that experience the highest HDI throughout their annual cycle are Australian endemics (0.946), many of which are drab and at risk of extinction—e.g., Southern Whiteface (*Aphelocephala leucopsis*), Bower's Shrike-thrush (*Colluricincla boweri*), and Red-colored Whistler (*Pachycephala rufogularis*). Australia averages low color diversity in general (Cooney et al. 2022) which, coupled with high endemism, a number of biodiversity threats (Birdlife International 2025), leads to the expectation that it would have many drab but imperiled species.

Aside from the nuances of geographical variation in colorfulness and extinction risk, the overall positive relationship we found tended to be very robust to methodological assumptions (Supporting Information), including phylogenetic relatedness, the sex of the specimens, and the choice of color metric. We chose to represent colorfulness based on the objective measurement of color reflectance from real specimens (Cooney et al. 2022), as opposed to quantification of illustrations (Dale et al. 2015; Senior et al. 2022), or personal preferences for attractiveness or “aesthetic salience” (Santangeli et al. 2023; Fischer et al. 2025). In particular, we wanted to avoid more subjective measures because surveys of human opinions of birds are biased towards temperate regions (Haukka et al. 2023; Fischer et al. 2025) and so are unlikely to be representative of most interactions between humans and birds, such as trappers in the tropics.

Finally, our study was limited to around two-thirds of passerines, a fact which could bias our results. However, in our sensitivity analysis that included species with missing color data where we

assumed colorfulness to be similar among close relatives, we still found the strong positive relationship between extinction risk and colorfulness (Fig. S4). It is possible that species missing data average less colorful than congeners with data—owing to biases in the collection of the Natural History Museum of London—however we did not find that families missing color data for more species were less colorful on average or contained more imperiled species (Supporting Information). We thus think that having data for all passerines would be unlikely to change our main finding. Beyond passerines, our main result would likely hold among landbirds in general, given documented trapping preferences for colorful parrots (Romero-Vidal et al. 2020). However, there would likely be changes to the observed relationships in different biogeographic realms, for example with the important trade in parrots in the Americas and Africa (Chan et al. 2021). Future studies should aim to quantify these relationships for an increasing number of bird groups.

Overall, we found a robust positive relationship between extinction risk and colorfulness for over a third of the world's birds. This finding has two important conservation implications. First, if more colorful birds are at greater risk of extinction, and many species do indeed go extinct in the future, we could see an erosion of color diversity around the world (Senior et al. 2022), including charismatic species that are banners for conservation. However, given how people value colorful birds (Santangeli et al. 2023; Fischer et al. 2025), the observed relationship could offer a conservation opportunity (Frynta et al. 2010). Colorful and charismatic birds are known to be suitable flagship species for conservation (Veríssimo et al. 2009, 2014; Garnett et al. 2018) which can then in turn benefit less charismatic species per the “umbrella effect” (Bennett et al. 2015). Thus, by making colorful birds flagship species, we can simultaneously protect the most endangered and most appreciated songbirds on earth.

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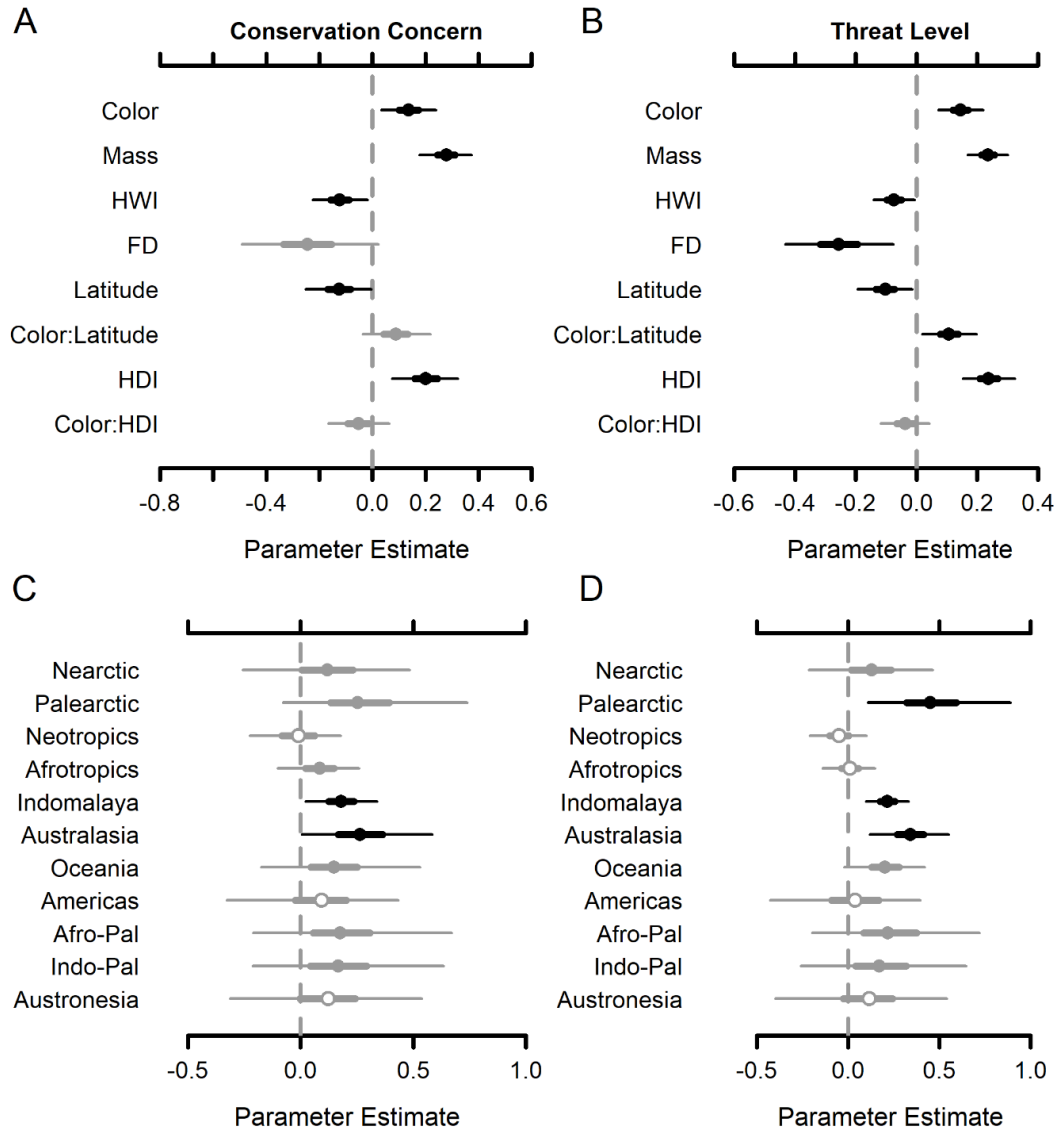


