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Biological Correlates of Extinction Risk in Resident Philippine Avifauna

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The majority of the world's biodiversity occurs in the tropics, but human actions in these regions have precipitated an extinction crisis due to habitat degradation, overexploitation, and climate change. Understanding which ecological, biogeographical, and life-history traits predict extinction risk is critical for conserving species. The Philippines is a hotspot of biodiversity and endemism, but it is a region that also suffers from an extremely high level of deforestation, habitat degradation, and wildlife exploitation. We investigated the biological correlates of extinction risk based on the IUCN Red List threat status among resident Philippine birds using a broad range of ecological, biogeographical, and life history traits previously identified as correlates of extinction risk in birds. We found strong support across competing models for endemism, narrower elevational ranges, high forest dependency, and larger body size as correlates significantly associated with extinction risk. Additionally, we compared observed threat status with threat status fitted by our model, finding fourteen species that are not currently recognized by the IUCN Red List as threatened that may be more threatened than currently believed and therefore warrant heightened conservation focus, and predicted threat statuses for the four Philippine Data Deficient bird species. We also assessed species described in recent taxonomic splits that are recognized by BirdLife International, finding 12 species that have a fitted threat status more severe than their IUCN-designated ones. Our findings provide a framework for avian conservation efforts to identify birds with specific biological correlates that increase a species' vulnerability to extinction both in the Philippine Archipelago and elsewhere on other tropical islands.

Keywords: cryptic species, deforestation, island biogeography, bird conservation, endemism, elevational range, forest dependency, body size

INTRODUCTION

The majority of the world's biodiversity is found in the tropics (Myers et al., 2000; Brown, 2014; Barlow et al., 2018), but human actions in these regions are expected to precipitate an extinction crisis as habitats are diminished and degraded (Pimm and Raven, 2000; Barlow et al., 2018). Extinction risk among taxa is phylogenetically non-random (e.g., Russell et al., 1998; Hughes, 1999; Von Euler, 2001; Yessoufou et al., 2012; Wang et al., 2018) and influenced by species' biology, specifically ecological, biogeographical, and life history traits (hereafter "biological correlates"). Such ecological variables that impact extinction risk include poor dispersal ability

(Weerd et al., 2003; Moore et al., 2008; Lees and Peres, 2009), ecological specialization (Norris and Harper, 2004; Şekercioğlu, 2007, 2011), and large body size (Gaston and Blackburn, 1995; Bennett and Owens, 1997; Wang et al., 2018). Biogeographical variables associated with high extinction risk include small geographical and elevational range size (Manne et al., 1999; Purvis et al., 2000; Şekercioğlu et al., 2008; White and Bennett, 2015), and endemism (Myers et al., 2000; Boyer, 2008). Life history and breeding biology variables associated with high extinction risk include nest type (Terborgh, 1974; Wilcove, 1985; Boyer, 2008) and slow life histories (Purvis et al., 2000; Webb et al., 2002; Tobias et al., 2013), including low fecundity (Bennett and Owens, 1997; Purvis et al., 2000; Kruger and Radford, 2008) which can impact a species' vulnerability to extinction both via increased predation risk of open nests and slower population recovery from a severe reduction in numbers.

For birds, habitat specialists are most at risk from habitat loss and degradation (Sodhi et al., 2004), which reduces niche availability (Norris and Harper, 2004). Of habitat specialists, forest interior (Turner, 1996; O'Dea and Whittaker, 2007), understory, and ground-dwelling bird species are particularly sensitive to habitat changes (Lambert and Collar, 2002; Visco et al., 2015), forest fragmentation (Şekercioğlu, 2002; Şekercioğlu and Sodhi, 2007), and compression of trophic niche-widths (Edwards et al., 2013) that results from habitat degradation. Larger bird species are also at heightened risk due to having low population sizes, slower life histories, requiring larger home ranges, and tending to occupy higher trophic niches (Gaston and Blackburn, 1995). Widely distributed species, on the other hand, are usually able to exploit a wider range of habitats than those with narrow distributions and may thus be less prone to extinction (Manne et al., 1999). Forest fragmentation and deforestation can compound species' poor dispersal abilities (Barlow et al., 2006; Şekercioğlu, 2007; Moore et al., 2008; Lees and Peres, 2009; Visco et al., 2015; Sheard et al., 2020) and push forest interior species upslope to more suitable habitat (Ocampo-Peñuela and Pimm, 2015), resulting in the extinction of small, isolated populations that are constrained by elevation (Kattan et al., 1994).
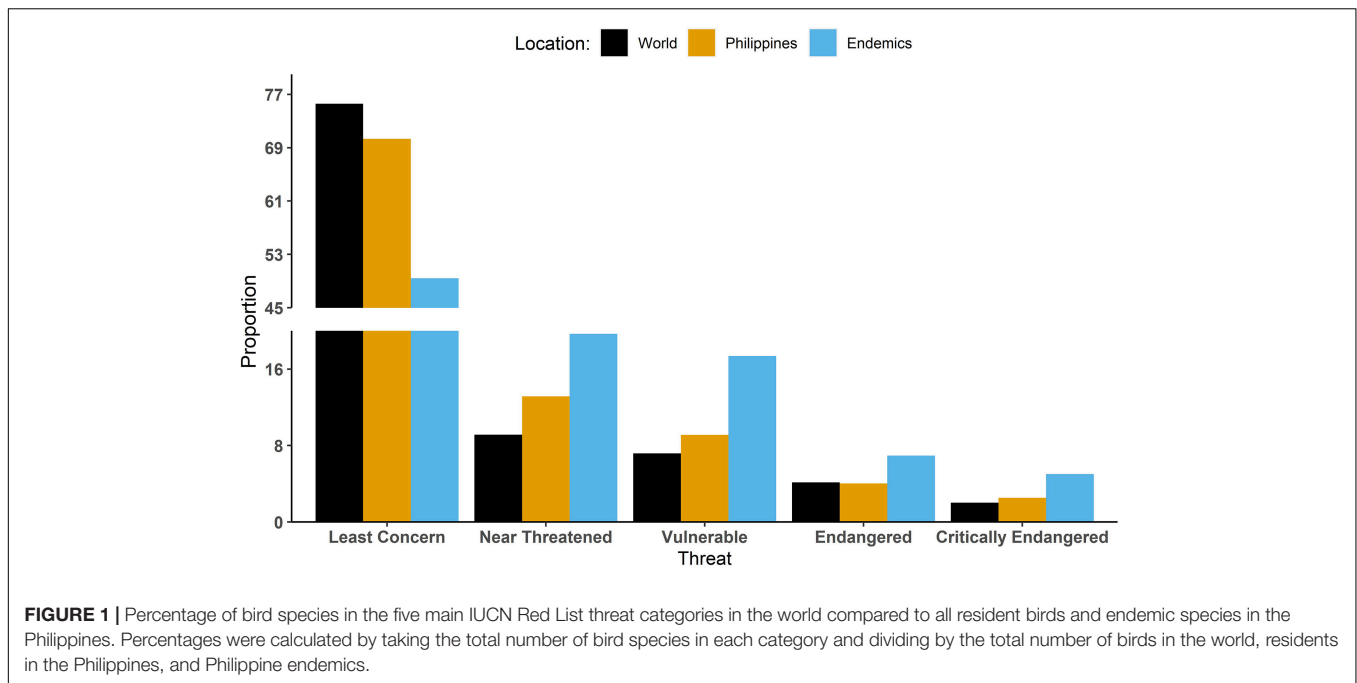
Most studies examining biological correlates of extinction risk in birds have only assessed single traits individually in models (e.g., Bennett and Owens, 1997; Norris and Harper, 2004; Şekercioğlu et al., 2004; Kruger and Radford, 2008). Yet, traits analyzed in isolation are limited in their power to predict a species' vulnerability (Henle et al., 2004; Wang et al., 2015, 2018), making it more difficult to determine the relative importance of individual traits that may predispose species to extinction (Bennett and Owens, 1997). Furthermore, some studies have found strong synergistic interactions between natural abundance and habitat specificity, and between body size and hunting vulnerability (Wang et al., 2015, 2018), though these studies used a maximum of two traits in each model. Therefore, there is a need to analyze the combined effects of multiple traits on a species' extinction proneness (Davies et al., 2004; Henle et al., 2004; Wang et al., 2015). Globally, the International Union for the Conservation of Nature (IUCN) Red List has become the standard for assessing extinction risk in species

