Identifying global research and conservation priorities for Columbidae: a quantitative approach using random forest models

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The family of Columbidae, including pigeons and doves, remains understudied despite their patrimonial value and high ecological and conservation relevance. Currently, 353 extant columbid species are listed in the IUCN red list, with about 20% of them being threatened with extinction. However, there has been little effort so far to synthetize the available information on factors influencing extinction risk and the allocation of research effort among columbid species. In this context, using random forest models, the present study aims at quantitatively assessing to what extent environmental, life history and socio-political factors may drive the extinction risk of pigeons and doves and explain differences in scientific attention among species. We found that high risk of extinction in columbids is associated with small historical range, exposure to invasive alien mammals and living in isolated islands and/or at low altitudes, while the probability of population decline is associated with species body size, surrounding human density and narrow habitat breadth. We also evidenced a large disparity between species or population extinction risk and scientific interest. Indeed, most of the studies on columbids have been conducted by scientists from North America and Western Europe on their local species, whereas species from biodiversity hotspots, which are more at risk of extinction, have comparatively received little attention. This unequal acquisition of knowledge creates gaps that deserve to be filled in order to have a good appreciation of extinction risk in columbids and associated threats, through fair transnational cooperation, academic training and regional coordination in conservation-oriented research on columbids.

KEYWORDS

biogeography, doves, endangered species, extinction risk, pigeons, scientific attention, threatened species

1 Introduction

The rate of biodiversity loss is currently increasing at an unprecedented rate, as a direct consequence of habitat loss, fragmentation and degradation, biological invasions, and climate change (Balmford et al., 2003; Barnosky et al., 2011). However, the extent and rate of biodiversity loss are not uniform around the globe (Howard et al., 2020), nor across taxa (Pimm et al., 2014). As available funding for conservation research and actions is limited (Evans et al., 2012; Waldron et al., 2013), there is an obvious need to define priorities for optimizing resource allocation (Brooks et al., 2006). Ideally, prioritization mechanisms should be based on sound and reliable scientific evidence (Williams et al., 2020). However, important gaps in knowledge still exist, particularly in several biodiversity-rich countries, such as Haiti or sub-saharan African countries, where ongoing conflicts, political instability and poor access to facilities and funding severely hamper the development of field research and monitoring programs (Hanson et al., 2009; Siddig, 2014; Conteh et al., 2017; dos Santos et al., 2020; Vallès et al., 2021). In addition to spatial bias, the conservation literature tends to give a disproportionate attention to emblematic, charismatic, and flagship species (Andelman and Fagan, 2000; Brambilla et al., 2013; Mammides, 2019; Habel et al., 2021). Consequently, there is a certain mismatch between research efforts and conservation priorities (Christie et al., 2021).

Avian conservation biology research is no exception to the rule (de Lima et al., 2011; Ducatez and Lefebvre, 2014; Murray et al., 2015; Roberts et al., 2016; Buechley et al., 2019). Various factors, such as environmental conditions, phylogeny, life-history traits, levels of anthropogenic pressure, or socio-political factors, independently or jointly, can affect the risk of extinction of avian species (Owens and Bennett, 2000). For instance, extinction risk is not distributed randomly among avian families and in relation to fecundity and body size (Bennett and Owens, 1997). On the other hand, the severity of extinction risk of avian species varies in relation to socioeconomic factors and human pressure (Olah et al., 2016; Chen et al., 2019). Similarly, variation in the level of scientific attention among bird species is significantly influenced by phylogeny, geographic range and ecological life history traits, with non-threatened species being studied twice as much as threatened ones (Ducatez and Lefebvre, 2014). For instance, although the Andean Flamingo, *Phoenicoparrus andinus*, is the least abundant flamingo in the world and is listed as Vulnerable by the IUCN Species Survival Commission (Derlindati et al., 2014), it has received far less attention than the Least Concern Greater Flamingo, *Phoenicopterus roseus* (Johnson and Cézilly, 2007; Geraci et al., 2012). In addition, the majority of avian conservation research is conducted in developed countries and/or by North American and western European researchers, confirming the mismatch between priorities and capacity for research and conservation (Brito and Oprea, 2009; Vallès et al., 2021).

In particular, Columbidae, the only extant family of Columbiformes, is particularly understudied, despite its patrimonial value and high ecological and conservation relevance (Walker, 2007; McKenzie and Robertson, 2015; Devenish-Nelson et al., 2019; Yarwood et al., 2019). Pigeons and doves are one of the oldest and most diverse extant lineages of birds. However, their evolutionary radiation and phylogeny remain poorly resolved (Soares et al., 2016), with the creation of new genus or species and the slimming of other genus based on molecular or paleontological evidence (Johnson et al., 2001; Banks et al., 2013; Sangster et al., 2018; Steadman and Takano, 2020). Currently, the family Columbidae includes about 370 species that are distributed on all continents, except for the high Artic and Antarctica (del Hoyo et al., 1997; BirdLife International, 2022). They occur in various habitats (del Hoyo et al., 1997; Gibbs et al., 2001; Carvalho et al., 2015; Fey et al., 2015; Monterrubio-Rico et al., 2016), where they provide important ecosystem services, particularly through seed dispersal (Meehan et al., 2005; Wotton and Kelly, 2012; Costan and Sarasola, 2017; Ando et al., 2021). However, a significant proportion of columbid species are endangered or threatened with extinction (Bennett and Owens, 1997; Walker, 2007; Rivera-Milán et al., 2015; Lees et al., 2021). This results in habitat fragmentation and degradation, introduced predators, competition with invasive columbid species, excessive hunting pressure and ineffective management, and trade (Walker, 2007; Carvalho et al., 2015; Camacho-Cervantes and Schondube, 2018; Lamelas-López et al., 2020; Lormée et al., 2020; Moreno-Zarate et al., 2021; Bacon et al., 2023). The conservation status of several species remains uncertain, mainly due to lack of data (del Hoyo et al., 1997; Walker, 2007). This is particularly true of secretive species or species with very restricted geographical range for which traditional study methods might not be appropriate (Cambrone et al., 2021). More to the point, little effort has been made so far to synthetize the available information on the factors influencing the conservation status of columbid species and research effort. To the best of our knowledge, only Walker (2007) provided a short review of the main drivers of extinction risk for columbid species based on a relatively simple statistical analysis of data available from BirdLife International, emphasizing the vulnerability of insular species. We went further in the present study by quantitatively assessing to what extent environmental, life history traits and socio-political factors may (i) drive the extinction risk of pigeons and doves and (ii) explain differences in scientific attention among species. To that end, we relied on random forest (RF) models and an updated database (including both IUCN conservation status and population trends of columbid species) especially compiled for this study.