Figure 1. Predictors of extinction risk for 4334 passerine bird species around the world. Each plot shows parameter estimates from Bayesian hierarchical models. Covariate coefficients are shown for (A) conservation concern (whether species were Least Concern or otherwise) and (B) mean threat level. Coefficients for the effect of colorfulness are then shown by biogeographic realm for (C) conservation concern and (D) mean threat level. Each parameter is represented by a mean, interquartile range, and 95% Bayesian credible interval (CrI). Points are filled when the interquartile range doesn't overlap 0, and parameters are black when the CrI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

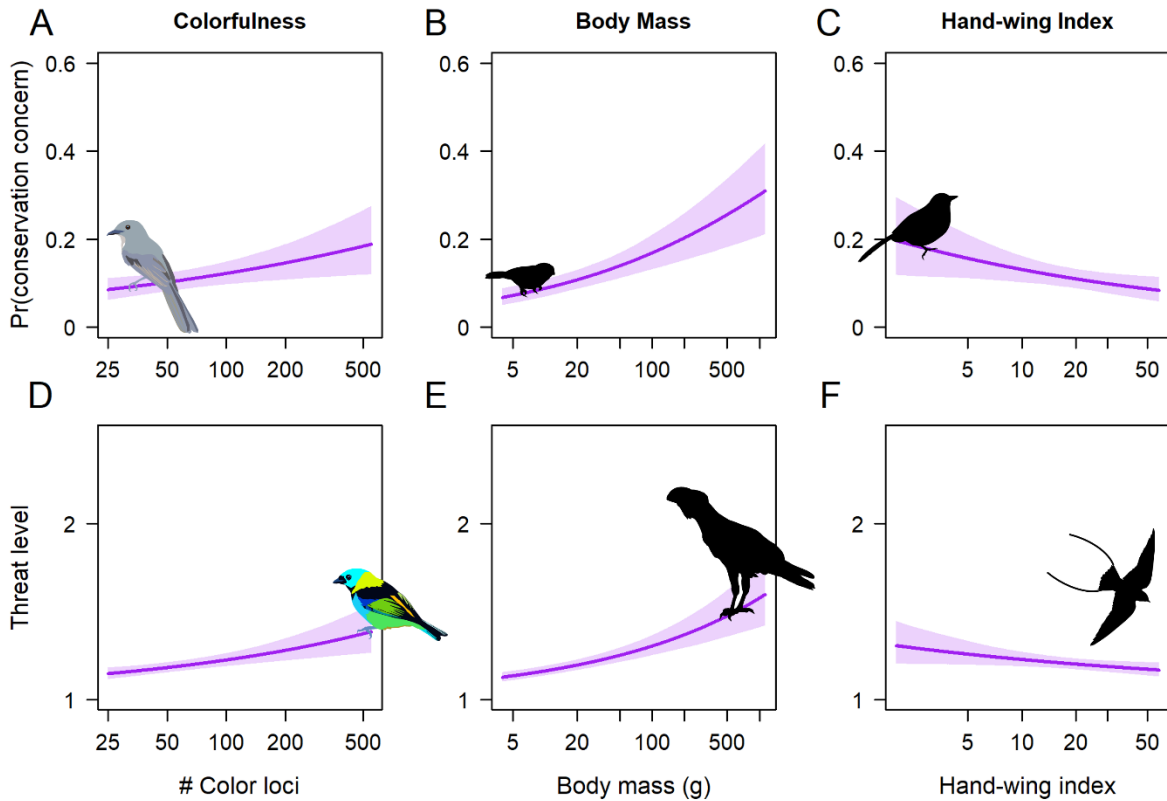


Figure 2. The relationships between extinction risk and functional traits for 4334 passerine bird species. For both (A-C) conservation concern and (D-F) threat level, colorfulness (A,D) and body mass (B,E) were positive predictors while hand-wing index (C,F) was a negative predictor. Ribbons show the 95% Bayesian credible intervals. Example species include the drab Greyish Mourner (*Rhytipterna simplex*), the colorful Green-headed Tanager (*Tangara seledon*), the small Pygmy Tit (*Psaltria exilis*), the large Thick-billed Raven (*Corvus crassirostris*), the low-dispersal Grey-sided Laughingthrush (*Pterorhinus caerulatus*), and the high dispersal Wire-tailed Swallow (*Hirundo smithii*). Species names follow BirdLife International.