(Le Breton et al., 2019). IUCN Red List criteria consist of three main components: a species' population decline rate, geographic range size, and population size (Mace et al., 2008; Le Breton et al., 2019; International Union for Conservation of Nature and Natural Resources, 2020).

Southeast Asia is predicted to lose over a third of its biodiversity over the next century due to elevated rates of deforestation (Brook et al., 2003; Sodhi et al., 2010), with the resident avifauna of the region being the most extinction-prone in the world after that of oceanic islands (Şekercioğlu et al., 2004). This is particularly true in the Philippines, where extreme habitat loss and other human actions threaten the nation's highly endemic birdlife (Oliver and Heaney, 1996; Panopio and Pajaro, 2014). The Philippines is one of the most biodiverse countries in the world (Posa et al., 2008); a vast archipelago with diverse habitats which form a global hotspot of species diversity and endemism (Heaney, 1993; Oliver and Heaney, 1996; Stattersfield et al., 1998; Myers et al., 2000). Furthermore, the bird diversity recognized in the Philippines continues to increase with successive taxonomic revisions. The country now possesses some of the highest richness of recently split threatened species in the world (Simkins et al., 2019). Furthermore, recent genetic and phenotypic analyses have indicated that alpha taxonomy may underestimate the quantity of bird species in the Philippines by at least 50% as a result of numerous cryptic endemic species in the country (Lohman et al., 2010; Campbell et al., 2016). Bird species limits in the Philippines are complicated by the country's large number of islands and mountains that have driven allopatric diversification (Collar, 2011; Rasmussen et al., 2012; Neate-Clegg et al., 2021).

With 594 species, the Philippines is ranked 58th in the world for bird species richness (BirdLife International, 2021). However, 93 (15.6%) Philippine bird species are threatened with extinction (BirdLife International, 2021), ranking the country 8th for globally threatened species (Vulnerable, Endangered, or Critically Endangered; **Figure 1**). For endemic species, the outlook is even more dire, with 75 of the 258 (29.1%) endemic species considered threatened. However, there has been minimal research assessing the extinction proneness of Philippine avifauna or even Southeast Asian avifauna as a whole (Sodhi and Brook, 2006). At the current rate of habitat destruction and biodiversity loss within the Philippines, we may lose a large amount of diversity before many cryptic species are even described (Lohman et al., 2010).

In this study, we examined the biological correlates of extinction risk among all resident Philippine bird species. As a natural archipelago of diverse topography and ecosystems, a global biodiversity hotspot rich in endemism, and a nation facing numerous threats that are driving rapid wildlife population declines, the Philippines is a high priority country to assess the relationships between ecological, biogeographical, and life history traits and extinction risk in birds. We analyzed a broad range of traits that have previously been linked to extinction risk, comparing the effects of multiple traits simultaneously. We predicted that species at greater risk of extinction in the Philippines would be endemic (Myers et al., 2000; Boyer, 2008), restricted to lower elevations or to limited

FIGURE 1 | Percentage of bird species in the five main IUCN Red List threat categories in the world compared to all resident birds and endemic species in the Philippines. Percentages were calculated by taking the total number of bird species in each category and dividing by the total number of birds in the world, residents in the Philippines, and Philippine endemics.

elevational ranges (Manne et al., 1999; Şekercioğlu et al., 2008; White and Bennett, 2015), large-bodied (Bennett and Owens, 1997; Boyer, 2008; Wang et al., 2018), have limited dispersal ability (Moore et al., 2008; Lees and Peres, 2009; Sheard et al., 2020), be ecologically specialized (Weerd et al., 2003; Norris and Harper, 2004; Şekercioğlu, 2011), have exposed nests or nest on the ground (Terborgh, 1974; Wilcove, 1985; Boyer, 2008), or have low fecundity (Bennett and Owens, 1997; Kruger and Radford, 2008). While we are assessing all of the resident birdlife in the Philippines, we especially focused on species that have either been split within the last decade or have been proposed to consist of cryptic populations that may warrant species-level status (Lohman et al., 2010; Collar, 2011; Rasmussen et al., 2012; Hosner et al., 2013; Campbell et al., 2016). We also aim to identify Philippine bird species which are not currently recognized as threatened by the IUCN but may be at risk of extinction in the near future.