2 Materials and methods

2.1 Database creation

2.1.1 Information about columbid species

We obtained data for the 369 species from three main sources: Birdlife international (BirdLife International, 2021), the website *Birds of the World* (https://birdsoftheworld.org) and *Pigeons and Doves: A Guide to the Pigeons and Doves of the World* (Gibbs et al., 2001). We extracted information on biological, ecological and environmental traits that are likely to influence extinction risk (see Buechley et al., 2019). We classified explanatory variables into four categories: "environment", "behavior and life history",

"anthropogenic pressure" and "socio-political indicators" (Table 1). In order to estimate each species' extinction risk, we relied on IUCN Red List categories and global population trends (BirdLife International, 2021). We classified species as threatened (critically endangered *CR*, endangered *EN* and vulnerable *VU*), non-threatened (near-threatened *NT* and least-concern *LC*), extinct (extinct *EX* and extinct in the wild *EW*), or data deficient. Because non-threatened species do not necessarily show stable or increasing population trends (Figure 1), we used global population trends of species (Rodrigues et al., 2006) as a second proxy of extinction risk. Species were thus classified as increasing, stable or decreasing according to BirdLife International (2021).

2.1.2 Scientific attention

In order to quantify scientific attention given to each columbid species, we relied on the number of peer-reviewed articles retrieved from an extensive bibliographic search on all databases of the Web of Science (conducted by mid-2021). We performed searches using current and past binomial scientific names, vernacular names in English, French and Spanish and all recognized synonyms. To compile all possible names of species, we used the websites *Avibase* (https://avibase.bsc-eoc.org) and *Birds of the World*. We considered several "research areas", as defined in the Web of Science, as all studies bringing ecological knowledge about a species may be of help for its conservation (Courchamp et al., 2015). Each search was conducted using the following procedure:

"TS="

(in order to search following terms in title, abstract and keywords of articles)

+

Full binomial scientific names, vernacular and all recognized synonyms in independent quotes, separated by "OR"

+

"AND SU=("Ecology" OR "Biodiversity and Conservation" OR "Ornithology" OR "Evolutionary Biology" OR "Zoology")"

(to limit searches to studies related to following science disciplines: Ecology, Conservation Biology, Ornithology, Evolutionary Biology/Ecology and Zoology)

+

"NOT SU=("Veterinary Sciences" OR "Neurosciences and Neurology" OR "Anthropology")"

(to exclude any study related to veterinary sciences, neurosciences and neurology, and anthropology).

We also performed a global search in order to estimate national contributions to research on Columbidae, assessed from the affiliations of authors of peer-reviewed articles. To that end, we used the same search nomenclature, except that we replaced names of species and their synonyms by "Columbidae", "Columbiformes", "Pigeon" and "Dove", separated by the Booleans operator "OR". In order to exclude all articles on Pigeon pea (*Cajanus cajan*), we added: NOT TS=("Pigeon*pea*" OR "*Cajanus cajan*").

2.1.3 Spatial analyses (GIS)

We used QGIS (3.10.11) to calculate spatial statistics for explanatory variables used in our analyses (Table 1 and Supplementary Material 1, Method A1). We obtained various raster and polygon files for historical species range from several sources (Table 1), and rasterized polygons representing area distribution of species using scientific attention (log[number of articles + 1]) as value for the raster unit (square of 400km²). Since, polygons of several species may overlap, we beforehand calculated the mean of scientific attention per raster unit.

2.2 Random forest models

We relied on random forest models because this machine-learning technique has been increasingly used in ecological and macro-ecology studies (Cutler et al., 2007; Kampichler et al., 2010) to assess the impact of various drivers on the extinction risks of a given group of species (Davidson et al., 2012; Di Marco et al., 2014; Di Marco et al., 2018; Buechley and Şekercioğlu, 2016; Buechley et al., 2019). In particular, the method is robust to both phylogenetic inertia and outliers, and can include both continuous and categorical variables (Murray et al., 2011; Davidson et al., 2012; Buechley et al., 2019). This technique is therefore particularly suitable for columbids given that their phylogenetic relationships are not fully resolved due to scarce sampling of taxa and limited availability of sequence data (Khan and Arif, 2013; Bruxaux et al., 2018).

We excluded extinct species and data deficient species from our analyses relying on RFs (Figure 1). We performed three different RF models to identify the factors influencing extinction risk, population trends, and scientific attention among columbids, including all traits listed and detailed in Table 1 as explanatory variables. We considered a wider range of threats than the ones considered by IUCN, thus reducing the risk of circularity when using IUCN status as a proxy of extinction risk of columbid species. All models were performed using the R software (v4.1.1, R Core Team, 2021), using RandomForest package (Liaw and Wiener, 2002). Forests consisted of 10,000, 10,000 and 1,000 classification trees for models implying respectively extinction risk, population trends and scientific attention, in order to reach the lowest value of Out Of Bag errors (OOB; i.e., the percentage of error in predicting the class of these statistical individuals across the random forest formation, see Supplementary Material 1, Method A2), which was also stable throughout the formation of the forest. To evaluate the accuracy of our classification models, we relied on the percentage of species correctly classified (i.e., 100% − OOB), Cohen's kappa statistic that tests the consistency between the actual and predicted classifications, and the sensitivity, specificity and the true skill statistic (TSS = sensitivity + specificity − 1; Allouche et al., 2006; Prasad et al., 2006; Gamer et al., 2019). For the RF addressing scientific attention (quantitative variable), we included the current IUCN category status (threatened/non-threatened) and population trends as explanatory variables. We relied on the percentage of variance explained (R²) as accuracy metrics to assess the performance of the model. The number of variables tested at each split was determined by the program (*mtry*; root-squared of the total number of explanatory variables). We estimated the relative importance of each explanatory variables implied in RF

TABLE 1 Traits used as explanatory variables in random forest models.