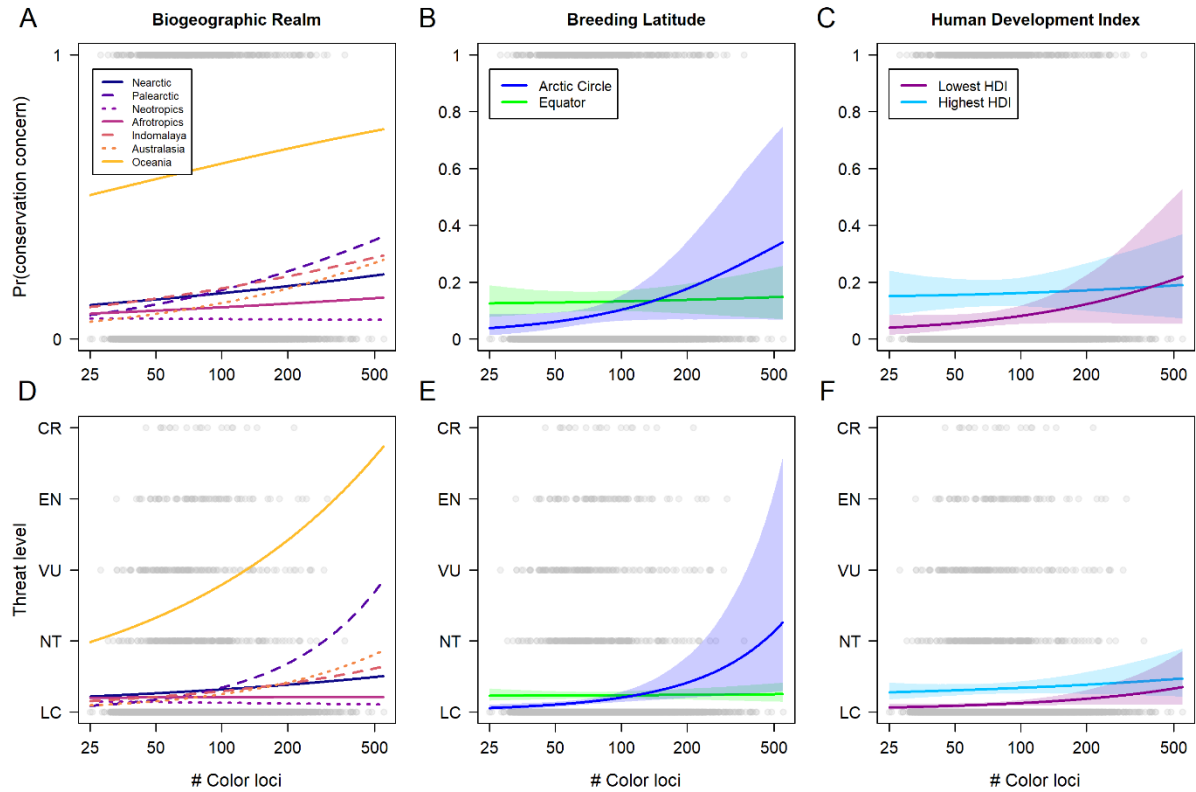


Figure 3. Geographical variation in the relationship between extinction risk and colorfulness across 4334 passerine bird species. The relationship between conservation concern varied by (A) biogeographic realm, (B) absolute breeding latitude, and (C) average human development index (HDI), with similar patterns for threat level (D-F). For realm, each line represents the effect of color in each realm. For breeding latitude, the two lines (and 95% Bayesian credible intervals) represent the effect of color at the Equator (green) and Arctic Circle (blue). For HDI, the two lines represent the effect of color at the lowest (Somalia endemic) and highest (Australia endemic) mean HDI across a species' range.