MATERIALS AND METHODS

Dataset and Biological Correlates

We compiled a dataset of the 446 resident Philippine bird species (**Supplementary Table 1**) after excluding 148 species that are fully migratory and do not breed on any of the islands in the Philippines. Taxonomic classifications were based on BirdLife International (2021), which maintains its own list of the world's bird species, reviewed and adopted by the BirdLife Taxonomic Working Group (BirdLife International, 2021) and utilized by the IUCN Red List (2020). IUCN Red List threat status for each species consists of Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), or Data Deficient (DD). We then collated data on 11 ecological,

biogeographical, and life-history traits: endemism, elevational range, average elevation, body mass, hand-wing index, habitat breadth, forest dependency, primary diet, dietary breadth, nest type, and average clutch size. While there is a strong relationship between geographic range size and extinction risk (**Figure 2**), we did not include geographic range size in our analyses to avoid potential circularity with a species' IUCN threat status. Most of the data were extracted from a global dataset of avian ecological traits (**Table 1**; see Şekercioğlu et al., 2004, 2019 for more details of these methods and a description of this dataset) which compiled information from the literature, including ornithological books (e.g., Del Hoyo et al., 1992-2013; Kennedy et al., 2000), BirdLife International (2021), and field guides (e.g., Robson, 2000). Hand-wing index (HWI) data were taken from Sheard et al. (2020). HWI is a measure of a bird wing's pointiness and is a proxy for dispersal ability (Sheard et al., 2020), and this dataset was also used to fill gaps in body mass. If no additional data were available, we used conspecific or congeneric values where possible to fill in gaps.

We used Kennedy et al. (2000) for each species' elevational range in meters above sea level (hereafter "m asl"; Del Hoyo et al., 1992-2013) rather than generalizing lowland, foothill, or montane designations based on elevational ranges, as there are hundreds of islands in the Philippines and elevational ranges can vary greatly between islands and mountains (Rahbek et al., 2019). Since 71% of the species in our study are forest species, we used forest dependency ("high," "medium," "low," "non-forest"; BirdLife International, 2021) as an indicator of a species' habitat preference. We used primary diet as an indicator of a species' trophic level (Wang et al., 2018). However, because invertivores and vertivores tend to have different sensitivity to anthropogenic change than herbivores (Şekercioğlu et al., 2002; Bregman et al., 2016; Keinath et al., 2017; Atwood et al., 2020;
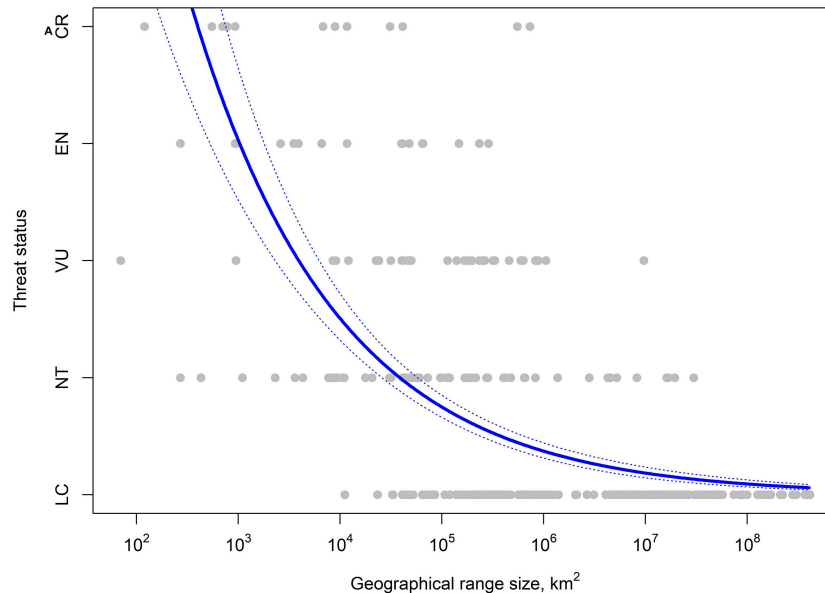
FIGURE 2 | The correlation between threat status and geographic range size in resident Philippine birdlife.

Sherry et al., 2020), we designated species as either "carnivores" or "herbivores." We grouped frugivores, nectarivores, and granivores as herbivores, and grouped piscivores, invertivores, and vertivores as carnivores. For the 14 omnivorous species, we used context to specify if a species was primarily an herbivore or carnivore. We used dietary breadth and habitat breadth to calculate the ecological specialization index (Şekercioğlu, 2011). Dietary breadth is a count of the number of food types a species consumes, with categories such as invertebrates and fruit (max = 7). Habitat breadth is a count of the number of major habitats that a species can occur in, with broad categories such as forest, woodland, and grassland (max = 10). Specialization is then quantified as $\log_{10}[100/(\text{dietary breadth} \times \text{habitat breadth})]$, with a maximum of 2 for species that eat only one type of food and live in one habitat (Şekercioğlu, 2011).

For traits related to a species' breeding biology, we used clutch size as a proxy for fecundity (Bennett and Owens, 1997; Wang et al., 2015). We also simplified our nest type categories into nests that are either open (i.e., cup, platform, scrape, or saucer nests) or closed (i.e., burrows, cavity, dome, pendant, sphere, or mound nests). Our final set of variables included ten ecological traits: endemism (yes/no), elevational range, average elevation, body mass, HWI, forest dependency, trophic level (carnivore/herbivore), ecological specialization, nest type (open/closed), and average clutch size.

Four species were listed by International Union for Conservation of Nature and Natural Resources (2020) as DD and lacked some trait data: Whitehead's Swiftlet (*Aerodramus whiteheadi*), Brown-banded Rail (*Lewinia mirifica*), Luzon Buttonquail (*Turnix worcesteri*), and Visayan Miniature Babbler (*Micromacronus leytensis*). Where possible, we filled in trait gaps for these four species with data from congeners. For body mass, we averaged the masses of all congeners.

To examine the threat status of recently split species, we identified the species in the literature that have been associated with taxonomic updates and proposed revisions within the last decade (**Supplementary Table 2**). This includes the 35 species recognized by BirdLife International (2021) that have recently been described as a result of species splits (Lohman et al., 2010; Collar, 2011; Rasmussen et al., 2012; Hosner et al., 2013; Campbell et al., 2016; Arndt et al., 2019) and, if applicable, the endemic Philippine parent species from which these birds were split (**Supplementary Table 2**). We also included the 19 species that consist of one or more cryptic populations that have been recommended to be split but have yet to be split and recognized by BirdLife International (2021) as separate species (**Supplementary Table 2**; Lohman et al., 2010; Collar, 2011; Campbell et al., 2016).