Class	Variables	Description	Source
Environment	Altitude	Averaged altitude at which species occurs (x10² m).	BirdLife International, 2021
Environment	Dist. to continent ‡	Distance to the closest continent (km). Species being even partially on continent are set at 0. This variable was normalized using log (x+1) transformation in order to improve graph quality.	Sayre et al., 2019; BirdLife International, 2021; data.gouv.fr
Environment	Endemicity ‡	Species occurring in one country (Yes/No).	BirdLife International, 2021
Environment	Hurricane frequency ‡	Number of hurricanes ranked at least 3 in the Saffir-Simpson scale per year, since 1980. Hurricanes are known to affect avifauna (Wunderle 1995).	Knapp et al., 2010
Environment	IBA	Overlap between historical species range and Important Bird and Biodiversity Areas (Yes/No).	BirdLife International, 2021
Environment	Prop. in islands ‡	Proportion of historical species range on islands. Islands species are usually more prone to extinction (Wood et al., 2017)	Sayre et al., 2019; data. gouv.fr
Environment	Prop. in biodiv. Hotspot ‡	Proportion of historical species range overlapping with biodiversity hotspots.	Hoffman et al., 2016
Environment	Range size ‡	Historical geographic range size of species (km²). This variable was normalized by log transformation in order improve on graph quality. This variable is a strong predictor of species vulnerability (Staude et al., 2020, Newsome et al., 2020)	BirdLife International, 2021
Environment	Island endemic ‡	Restriction of historical species range to a single country consisting of one or several islands (Yes/No). Island-endemic species are usually more prone to extinction (Wood et al., 2017)	Sayre et al., 2019; BirdLife International, 2021; data.gouv.fr
Environment	Prop. in tropical ‡	Proportion of historical species range between the northern and the southern tropics.	Manually created
Behaviour and Life history	Fecundity	Average clutch size.	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Diet	Seven diet categories: granivorous, frugivorous, herbivorous (parts of plants other than seeds or fruits. e.g., buds), invertebrates eaters, meat, fungi and/or reptiles. The last three diet are very rare. For models, they were coded for each 0 (not have this diet) and 1 (having this diet).	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Diet breadth	Number of diet categories per species	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Forest dependency	Forest dependency of species. (No forest sp. (No)< Low (Lo)< Medium (Mid)< High (Hi))	BirdLife International, 2021
Behaviour and Life history	Generation length	Generation length of species from Birdlife International. The variable is known to impact extinction risk in birds (Bird et al., 2020).	BirdLife International, 2021
Behaviour and Life history	Sociality	Sociality of species. (Gregarious (Greg.)/Occasionally gregarious (Occ.)/Solitary (Sol.))	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Life stratum	Stratum in which the species live (Arboreal (Arb.)/Ground (Gr.)/Both).	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Mass	Averaged body mass of species (g). This variable was normalized using log transformation to improve graph quality.	Birds or the world; Gibbs et al., 2001
Behaviour and Life history	Migration	Migration status: Full migrant (Full.)/Vagrant (Vag.)/Sedentary (Sed.)	BirdLife International, 2021; Birds of the world; Gibbs et al., 2001

(Continued)

TABLE 1 Continued

Class	Variables	Description	Source
Behaviour and Life history	Habitat breadth	Number of different habitats used, based on Habitat level 2 from Birdlife International.	BirdLife International, 2021
Pressure	Subsistence use	Species hunted for subsistence purpose, as defined by IUCN red list (Yes/No).	BirdLife International, 2021
Pressure	Handicraft use	Whole or parts of the species used for crafting jewellery, ornament, or any items (Yes/No).	BirdLife International, 2021
Pressure	HFP ‡	Geometric mean of human footprint values estimated in 2009 (see Di Marco et al., 2018 and Venter et al., 2016 for detailed explanation).	Venter et al., 2016; Venter et al., 2018
Pressure	IAS birds	Species impacted by invasive alien bird species (Reported/Not Reported).	BirdLife International, 2021
Pressure	IAS mammals	Species impacted by invasive alien mammals species (Reported/Not Reported).	BirdLife International, 2021
Pressure	IAS reptiles	Species impacted by invasive alien reptiles species (Reported/Not Reported).	BirdLife International, 2021
Pressure	Pets use	Use of species used as pet or display (Yes/No).	BirdLife International, 2021
Pressure	Sport hunting use	Species exposed to sport hunting (Yes/No).	BirdLife International, 2021
Socio-political indicator	GSI ‡	Governance stability index. This index is the average of six indices that measures governance (voice and accountability, political stability and absence of violence, government effectiveness, regulatory quality, rule of law, and control of corruption (Baynham-Herd et al., 2018).	World Bank database
Socio-political Indicator	HDI ‡	Human Development Index. This index is based on life expectancy, years of schooling and gross national income per capita.	World Bank database
Socio-political indicator	Human density ‡	Number of humans per km^2. Averaged over estimates for 2000, 2005, 2010 and 2020.	CIESIN, 2018

‡ means that data were extracted using GIS tools.

models based on the mean decrease Gini (when the dependent variable is qualitative or classes) or increase in node purity (when the dependent variable is quantitative), as a measure of how much model accuracy decreases when removing explanatory variables. The calculation is based on the Gini/node impurity value estimated from classification trees composing the forest. Detailed explanations about random forest modelling are provided in Supplementary Material 1, Method A2.

After inspecting partial dependence plots of relationships between explanatory and dependent variables, we restricted the analysis to the eight first most important variables, as the other ones were much less meaningful and did not present enough variation (Supplementary Material 2, Figure A4–A7). In order to compare and statistically assess the relative importance of explanatory variables and partial plots, we calculated 95% confidence interval (95%CI) by performing 1,000 independent bootstraps from the original dataset (Cumming and Finch, 2005). Results of inferential statistical tests (i.e., tests of Wilcoxon, Kruskal-Wallis, Kendall's correlation or Fisher) are presented in Supplementary Material 2 (Table A1–A3), for all explanatory variables.