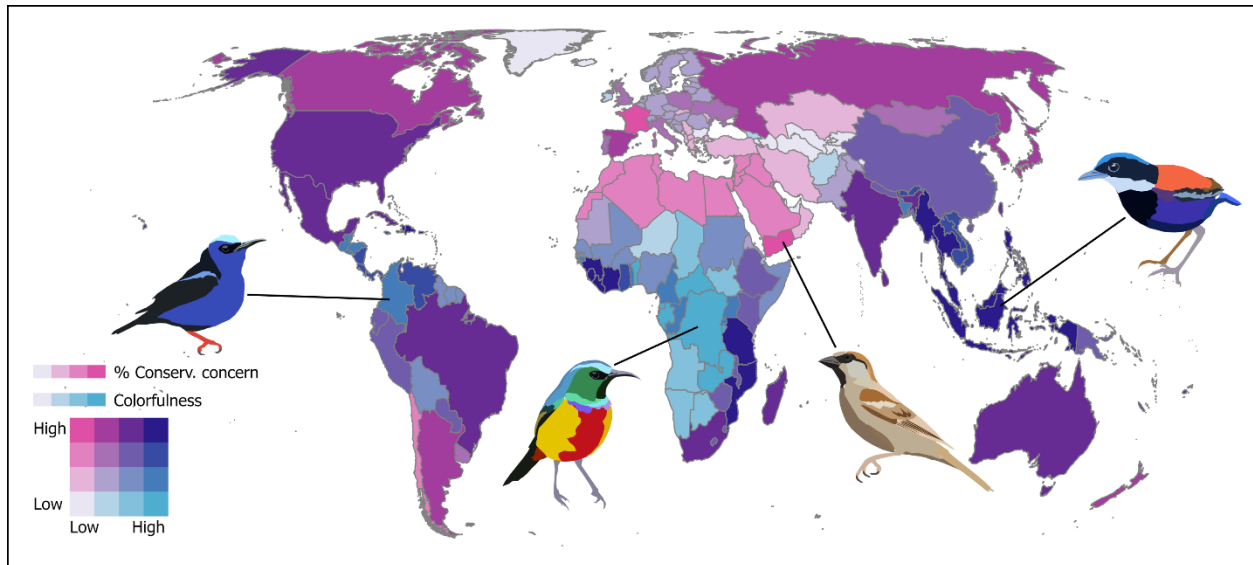


Figure 4. A bivariate map of concentration of colorfulness and extinction risk for passerine birds. Each country/territory is ranked based on both the average colorfulness of its passerines and the percentage of species of conservation concern (i.e., not Least Concern). Examples species shown from right to left: Blue-headed Pitta (*Hydrornis baudii*, Vulnerable), Abd Al Kuri Sparrow (*Passer hemileucus*, Vulnerable), Regal Sunbird (*Cinnyris regius*, Least Concern), and Red-legged Honeycreeper (*Cyanerpes cyaneus*, Least Concern). Species names follow BirdLife International.

Supporting Information

Choice of variables

To evaluate the robustness of our results to methodological decisions, we initially performed three sensitivity analysis. In the first, we used the (log) convex hull volume of visible color space as an alternate metric of colorfulness (Cooney et al. 2022), running four models identical in structure to the models of the main analysis (Fig. S2). In the second, we ran the same four models on the number of color loci of females instead of males (Fig. S3). In the third (Fig. S5), we ran two models (one including breeding latitude and human development index, the other biogeographic realm) using a binary response variable (and logit-link) where species were classified as threatened (1; Vulnerable, Endangered, or Critically Endangered) or not (0; Least Concern or Near Threatened).

All of these sensitivity analyses produced results qualitatively similar to our main results (Fig. S2, S3, S5). For convex hull volume, the relationship between conservation concern and colorfulness became less strong for Indomalaya (Fig. S2C). For females, the interaction between color and breeding latitude was stronger, likely owing to the latitudinal trend in plumage dimorphism (Fig. S3). For threatened species, the effect of colorfulness was slightly weaker (Fig. S5), with $\Pr(\beta_1 > 0) = 96.8\%$, likely owing to the smaller percentage (5%) of threatened species.

Passerines missing color data

The color data gathered by Cooney et al. represented ~65% of passerine species (Cooney et al. 2022). The data were taken from scans of museum skins at the Natural History Museum of London. These species may be representative of the world's passerines, but it is possible that biases in the collection could lead to biases in the results. For example, species missing from the collection may be more range

restricted (and therefore imperiled) or may be less colorful. If the dataset were missing a large number of drab birds of conservation concern, this would represent a potential bias in our results.

To assess this potential issue, we calculated the mean number of color loci for each bird family. We then quantified what percentage of each family was represented in the color dataset, and what percentage of each family were of conservation concern. We would have cause to consider museum sampling bias if the missing species were more likely to come from drab families with more species at risk of extinction. However, there was almost no correlation between families missing the most species and families with the most imperiled species (Pearson's $r = 0.05$), nor with more colorful families (Pearson's $r = -0.10$). Moreover, percent imperiled species (coefficient = 0.003, SE = 0.008, $Z = 0.346$, $p = 0.729$) and mean colorfulness (coefficient = -0.003503, SE = 0.006219, $Z = -0.563$, $p = 0.573$) did not predict percent of species with data in a binomial generalized linear model.

We also performed a sensitivity analysis of models to evaluate whether the results might change if we had data for all species. To do this, we began with all 6604 species of extant passerine (Birdlife International 2025). We then filled in missing data for body mass and HWI from AVONET (Tobias et al. 2022), for forest dependency from BirdLife International (Birdlife International 2025), for breeding latitude from (Cooney et al. 2022), and for realm and human development index (UNDP 2023). These steps resulted in a dataset of 6407 species, i.e., an addition of 2073 species. Over the original 4334 species, we calculated the mean number of color loci at both the genus level and family level. Then, for the 2073 species missing color data, we assigned the mean value of the genus or family (if no congeners had data). There were six families with no representatives with color data: Sapayoidae (one species), Atrichornithidae (two species), Dasyornithidae (three species), Rhagologidae (one species), Callaeidae (three species), and Nesospingidae (one species). The final dataset contained 6396 species. To this dataset, we ran the same set of four models as our main analysis. Our results were qualitatively very similar (Fig. S4), albeit with stronger effects of breeding latitude. The color coefficients for Australasia

were also less strong, suggesting that the addition of drab, imperiled species diluted the importance of colorfulness in this realm.

Phylogenetic analysis

In any analysis of traits it is important to consider phylogenetic non-independence among species. We took two steps to address this possible issue. Both steps utilized 500 random phylogenetic trees requested from birdtree.org (Jetz et al. 2012). In the first step, we used the function “*phylosig*” from the package *phytools* (Revell 2012) on every tree to calculate phylogenetic signal—Blomberg’s *K*, where 1 = Brownian motion and 0 = no signal—in the conservation concern response variable. We then calculated the mean and 95% confidence intervals of all estimates. We estimated a *K* of 0.028 (CI: 0.008 to 0.044), indicating very little phylogenetic signal in the response variable.

In the second step, we conducted phylogenetic generalized linear models (PGLMs) using the function “*phyloglm*” from the package *phylolm*. For each of the 500 trees, we conducted a PGLM using the same structure as model 1 in the main text. From the model we extracted the parameter coefficients for each variable. After iterating over all trees, we then calculated for each parameter the mean coefficient estimate, interquartile range of estimates, and 95% confidence interval. The results (Fig. S6) were very similar to those from our main model (Fig. 1A), indicating that our results were robust to phylogenetic non-independence. Notably, both the effect of forest dependency, and the interaction between colorfulness and latitude, became stronger.