Statistical Analyses

We created a series of generalized linear mixed-effects models (GLMMs) using the "glmer" function from the R package *lme4* (Bates et al., 2015) to test the relationships between IUCN threat status and our ten traits (Kruger and Radford, 2008). We excluded the four DD species, and then converted threat status into a continuous linear index from 0 to 4 (0 = LC, 1 = NT, 2 = VU, 3 = EN, 4 = CR), which served as our response variable. This numerical treatment for threat status and use of IUCN categories as surrogate measurements of extinction risk follows that of prior studies assessing predisposition to extinction in biodiversity (Purvis et al., 2000; Cardillo et al., 2004), including a recent examination of the correlates of extinction risk in birds (Wang et al., 2018). We also log-transformed body mass, since it increases geometrically, and clutch size, since this variable consists of count data; these two variables were approximately normally distributed following transformation. We then scaled

TABLE 1 | Resident Philippine bird species not currently listed as threatened by the IUCN Red List (i.e., Least Concern or Near Threatened) which possess traits identified as correlates of extinction risk with strong support across all competing models (endemism, elevational range, forest dependency, and body mass) and have a predicted threat status that would often result in the species being classified as threatened under the IUCN Red List. Three threatened species with higher predicted threats than their IUCN designated ones, as well as the four Data Deficient species are also included in the table.

Species	IUCN red list status	Endemic	Elevational range (m)	Forest dependency	Body mass (g)	Fitted threat	Predicted threat
Palawan Peacock-pheasant *Polyplectron napoleonis*	VU	Yes	800	High	379.00	2.62	EN
Luzon Bleeding-heart *Gallicolumba luzonica*	NT	Yes	1,000	High	190.00	1.68	VU
Philippine Green-pigeon *Treron axillaris*	LC	Yes	1,000	High	198.00	1.84	VU
Cream-bellied Fruit-dove *Ramphiculus merrilli*	NT	Yes	1,300	High	263.00	1.64	VU
Pink-bellied Imperial-pigeon *Ducula poliocephala*	NT	Yes	1,100	High	537.00	2.44	VU
Whitehead's Swiftlet *Aerodramus whiteheadi*	DD	Yes	800	High	14.00	0.99	NT
Brown-banded Rail *Lewinia mirifica*	DD	Yes	1,700	Low	95.67	0.20	LC
Calayan Rail *Gallirallus calayanensis*	VU	Yes	300	High	245.00	2.85	EN
Luzon Buttonquail *Turnix worcesteri*	DD	Yes	1,100	Non-forest	63.34	0.20	LC
Palawan Scops-owl *Otus fuliginosus*	NT	Yes	500	Medium	123.28	1.55	VU
Luzon Lowland Scops-owl *Otus megalotis*	LC	Yes	900	High	248.33	1.88	VU
Mindoro Scops-owl *Otus mindorensis*	NT	Yes	630	High	123.28	2.11	VU
Philippine Eagle-owl *Bubo philippensis*	VU	Yes	650	High	1392.15	3.41	EN
Philippine Honey-buzzard *Pernis steerei*	LC	Yes	1,310	High	708.50	1.72	VU
Philippine Serpent-eagle *Spilornis holospilus*	LC	Yes	500	Medium	637.50	2.73	EN
Writhed Hornbill *Rhabdotorrhinus leucocephalus*	NT	Yes	200	High	1153.50	4.61	CR
Luzon Hornbill *Penelopides manillae*	LC	Yes	900	High	454.75	1.65	VU
Mindanao Hornbill *Penelopides affinis*	LC	Yes	900	High	479.50	2.07	VU
Visayan Miniature Babbler *Micromacronus leytensis*	DD	Yes	800	High	6.0	0.77	NT
Stripe-breasted Rhabdornis *Rhabdornis inornatus*	LC	Yes	200	High	39.10	1.71	VU

See methods for how body mass for the Data Deficient species were estimated, as well as how fitted threat values were calculated and the numerical ranges associated with each threat status. DD, Data Deficient; LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.
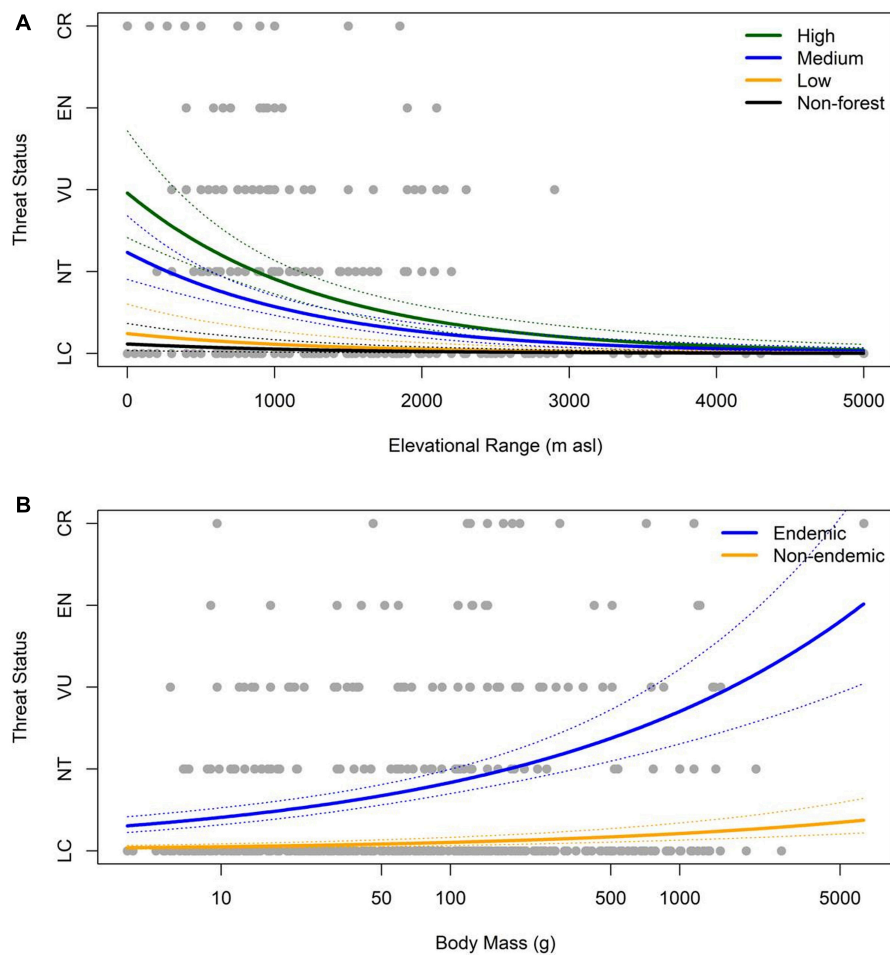
FIGURE 3 | The correlation between threat status and **(A)** a species' elevational range size and forest dependency, and **(B)** a species' endemicity and body mass in resident Philippine birdlife. We hold the other variables from our top model to be equal to their mean values (0). All four variables were significantly correlated with threat status: endemism (1.560 ± 0.276, $z = 5.656$, $p < 0.001$), elevational range (–0.541 ± 0.097, $z = -5.603$, $p < 0.001$), forest dependency ($\chi^2 = 16.361$, $p = 0.001$), and body mass (0.451 ± 0.069, $z = 6.550$, $p < 0.001$).