Although accuracy metrics were calculated for each RF model, we assessed the prediction capacity of models addressing extinction risk and evaluated overfitting issues by randomly splitting the original dataset into a training dataset (80% of the original dataset) and a dataset that was used to make predictions about extinction risk (i.e., the remaining 20% of the original dataset). Thereafter, we compared predicted results to actual ones by calculating sensitivity, specificity and TSS. This process was renewed 1,000 times in order to calculate the mean and 95% confidence interval of the three performance statistics. Thereafter, we predicted extinction risk for all columbid species by excluding one by one each species from the training dataset (i.e., all species, excepted the species tested). As we found mismatches between predicted and actual extinction risk for some species, we assessed to what extent this was related to levels of scientific attention. To that end, we considered two groups based on the median of scientific attention (i.e., one). The first group then consisted of species for which more than one published scientific article was available whereas the second one corresponded to species for which one or zero scientific article was available. We then tested for differences in the relative proportions of mismatches and correctly evaluated species between the two groups using a Chi-square test. For both analyses, significance level was set at 0.05.
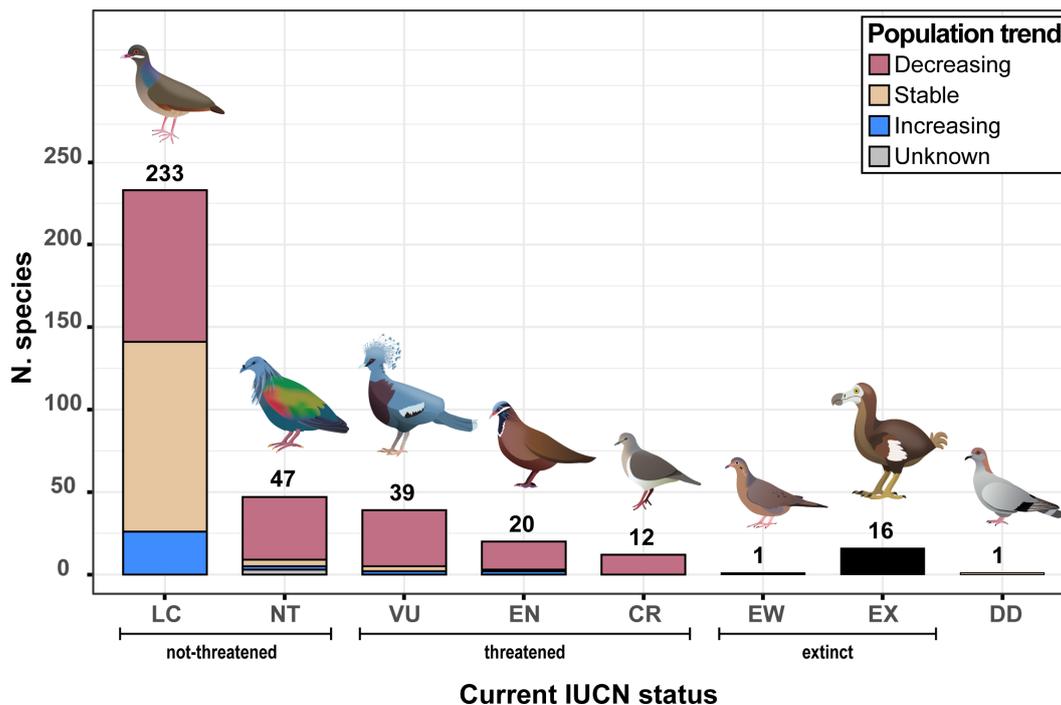
FIGURE 1
Distribution of columbid species according to their current IUCN status and their current population trend. From left to right, columbid species illustrations correspond to: Bridled Quail-Dove (*Geotrygon mystacea*), Nicobar Pigeon (*Caloenas nicobarica*), Victoria Crowned-Pigeon (*Goura victoria*), Blue-headed Quail-Dove (*Starnoenas cyanocephala*), Grenada Dove (*Leptotila wellsi*), Socorro Dove (*Zenaida graysoni*), Dodo (*Raphus cucullatus*) and Somali Pigeon (*Columba oliviae*).

3 Results

Among the 369 described columbid species, 76% are considered by IUCN as non-threatened and 19% as threatened, and 5% as extinct or extinct in the wild (Figure 1). In terms of population trends, 52% of species are declining, while 33% are stable and 9% are increasing. As expected, the relative proportions of declining, stable, and increasing species differed between threatened and non-threatened ones [threatened species: 89%, 6%, and 5%, respectively; non-threatened species: 46%, 43%, and 11%, respectively; Fisher's exact test, P< 0.0001].

3.1 Extinction risk

3.1.1 Threatened *vs*. non-threatened species

The RF model classifying species either as non-threatened or threatened correctly classified 87% of the species based on the 38 explanatory variables used (Table 1). RF model sensitivity and specificity respectively indicated that 87% of actual non-threatened species and 82% of actual threatened species were correctly identified. Cohen's kappa statistics and TSS further indicated that the classification of species significantly differed from a random classification [Cohen's kappa = 0.51, P< 0.0001; TSS = 0.70], while the OOB error was 13%. The eight most important variables influencing extinction risk were in decreasing order: species historical range size, impact of invasive alien mammals, distance to closest mainland, altitude distribution of the species, HFP, human density, proportion of species historical range in current biodiversity hotspots, and species body mass. Based

on the 95% CI comparison, only historical geographic range size had a relative importance significantly higher than the other variables (Figure 2A, see Supplementary Material 2, Figure A4 for all variables importance values). Based on partial dependence plots, species with the smallest historical range size, exposed to invasive alien mammals, living the farthest to mainland and/or at the lowest altitudes were associated to a greater risk of extinction (Figure 3A). Although other variables were relatively important in the prediction of species' risk extinction based on the RF model, their variation did not seem to be directly associated to extinction risk (Figure 3A; see Supplementary Material 2, Figure A5 for all variables).