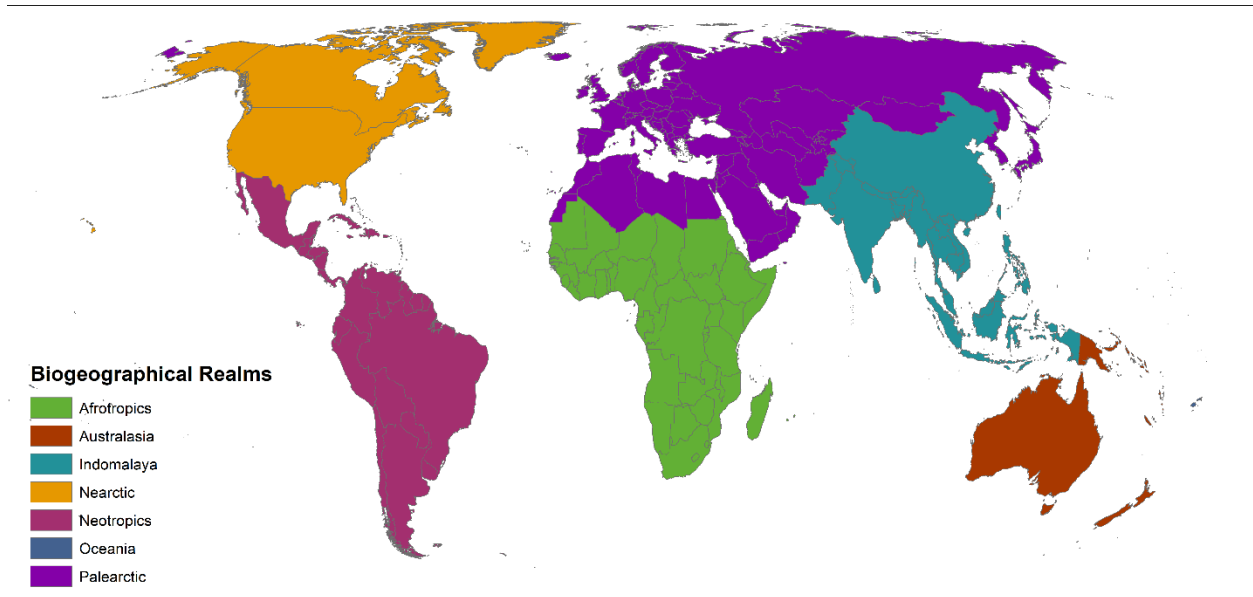


Figure S1. A map of biogeographic realms used in the analysis of color and extinction risk. Each country/territory was assigned to one of seven realms.