all of our numerical variables to have a mean of 0 and a standard deviation of 1.

We then constructed a GLMM with a Poisson error structure. We used a Poisson GLMM because threat status was not normally distributed, consisted of integer values, and was zero-bound and zero-inflated. To control for phylogeny, we included bird genus nested within family as random intercept effects in our models. In our general model, we included all ten biological correlates, excluding any species which had gaps in data for forest dependency, nest type, or clutch size. Removing these birds with gaps, we therefore had sufficient data for 371 species to run in this model. However, due to the large number of species for which we lacked information on clutch size, we created another model for this dataset that excluded clutch size, to test the significance of this variable. We compared these two models using a likelihood ratio test and, since clutch size was not significant ($\chi^2 = 0.482$, $p = 0.487$), we removed it from the general model. We then created a second general GLMM with an

expanded dataset that included species with no clutch size data ($n = 421$). We investigated variance inflation factors for the nine variables in our expanded GLMM using the function "vif" from the R package *car* (Fox and Weisberg, 2019), and all were below 3 (Zuur et al., 2010).

Next, we used the function "dredge" from the R package *MuMIn* (Bartoń, 2020) on the general model to run models for every possible subset of variables (512 models), to rank these models based on AIC_c, and to provide model weights for each model (Burnham and Anderson, 2002). We then subsetted these possible models to those with $\Delta AICc < 6$ (Harrison et al., 2018). We considered the model with the lowest AIC_c to be the model best supported by the data. We used a likelihood ratio test to determine significance for any categorical variables with more than two categories.

We compared observed threat status with predicted (fitted) threat status from the model for two groups of species to evaluate whether some species may be more threatened than currently

TABLE 2 | Endemic Philippine bird species, described within the last decade as a result of a taxonomic split and recognized by BirdLife International (2021) or species that consist of one or more cryptic populations, which possess traits identified as correlates of extinction risk with strong support across all competing models (endemism, elevational range, forest dependency, and body mass) and have a predicted threat status that is numerically higher than their current IUCN designated one.

Species	IUCN red list threat	Endemic	Elevational range (m)	Forest dependency	Body mass (g)	Taxonomic status	Fitted status	Predicted status
White-eared Brown-dove *Phapitreron leucotis*	LC	Yes	1,500	Medium	111.00	Parent	0.70	NT
Buff-eared Brown-dove *Phapitreron nigrorum*	LC	Yes	1,600	Medium	112.50	Split	0.61	NT
Short-billed Brown-dove *Phapitreron brevirostris*	LC	Yes	1,600	Medium	104.00	Split	0.59	NT
Philippine Green-pigeon *Treron axillaris*	LC	Yes	1,000	High	198.00	Split	1.84	VU
Red-crested Malkoha *Dasylophus superciliosus*	LC	Yes	700	Medium	198.00	Cryptic	1.07	NT
Luzon Lowland Scops-owl *Otus megalotis*	LC	Yes	900	High	248.33	Parent	1.88	VU
Mindanao Lowland Scops-owl *Otus everetti*	LC	Yes	1,550	High	150.00	Split	1.17	NT
Buff-spotted Flameback *Chrysocolaptes lucidus*	LC	Yes	1,500	Medium	127.00	Parent, Cryptic	0.62	NT
Luzon Flameback *Chrysocolaptes haematribon*	LC	Yes	1,000	Medium	127.50	Split	1.06	NT
Philippine Oriole *Oriolus steerii*	LC	Yes	1,200	Medium	70.91	Parent	0.74	NT
White-lored Oriole *Oriolus albiloris*	LC	Yes	1,200	Medium	70.91	Split	0.84	NT
Blue-headed Fantail *Rhipidura cyaniceps*	LC	Yes	1,000	Medium	13.80	Parent	0.61	NT
Visayan Fantail *Rhipidura albiventris*	LC	Yes	500	Medium	14.00	Split	0.87	NT
Mindanao Blue Fantail *Rhipidura superciliaris*	LC	Yes	1,200	High	12.66	Parent	0.67	NT
Visayan Blue Fantail *Rhipidura samarensis*	LC	Yes	1,200	High	12.60	Split	0.67	NT
Philippine Pied Fantail *Rhipidura nigritorquis*	LC	Yes	800	Medium	16.40	Split	0.53	NT
Cordillera Ground-warbler *Robsonius rabori*	VU	Yes	800	Medium	61.00	Parent	1.33	NT
Sierra Madre Ground-warbler *Robsonius thompsoni*	LC	Yes	1,300	Medium	58.75	Split	1.06	NT
Stripe-breasted Rhabdornis *Rhabdornis inornatus*	LC	Yes	200	High	39.10	Parent	1.71	VU
Grand Rhabdornis *Rhabdornis grandis*	LC	Yes	1,250	High	45.50	Split	0.79	NT
White-browed Shama *Kittacincla luzoniensis*	LC	Yes	1,000	High	24.00	Parent	0.88	NT
Visayan Shama *Kittacincla superciliaris*	LC	Yes	1,000	High	24.05	Split	0.88	NT