3.1.2 Population trends

The RF model correctly classified 73% of species according to population trends, with a OOB error of 27%. In addition, the percentage of true positive was of 74%, 69% and 64% for decreasing, stable and increasing species, respectively. On the other hand, the percentage of true negative was of 80%, 89% and 94% for decreasing, stable and increasing species' population trends, respectively. Although goodness-of-fit was lower than for the previous model, Cohen's kappa still indicated a species classification differing from a random classification [Cohen's kappa = 0.48, P< 0.0001]. The eight most important variables predicting population trends were in decreasing order: human density within the species historical geographic range distribution, species body mass, HFP, species historical geographic range size, species habitat breadth, GSI, species altitude distribution, and HDI (Figure 2B). Based on the comparison of 95%CI, these eight variables
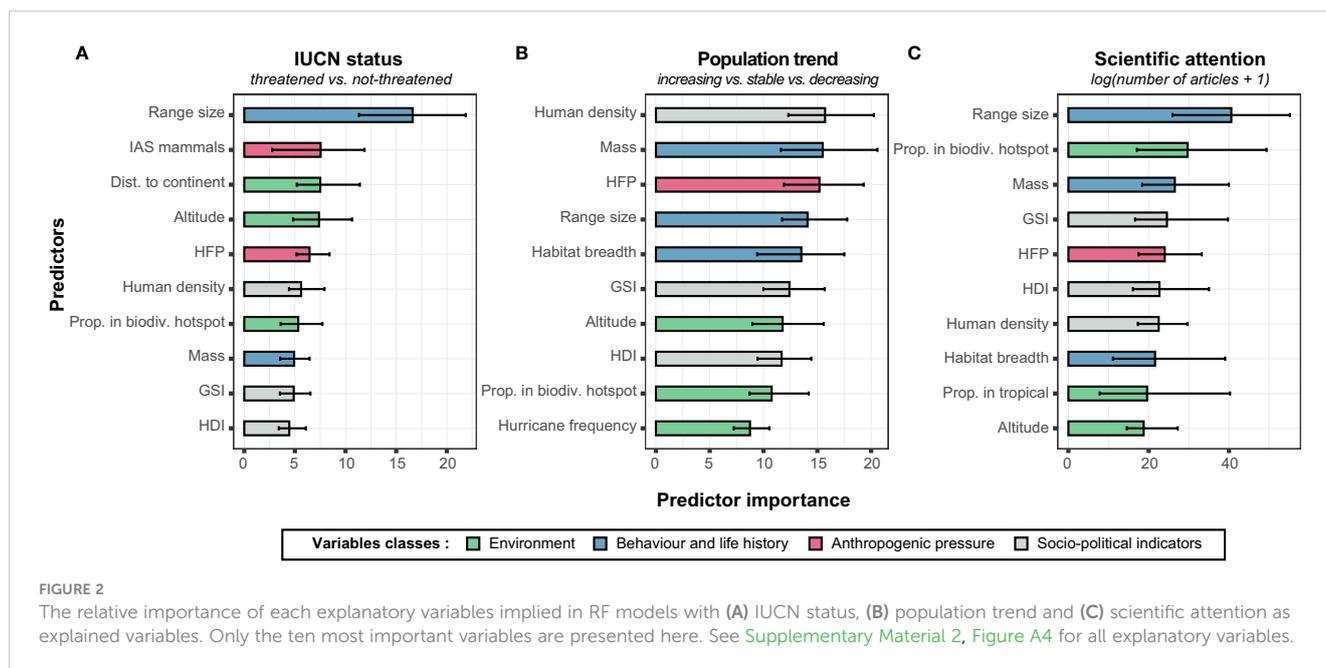
did not seem to significantly differ in terms of importance (Figure 2B, see Supplementary Material 2, Figure A4 for all variables importance values). Based on partial dependence plots, risk of population decline was significantly lower for species with a low body weight living in areas characterized by high human density (Figure 3B). In addition, a higher risk of decline was associated with species with narrow habitat breadth and living at low altitudes (Figure 3B). Although other variables were important in predicting species' risk of decline based on the RF model, partial dependent plots suggest that they are not directly associated to it (Figure 3B; see Supplementary Material 2, Figure A6 for all variables).

3.2 Scientific attention

Our literature survey resulted in 3,537 research articles across the 369 Columbidae species, in scientific disciplines related to environment, ecology and evolution. From these articles, 405 concerned multiple species. Scientific attention (assessed from the number of published articles) differed markedly between columbid species, ranging from 0 to 1363 (median = 1, interquartile = 3). Overall, 10 species (about 3% all species) accounted for 77% of all research articles published since 1966. The most commonly studies species were the Common Wood Pigeon (*Columba palumbus*, 1363 articles), the Rock Pigeon (*Columba livia*, 1079), the Mourning Dove (*Zenaida macroura*, 309), the European Turtle-Dove (*Streptopelia turtur*, 121), the Eurasian Collared-Dove (*Streptopelia decaocto*, 117), the Common Ground Dove (*Columbina passerina*, 115), the Malagasy Turtle Dove (*Nesoenas picturatus*, 93), the Zenaida Dove (*Zenaida aurita*, 79), the White-winged Dove (*Zenaida asiatica*, 65) and the Plain-breasted Ground Dove (*Columbina minuta*, 46). Among them, only the Eurasian Turtle Dove is listed as vulnerable with a high risk of extinction, whereas the nine other species are considered of least-concern. In contrast, we did not find any article for 151 (41%) species. Overall, scientific attention was negatively associated with IUCN status [Jonckheere-Terpstra test, JT= 13864, P = 0.006].

Research laboratories in North America and Europe contributed the most to research on columbid species, accounting for, respectively, about 43% and 32% of articles published in peer-reviewed journals. Scientific attention by country was positively correlated with GSI and HDI, but negatively with HFP (Supplementary Material 2, Table S5). Based on geographic distribution of species, species inhabiting close to "hotspots" of research on columbid species were the most studied (Figure 4, 5). The geographic distribution of scientific attention was also positively correlated with GSI and HDI, and, contrary to scientific attention *per se*, to HFP (Figure 4). Accordingly, the vast majority of unstudied species were located in the southern hemisphere, while most of the 10 most studied species were totally or partially located in the northern hemisphere (Figure 5).