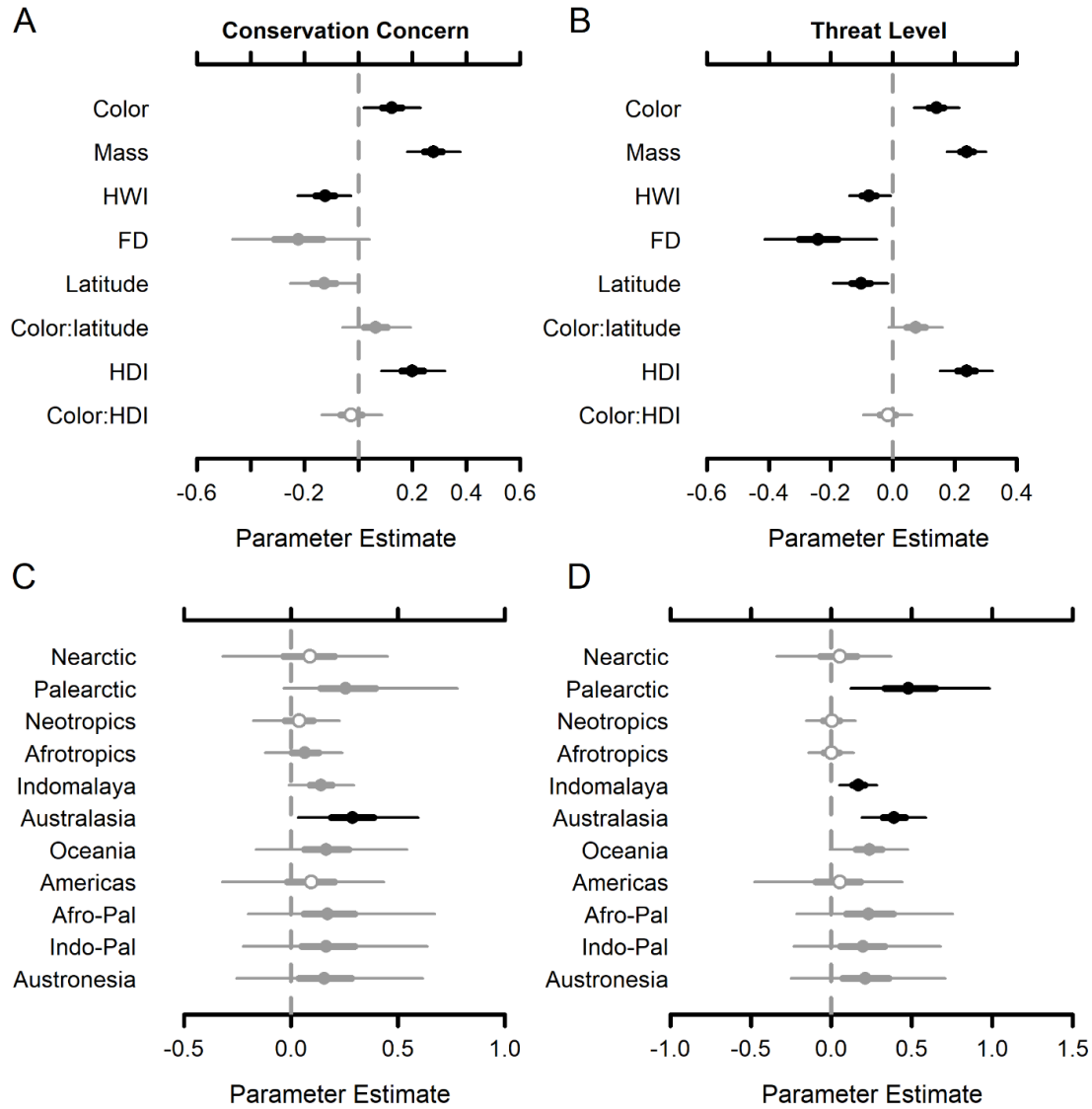


Figure S2. Predictors of extinction risk for 4334 passerine bird species around the world where color is represented by the convex hull volume of visible color space. Each plot shows parameter estimates from Bayesian hierarchical models. Covariate coefficients are shown for (A) conservation concern (whether species were Least Concern or otherwise) and (B) mean threat level. Coefficients for the effect of colorfulness are then shown by biogeographic realm for (C) conservation concern and (D) mean threat level. Each parameter is represented by a mean, interquartile range, and 95% Bayesian credible interval (CrI). Points are filled when the interquartile range doesn't overlap 0, and parameters are black when the CrI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

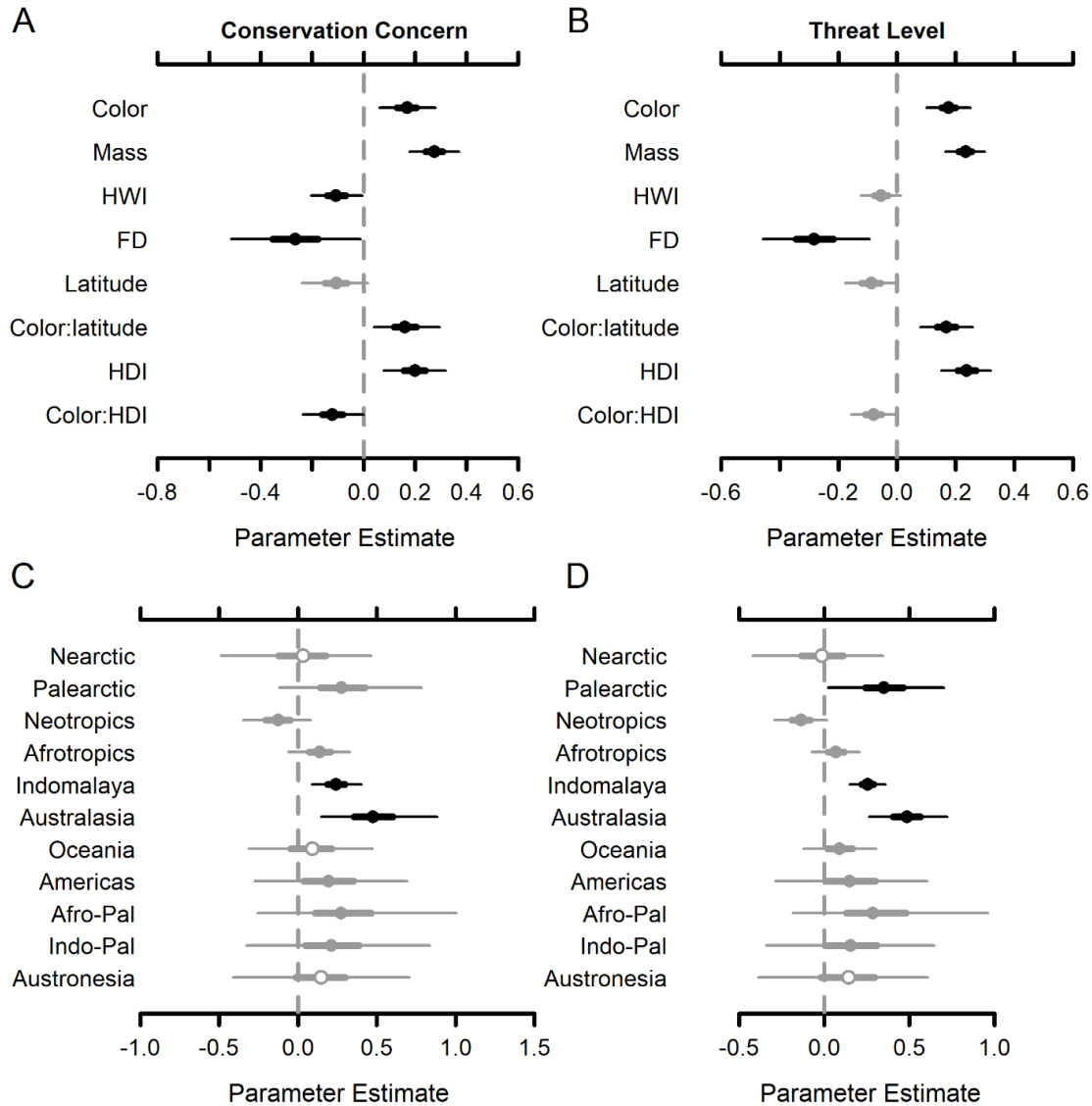


Figure S3. Predictors of extinction risk for 4334 female passerine bird species around the world. Each plot shows parameter estimates from Bayesian hierarchical models. Covariate coefficients are shown for (A) conservation concern (whether species were Least Concern or otherwise) and (B) mean threat level. Coefficients for the effect of colorfulness are then shown by biogeographic realm for (C) conservation concern and (D) mean threat level. Each parameter is represented by a mean, interquartile range, and 95% Bayesian credible interval (CrI). Points are filled when the interquartile range doesn't overlap 0, and parameters are black when the CrI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