See the methods for how fitted threat values were calculated and the numerical ranges associated with each threat status. If a split bird has a parent species that occurs in the Philippines, the parent has been paired with the split. LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered; Split, a newly described species in the last decade whose population was split out of an existing species; Parent, a species from which a recently described bird was split; Cryptic, a species consisting of one or more populations representing cryptic species that have yet to be split and recognized by BirdLife International (2021) as full species.

designated. We first assessed LC and NT species and determined whether the fitted threat status exceeded the observed threat status. For our thresholds for fitted threat status, we chose a range between 0.5 and 1.5 to indicate a species was NT, 1.5–2.5 for VU, 2.5–3.5 for EN, and 3.5 and higher for CR; a range of 0.0–0.5 indicated LC. We also used the same approach to extract and assess fitted threat values for 35 species (and their parent species, if applicable) recognized by BirdLife International (2021) that were recently split (Lohman et al., 2010; Collar, 2011; Rasmussen et al., 2012; Hosner et al., 2013; Campbell et al., 2016; Arndt et al., 2019), as well as the 19 species which consist of populations of one or more cryptic species (Lohman et al., 2010; Collar, 2011; Campbell et al., 2016) that have not yet been recognized by BirdLife International (2021). Finally, we used our model, which had excluded DD species, to predict the threat status of the four DD species.

All statistical analyses and graphing were conducted in R (version 4.0.2, 2020-06-22; R Core Team, 2020).

RESULTS

Our general model contained 421 species. Following multi-model comparison, we found 29 competing models within ΔAICc <6. The top-ranked model contained four covariates that had a significant effect on threat status: endemism, elevational range, forest dependency, and body mass. These covariates were present in all 29 competing models. Specialization (0.173 ± 0.097, $z = 1.783$, $p = 0.075$) was also included in our top-ranked model, but it was non-significant.

Endemism was significantly associated with threat status in our top-ranked model (**Figure 3B**; 1.560 ± 0.276 se, $z = 5.656$, $p < 0.001$), with endemic species being more threatened with extinction than non-endemic residents (average threat: endemic = 1.00, non-endemic = 0.11). Elevational range was significantly associated with threat status in our top-ranked model (**Figure 3A**; −0.541 ± 0.097 se, $z = -5.603$, $p < 0.001$), with species that have narrower elevational ranges being more threatened than those that occur at broader elevational ranges. Forest dependency was significantly associated with threat status in our top-ranked model (**Figure 3A**; $\chi^2 = 16.361$, $p = 0.001$), such that species that have high forest dependency are more threatened than species with lower forest dependency (average threat: high = 1.20, medium = 0.50, low = 0.10, non-forest = 0.06). Finally, body mass was significantly associated with threat status in our top-ranked model (**Figure 3B**; 0.451 ± 0.069, $z = 6.550$, $p < 0.001$), with larger-bodied species more threatened than smaller-bodied birds.

We found 84 species of resident Philippine birds not listed as threatened by the International Union for Conservation of Nature and Natural Resources (2020) that had fitted numerical threats more severe than their currently designated ones, including 71 LC species that would classify as NT. Of these 84 species, fourteen had a predicted threat status that would result in the species being classified as threatened under the IUCN Red List (**Table 1**). In particular, Philippine Serpent-eagle (*Spilornis holospilus*) would classify as EN, while Writhed Hornbill

(*Rhabdotorrhinus leucocephalus*) would classify as CR (**Table 1**). There were also three threatened species, all currently designated as VU, which would classify as EN (**Table 1**): Palawan Peacock-pheasant (*Polyplectron napoleonis*), Calayan Rail (*Gallirallus calayanensis*), and Philippine Eagle-owl (*Bubo philippensis*). Finally, for the four DD species, we predicted a fitted threat of LC for Brown-banded Rail and Luzon Buttonquail, and NT for Whitehead's Swiftlet and Visayan Miniature Babbler (**Table 1**).

Additionally, we found 12 species, which are all products of recent splits (Collar, 2011; Rasmussen et al., 2012; Hosner et al., 2013; Campbell et al., 2016) and are recognized by BirdLife International (2021) that have predicted threat statuses more severe than their current IUCN-designated statuses (**Table 2**). Similarly, we found two species, Red-crested Malkoha (*Dasylophus superciliosus*) and Buff-spotted Flameback (*Chrysocolaptes lucidus*), each consisting of one or more cryptic populations with high phenotypic divergence (Campbell et al., 2016), that had a higher predicted threat status than their IUCN-designated one (**Table 2**). Eleven parent species from which one or more species were recently split also had a more severe predicted threat status than their IUCN ones (**Supplementary Table 2**).

DISCUSSION

In biodiverse regions threatened with anthropogenic change, it is critical to assess the predictors of extinction risk. In this study, we conducted the first comprehensive investigation into the biological correlates of extinction risk in the Philippine avifauna. For resident Philippine birds, we found strong support across competing models for endemic, elevationally-restricted, highly forest dependent, and larger-bodied species being predisposed to extinction (**Figure 3**).

Endemic species tend to be well-adapted to their local environments, but become rare when rapid changes create new habitats (Jones et al., 2001) or forest fragments (Weerd et al., 2003) to which they often cannot adapt. Endemic species also tend to have smaller geographic ranges than co-occurring resident, non-endemic species. While a number of Philippine endemics have large ranges across the archipelago and are not listed as globally threatened, geographic range size is one of the main criteria used by the IUCN to assess a species' extinction risk (Mace et al., 2008; Le Breton et al., 2019; International Union for Conservation of Nature and Natural Resources, 2020). Consequently, many Philippine endemic birds are restricted to a single island such as Palawan or Luzon. We also found that birds which occur at narrower elevational ranges are at a heightened risk of extinction, consistent with prior studies (Şekercioğlu et al., 2008; White and Bennett, 2015). This may be amplified by the fact that eighty-seven percent of Philippine bird species occur in lowland areas below 500 m asl (**Supplementary Table 1**), with many species with narrow elevational ranges occurring partially or entirely across lower elevations. Deforestation for timber and crop cultivation (Kummer, 1992; Weerd et al., 2003; Panopio and Pajaro, 2014) has reduced the extent of lowland forest in the Philippines by over 90% (Ong et al., 2002; Tanalgo et al., 2015).