Based on RF models, explanatory variables accounted for 45% of the observed variation in scientific attention among columbid species. The most important variables were species historical geographic range size, proportion of species range in current biodiversity hotspots, species body mass, GSI, HFP, HDI, human density within species range, and species habitat breadth (Figure 2C). In terms of relative importance, the historical range size of species did not differ from the proportion of species range in current biodiversity hotspots, species body mass of species, GSI, and species habitat breadth, as evidenced by their 95%CI (Figure 2C). The importance of other variables was lower (Supplementary Material 2, Figure A4). Partial dependence plots show that species with important range size, high body mass, occurring in countries with highest values of GSI, and located in ecosystems highly impacted by human activities (high HFP value) have been the most studied (Figure 4). Although no clear association was observed with the proportion of species range within hotspots of biodiversity, there was a trend for species exclusively occurring in biodiversity of hotspots to be less studied than others (Figure 4). In addition, we observed a positive trend relating scientific attention to species habitat breadth (Figure 4). Although the others variables were more or less important to explain scientific attention variation based on RF model,
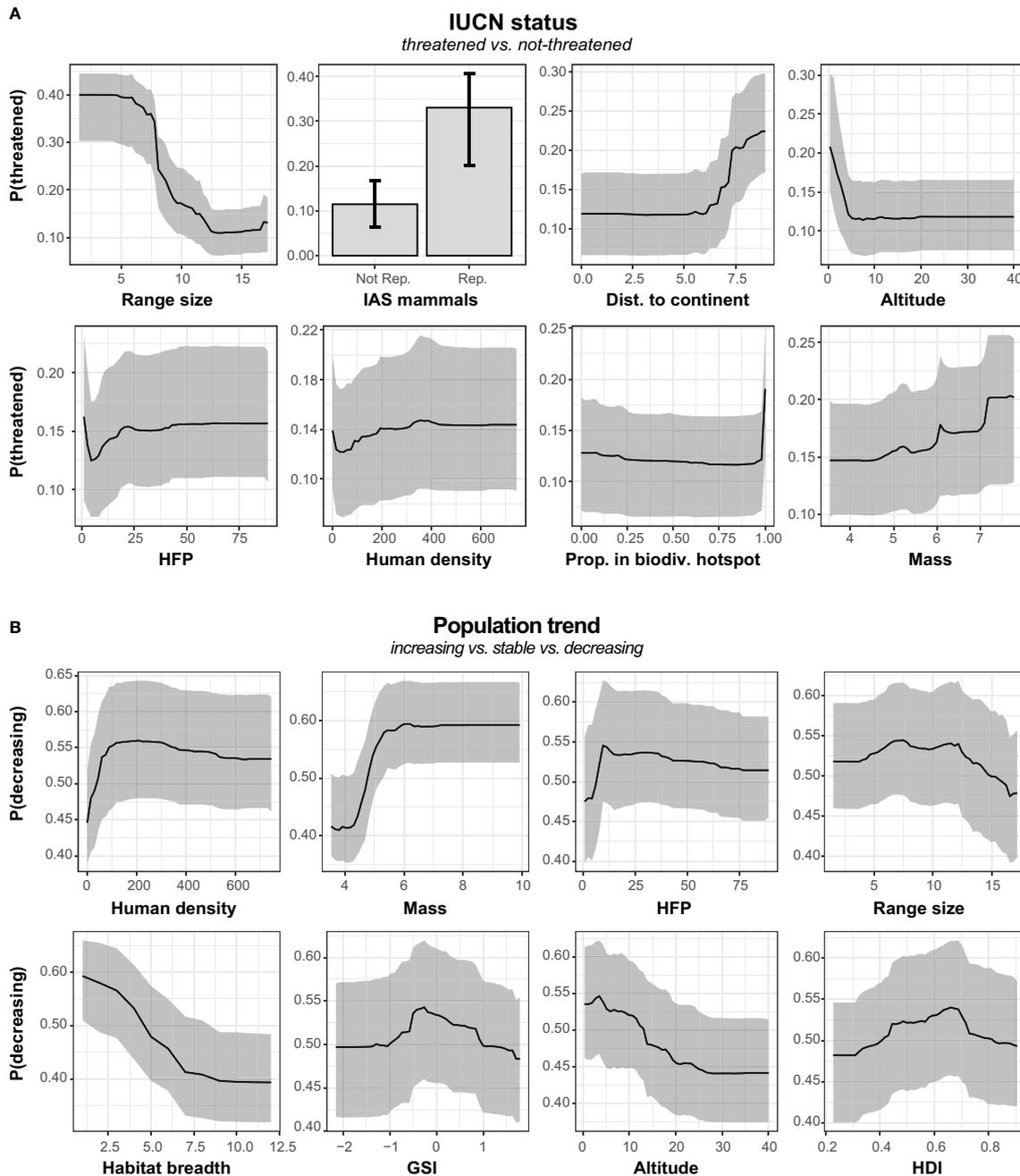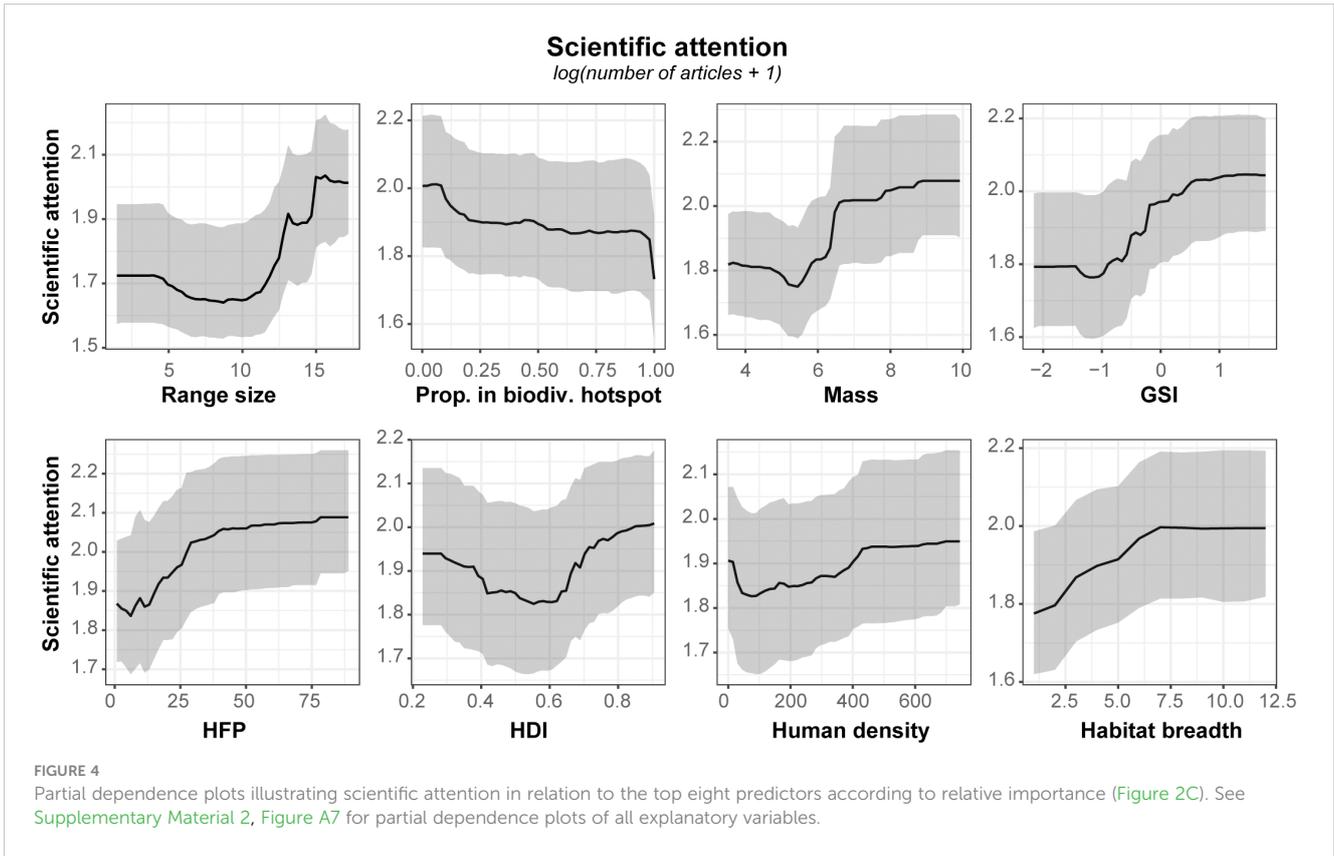
FIGURE 3
Partial dependence plots illustrating **(A)** the probability to be threatened and **(B)** the probability to have decreasing population trend in relation to the top eight predictors according to relative importance (Figures 2A, B). See Supplementary Material 2, Figure A5–A6 for partial dependence plots of all explanatory variables.