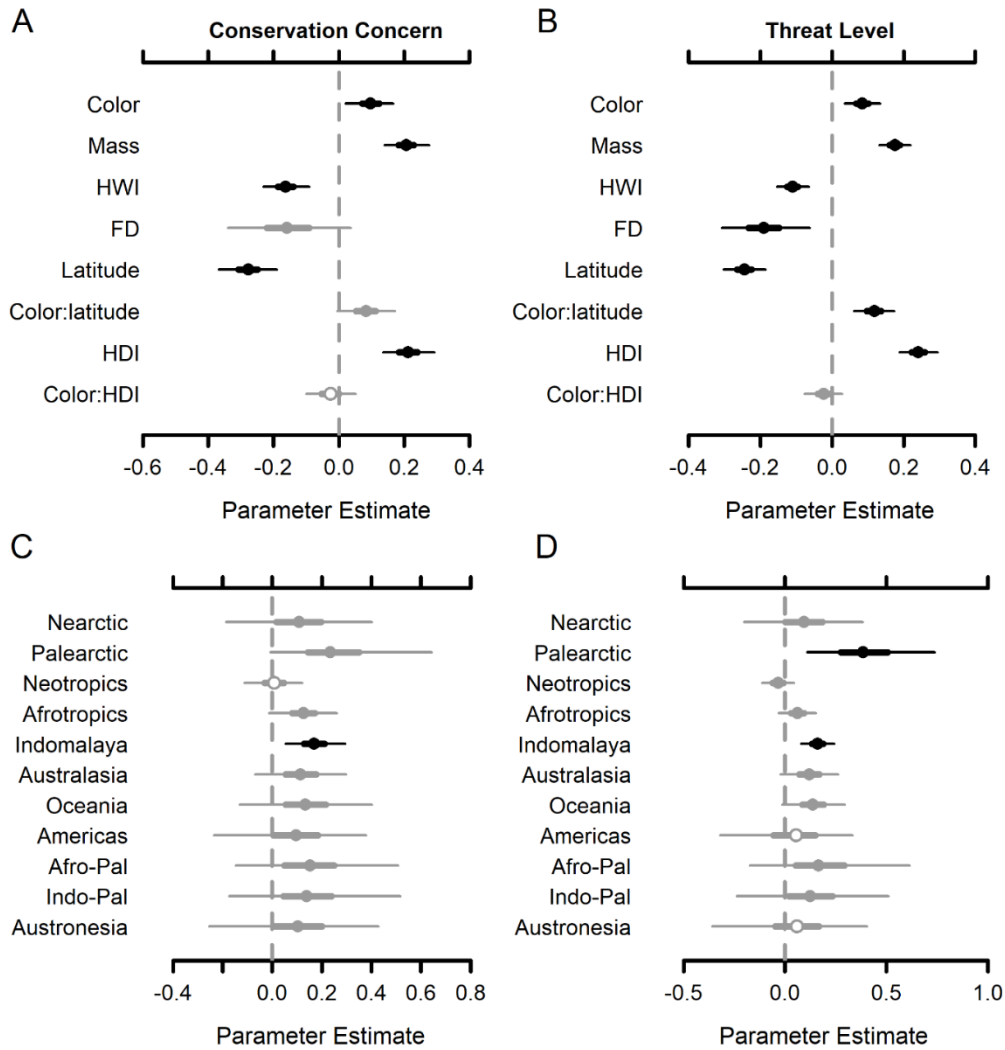


Figure S4. Predictors of extinction risk for 6396 passerine bird species around the world. In this analysis, species missing color data were inferred from the genus or family level. Each plot shows parameter estimates from Bayesian hierarchical models. Covariate coefficients are shown for (A) conservation concern (whether species were Least Concern or otherwise) and (B) mean threat level. Coefficients for the effect of colorfulness are then shown by biogeographic realm for (C) conservation concern and (D) mean threat level. Each parameter is represented by a mean, interquartile range, and 95% Bayesian credible interval (CrI). Points are filled when the interquartile range doesn't overlap 0, and parameters are black when the CrI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