Between 2002 and 2020, the Philippines lost 151kha of humid primary forest (Turubanova et al., 2018). This level of habitat destruction may especially impact species that have smaller elevational ranges and are thus constrained by elevation (Kattan et al., 1994). Extensive habitat destruction also greatly reduces niche availability, and species with narrow ecological niches are less adaptable to the changes brought about by habitat loss and degradation (McKinney, 1997; Kruger and Radford, 2008; Edwards et al., 2013). We likewise found that high forest dependency was a correlate of extinction risk in Philippine birds.
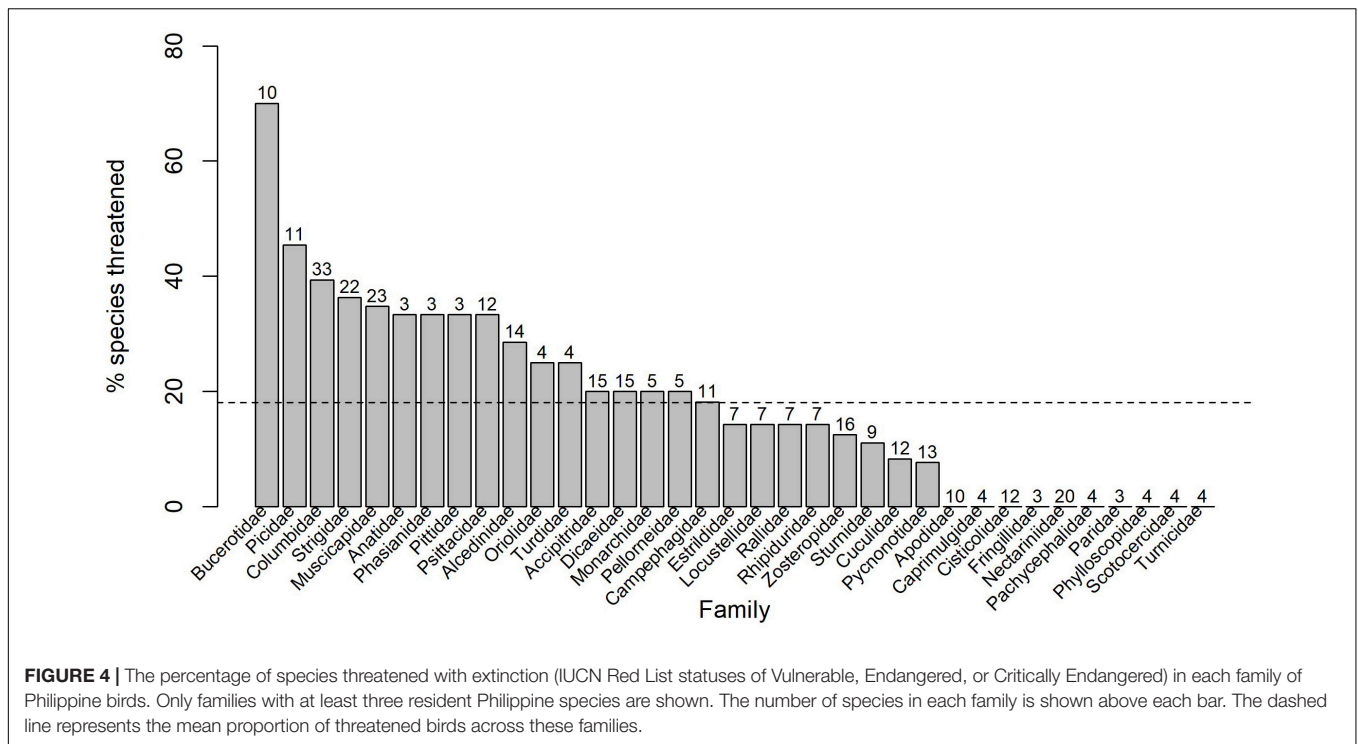
We found that larger-bodied birds are at increased risk of extinction, consistent with previous studies (e.g., Gaston and Blackburn,1995; Bennett and Owens, 1997; Wang et al., 2018). Larger species may recover more slowly from reductions in population size as a result of slower life histories (Gaston and Blackburn, 1995; Bennett and Owens, 1997), particularly in insular species (Boyer, 2008). Likewise, larger body size may limit population density and therefore a species' total population size on islands (Boyer, 2008). Since population size is one of the main criteria used by the IUCN to assess a species' extinction risk (Mace et al., 2008; Le Breton et al., 2019; International Union for Conservation of Nature and Natural Resources, 2020), both of these effects of larger body size would be important for predisposition to extinction. Additionally, larger species are often targeted for hunting and the pet trade, such as Visayan Hornbill (*Penelopides panini*), Philippine Cockatoo (*Cacatua haematuropygia*), Blue-naped Parrot (*Tanygnathus lucionensis*), and Philippine Serpent-eagle (Asian Development Bank, 2018) are thus more susceptible to overexploitation than are smaller species (Beissinger, 2000; Peres and Palacios, 2007; Wang et al., 2018). For example, three large pigeon species disappeared in the early twentieth century from Sibuyan Island in the Philippines, species that were likely locally extirpated despite their broad elevational ranges (Goodman et al., 1995). Intense hunting pressure coupled with the destruction of lowland habitat could have played a large part in the disappearances of these three pigeons (Goodman et al., 1995).

When examining predicted threat status, we found fourteen Philippine endemics not currently listed as threatened by the IUCN Red List (2020) that have predicted threat statuses that would qualify these birds as globally threatened according to our model (**Table 1**). We also found three threatened species that had higher predicted threats than their current designated ones. These fifteen species may be more threatened with extinction than currently believed based on their ecological correlates of extinction risk, and so should receive heightened conservation attention. Of particular note, we predicted that the LC Philippine Serpent-eagle and NT Writhed Hornbill are, respectively, EN and CR. Both birds are recognized as undergoing population declines, though Philippine Serpent-eagle is not classified as threatened since it occurs over a large range whereas it is noted that Writhed Hornbill is a poorly known species that should be carefully monitored (BirdLife International, 2021). These two species should therefore become bird conservation priorities in the Philippines.