their variations were not directly associated to scientific attention (see Supplementary Material 2, Figure A7 for all variables).

3.3 Extinction risk predictions biased by scientific attention

Bootstrapped sensitivity and specificity [95% CI] of the extinction risk model respectively indicated that 78% [46%;

100%] of actual non-threatened species and 87% [78%; 95%] of actual threatened species were correctly identified when randomly using 80% of original dataset as training data, and the remaining 20% as tested data. Moreover, bootstrapped TSS [95% CI] was significantly different from zero (0.649 [0.328; 0.902]) showing that random training datasets classified species better than a random classification. Besides, these values were not significantly different from those calculated from the global model, thus suggesting an absence of overfitting.

FIGURE 4
Partial dependence plots illustrating scientific attention in relation to the top eight predictors according to relative importance (Figure 2C). See Supplementary Material 2, Figure A7 for partial dependence plots of all explanatory variables.

Among the 352 extant columbid species, the prediction of extinction risk of 50 species (14%) was inconsistent with their actual status (see Supplementary Material 2, Table A5 for a detailed list). On the one hand, the model predicted a higher extinction risk than that indicated by the IUCN red list for eight of them (16%), with estimated probabilities to be classified as "threatened" by the model being above or equal to 50%. On the other hand, the model suggested to downlist most of these species (42, 84%) as "not threatened". However, their average estimated probability to be classified as "threatened" by the model was 30% ± 13% (SD), and only ten of them had an estimated probability to be classified as "threatened" inferior to 20%. Importantly, we found that mismatches predictions in term of extinction risk were significantly related to scientific attention. Species with

FIGURE 5
Maps illustrating the geographical distribution of the top 10 studied species and not studied species. The two most important research hotspots correspond to the regions of North America (USA + Canada) in the left, and of Western Europe in the right. They represent about 70% of the scientific production in natural sciences among the first 50 countries according to the Nature index database (https://www.nature.com/nature-index).

mismatches prediction were in fact less studied than those with predictions consistent with the IUCN red list [Chi-square test, $X^2_{(1)}$ = 7.336, P = 0.007]. The only species classified as data deficient in the IUCN red list, *Columba oliviae*, was classified as "not threatened" by the model, with a probability of 79%.

4 Discussion

Since Walker (2007), the number of identified species of Columbidae has increased from 317 to 370 species. Meanwhile, the proportions of extinct (4.30% in the present study and 3.70% in Walker, 2007), threatened (19.24% and 18.61%, respectively) or non-threatened species (75.88% and 77.29%, respectively) have however remained stable. Walker (2007) described the geographic distribution of columbid species across the world according to their extinction risk and associated threats, as listed in the IUCN red list. We went further by quantitatively assessing to what extent various biological, ecological, environmental and socio-political drivers influence extinction risk and population trends of columbid species as well as interspecific variation in levels of scientific attention. In addition, we showed, for the first time, that low scientific attention can be responsible for incorrect estimation of the conservation status of columbid species.