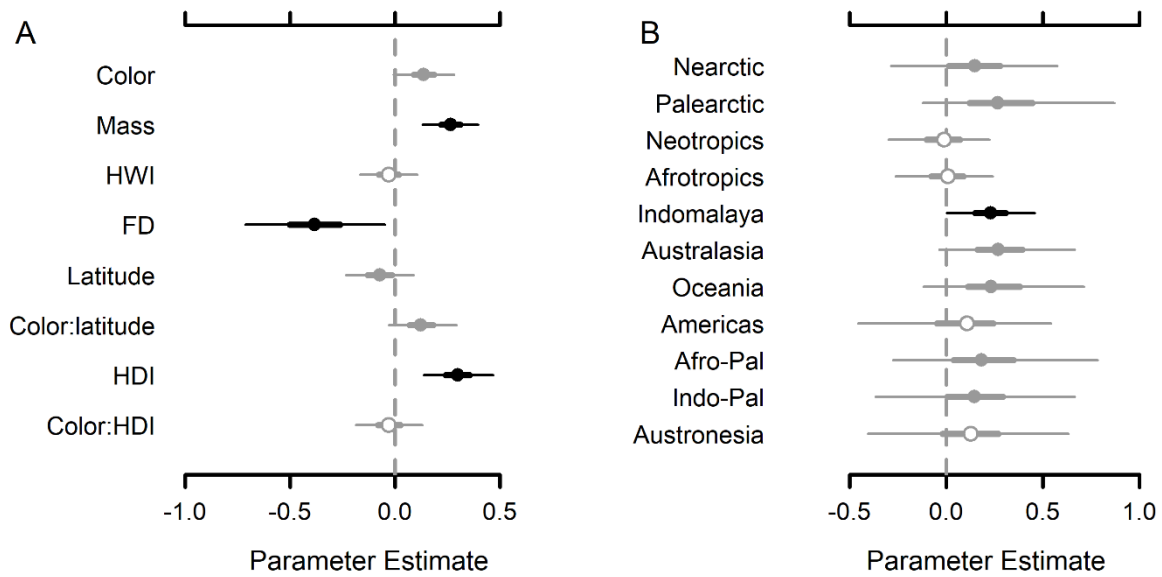


Figure S5. Predictors of threatened status for 4334 passerine bird species around the world. Each plot shows parameter estimates from Bayesian hierarchical models. The response variable was binary for whether species were threatened (Vulnerable, Endangered, or Critically Endangered) or not (Least Concern or Near Threatened). Covariate coefficients (A) are shown as are coefficients for the effect of colorfulness by biogeographic realm (B). Each parameter is represented by a mean, interquartile range, and 95% Bayesian credible interval (CrI). Points are filled when the interquartile range doesn't overlap 0, and parameters are black when the CrI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

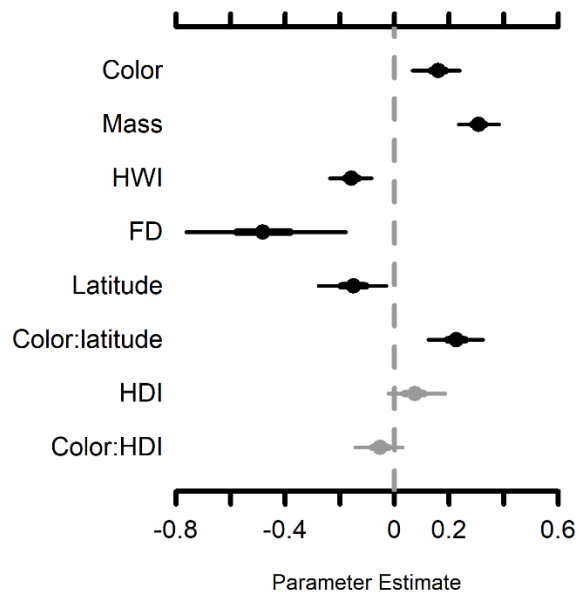


Figure S6. Predictors of conservation concern for 4334 passerine bird species around the world, based on a phylogenetic GLM (PGLM). Results come from 500 PGLMs, one per phylogenetic tree. Each parameter is represented by a mean, interquartile range, and 95% confidence interval (CI). Parameters are black when the CI doesn't overlap 0. HWI = hand-wing index, FD = forest dependency, HDI = human development index.

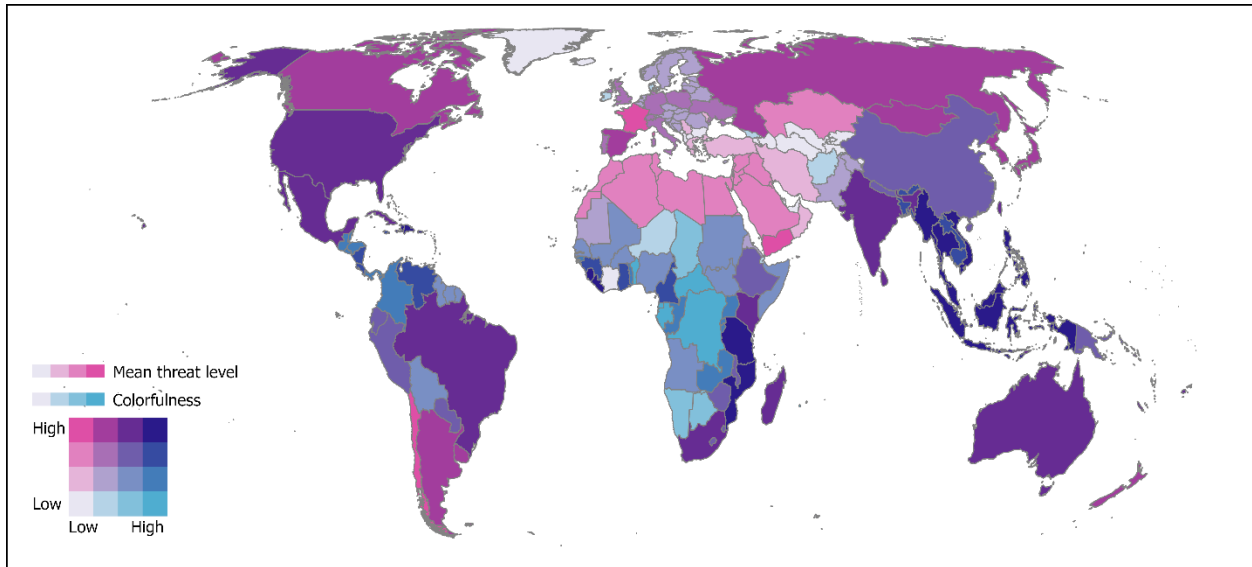


Figure S7. A bivariate map of variation in colorfulness and threat level for passerine birds. Each country/territory is ranked based on both the average colorfulness of its passerines and the average threat level (1-5).