Additionally, there are currently four DD birds in the Philippines, all of which are poorly known, with only a handful of records each within the last couple decades. Using our fitted model, we predicted that two of these birds would have a status of LC and the other two would have a status of NT (**Table 1**). However, there are some caveats with these findings. While we used congeners of these four species to help fill in information gaps for certain key traits, having more accurate trait information will allow for better predictions of threat status. We also know that IUCN threat status takes into account geographic range size and population size (Mace et al., 2008; Le Breton et al., 2019; International Union for Conservation of Nature and Natural Resources, 2020), which are both likely to be very small for these species. Likewise, elevational ranges used for these species may not be truly reflective for these birds with little-known distributions. Thus, these species are likely to be more threatened than estimated by our models. Future surveys should aim for a better understanding of the distributional limits and biological traits of these DD species in order to better predict and assess their threat status.

The Philippine avifauna has also undergone much taxonomic revision in recent years. In 2000, the number of endemic birds in the Philippines was 172 species (Kennedy et al., 2000), whereas today there are 258 endemic species (BirdLife International, 2021). Much of this change has occurred within the past decade, as birds have been split from extant recognized species (Lohman et al., 2010; Collar, 2011; Rasmussen et al., 2012; Hosner et al., 2013; Campbell et al., 2016; Arndt et al., 2019). We found 12 recently described splits (**Table 2**) and 11 parent species (**Supplementary Table 2**) which are likely to have worse threat statuses than their IUCN-designated ones. It is also predicted that the Philippines has a high number of cryptic species that have yet to be formally recognized (Lohman et al., 2010; Campbell et al., 2016), with recent proposals for some cryptic populations being elevated to species (**Supplementary Table 2**; Lohman et al., 2010; Collar, 2011; Campbell et al., 2016). We found two species with proposed cryptic splits that had higher predicted threat statuses than their IUCN-designated ones (**Table 2**). As bird species are split, newly split populations will have both a smaller number of individuals and more restricted geographic distributions (Robuchon et al., 2019) than the original parent species. For example, the Philippine clade of the LC parrot species *Tanygnathus sumatranus* was recently split (Arndt et al., 2019), resulting in the now endemic Blue-backed Parrot (*Tanygnathus everetti*) being designated as EN by the IUCN Red List (2020). We can therefore expect the number of threatened birds in the Philippines to increase in the future with new taxonomic arrangements.

Between 1988 and 2012, the number of threatened endemic birds in the Philippines increased from 34 (Collar and Andrew, 1988) to 84 species (Panopio and Pajaro, 2014). Today, 93 (36%) endemic species are threatened with extinction in the Philippine Archipelago (BirdLife International, 2021), a 10% increase in the number of endemic avifauna facing extinction in these islands in just under a decade. The families with the

FIGURE 4 | The percentage of species threatened with extinction (IUCN Red List statuses of Vulnerable, Endangered, or Critically Endangered) in each family of Philippine birds. Only families with at least three resident Philippine species are shown. The number of species in each family is shown above each bar. The dashed line represents the mean proportion of threatened birds across these families.

highest number of threatened birds in the Philippines are Columbidae, Muscicapidae, Strigidae, and Bucerotidae, with the latter having the highest proportion of threatened species (**Figure 4**). Approximately 71% of Philippine birds in our study are forest species, so the numbers of threatened birds can be expected to increase if deforestation and degradation of habitats continue at a rate similar to or greater than the recent trends of destruction.

Beyond the Philippines, Southeast Asia contains thousands of islands rich in diversity and endemism, and anthropogenic threats such as habitat degradation and exploitation are severe. In the Philippines, there are 258 endemic species (43% of resident avifauna) and 141 species (24%) with high forest dependence. Across Southeast Asia and Papua New Guinea, this number is 880 (34% of resident avifauna) and 852 species (33%) with high forest dependence. The median elevational range among Philippine avifauna is 1,100 m, and there are 222 species (37%) with a range of 1,100 or less meters. Likewise, there are 503 species (19%) across the broader region with a range of 1,100 or narrower. The median body mass of Philippine birds is also 53 g, and there are 223 species (38%) in the archipelago that weigh this much or more. Likewise, of the birds across the broader region for which there is available information on weight (65% of species), there are 441 species (26%) that have a large body size. Our findings thus have important conservation implications for birdlife on islands throughout Southeast Asia, Oceania, and the rest of the tropics. As human activities continue to cause global declines and losses in avian biodiversity, assessing and predicting extinction risk will be even more important as a pre-emptive conservation strategy.

CONCLUSION

In this study, we identify from a broad range of ecological, biogeographical, and life history traits the most important biological correlates of extinction risk in resident Philippine birdlife. Many species are typically affected by more than one type of threat (Davies et al., 2004; Henle et al., 2004; Wang et al., 2015, 2018), and our study is one of the few that collectively analyzes the effects of multiple traits in birds as potential correlates of extinction risk. Endemics, species with narrower elevational ranges, highly forest dependent species, and larger birds are most prone to population declines, and we can use our analyses to predict which species may be at more risk of extinction now and in the near future (**Tables 1**, **2**) to help bring attention to these species and better inform conservation strategies for Philippine birds. With many recently described bird species in the Philippines in the last decade and an increased understanding of the number of cryptic species in the archipelago that have yet to be elevated to species-level (Lohman et al., 2010; Collar, 2011; Campbell et al., 2016), identifying avian ecological traits of extinction risk can be crucial for the conservation of newly described species in the future. If deforestation continues and habitats are further diminished and degraded, particularly in lowland regions, species currently at risk in the Philippines may become extinct and the threat of extinction will expand to other species, including those that have yet to be described. Furthermore, we have a limited understanding of the effects of climate change on tropical birds and the future impacts of climate change on tropical montane forest endemics are likely to be underestimated (Harris et al., 2011; Wormworth and Şekercioğlu, 2011). Urgent action to curtail human

impact on biodiversity, especially deforestation, degradation, exploitation and climate change, is needed if the Philippine Archipelago is to retain its unique and diverse avian biodiversity.

DATA AVAILABILITY STATEMENT

The original dataset analyzed for this study can be found in **Supplementary Table 1** included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because our study relied on a dataset of trait-based information for bird species and did not involve handling of or experiments on animals.

AUTHOR CONTRIBUTIONS

KK wrote the manuscript with assistance from MN-C and ÇŞ. ÇŞ and MP conceived the original idea for the project, with later support from KK and MN-C. ÇŞ acquired funding and resources. JM, JB, KK, and MN-C compiled the dataset for this manuscript. KK and MN-C statistically analyzed the data and created the figures and tables. All co-authors contributed to and gave final approval of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021. 664764/full#supplementary-material

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