4.1 Extinction risk

4.1.1 Ecological and biological drivers

Overall, our results tend to agree with previous findings (Walker, 2007) about the main drivers of extinction risk. However, we show that the use of both IUCN status and population trends are complementary in the identification of these drivers. Using both of them allowed us to identify several biological and ecological traits that make columbid species more prone to extinction. First, range-restricted species appeared more prone to extinction than more geographically widespread ones. Such relationship might seem obvious when using IUCN status as a proxy of extinction risk, because geographic range size is considered in its assessment (Fisher and Owens, 2004). However, geographic range size of columbid species was also positively associated with risk of population decline, thus confirming this factor as an important predictor of global extinction risk. Although the impact of geographic range size on extinction risk is complex, small range size is often associated with restricted ecological niche and small population size. Indeed, the number of habitats or resources required for survival and reproduction of individuals and, hence, population growth, often covary with geographic range size (Gaston, 2003; Peterson et al., 2011; Saupe et al., 2015). Moreover, large-range species are overall less likely to be affected by human disturbance or destruction of their natural environment, or by stochastic events, in their entire geographic range at once (Gaston, 2003; Fisher and Owens, 2004). However, some particular migrating columbid species, despite having a large range size, might be vulnerable to disturbance or damage occurring in their breeding, wintering or stop-over areas, as shown in the case of the

Woodpigeon (*C. palumba*; Schumm et al., 2022; but see Bendjoudi et al., 2015) or the Turtle Dove (*S. turtur*; Eraud et al., 2013; Schumm et al., 2021). The negative relationship between extinction risk and geographic range size has been evidenced in a large range of terrestrial and marine vertebrate species (Davidson et al., 2012; Di Marco et al., 2014; Böhm et al., 2016; Buechley et al., 2019), and at different geological time scales (Harnik et al., 2012).

Second, island columbid species appeared to be more prone to extinction than continental ones, and even more so the further the distance of islands to mainland. Indeed, in addition to usually having smaller geographic range size than continental species, island-species have evolved in isolation, under particular selection pressures (e.g., relaxed predation and parasitism), making them particularly vulnerable to disturbances such as overexploitation and any kind of negative interactions with invasive species (Purvis et al., 2000a; Purvis et al., 2000b; Boyer, 2010; Loehle and Eschenbach, 2012). Introduced pathogens may also have a significant negative impact on the persistence of isolated populations. For instance, a pathogenic strain of *Trichomonas gallinae*, which might have been introduced in Mauritius Island, increased adult and nestling mortality in the endangered Pink Pigeon, *Neosoenas mayeri* (Swinnerton et al., 2005; Bunbury et al., 2007; Bunbury et al., 2008). In mammals and birds, 95% of known extinctions concerned island-species (Loehle and Eschenbach, 2012). However, smaller geographic range size of most insular species might be the most important variable in explaining species extinction risk (Manne et al., 1999). Among columbid species, all known extinct species inhabited islands, excepted for the Passenger Pigeon (*Ectopistes migratorius*), suggesting that being an island-species is at least as much important as geographic range size, especially when adding other sources of extinction such as overexploitation, invasive species or climate change (Courchamp et al., 2003; Courchamp et al., 2014; Wood et al., 2017). For instance, the two largest known and now extinct columbid species, the iconic Dodo, *Raphus cucullatus*, and the Rodrigues Solitaire, *Pezophaps solitaria*, were both endemic to Mauritius islands and flightless. Their extinction was probably due to a combination of factors, including large body size, island endemism, low population growth, small population size and small geographic range size, making them particularly vulnerable to habitat destruction, hunting and invasive species (Duncan et al., 2002; Fisher and Owens, 2004; Hume, 2006; Hilbers et al., 2016). Our results indeed suggest that the extinction risk of columbid species increases with their body mass, as shown in diverse taxa (Gaston and Blackburn, 1995; Davidson et al., 2009; Fritz et al., 2009; Böhm et al., 2016). The influence of body size could actually be multifactorial, and be exacerbated by other external factors like overexploitation. Indeed, larger species are often preferred as game species (Duncan et al., 2002; Whytock et al., 2016; Ripple et al., 2017).

Although hunting has been recognized among the most important threats within Columbidae, concerning 77% of threatened species (Walker, 2007), and that inferential statistics performed in this study (see Supplementary Material 2, Table A1–A2) showed that threatened species are significantly more exposed to it, our models did not identify hunting-related drivers (i.e.,

subsistence use and sport hunting) as important variables explaining extinction risk. This does not mean that the impact of hunting exposure is null, but that other variables provide a better discriminant classification into RF models to evaluate extinction risk of columbids. It is obvious that hunting has a direct influence on the mortality rate of harvested populations, and, hence, can be a contributing driver to extinction risk for some species (e.g., the European Turtle Dove, *Streptopelia turtur*, Lormée et al., 2020), especially when it is not regulated or not performed in a sustainable way. However, the assessment of extinction risk requires a more comprehensive approach, considering various drivers and threats, as discussed in management recommendations for the European Turtle Dove (Bacon et al., 2023). The global influence of hunting might thus be lower than that of other threats, such as habitat loss and invasive species. However, its impact on game populations might be exacerbated when combined with such threats (Romero-Muñoz et al., 2019; Romero-Muñoz et al., 2020; Bogoni et al., 2022). For instance, the extinction of the iconic Passenger Pigeon was caused by both unregulated commercial hunting and significant destruction of its breeding habitat (i.e., a decrease estimated about 53%; Stanton, 2014). Furthermore, a more precise metrics of hunting pressure would probably be more informative than mere exposure to hunting (Bellard et al., 2022) and could have enhanced the performance of our RF models. Unfortunately, such information is unavailable for a large majority of game columbids.

Habitat breadth also appeared to influence extinction risk, confirming a general trend (Norris and Harper, 2004; Devictor et al., 2008; Clavel et al., 2011; Callaghan et al., 2019). Although ecological specialization does not always limit the capacity of species to persist (Benito et al., 2020), it might be evolutionary disadvantageous in environments exposed to changes and perturbations (Davies et al., 2004; Colles et al., 2009; Clavel et al., 2011; Ducatez et al., 2014; Morelli et al., 2020). Indeed, specialist species often tend to be associated with small population size, restricted geographic range size and limited use of resources and habitats, what may make them particularly vulnerable when exposed to environmental changes and disturbances (McKinney, 1997; Davies et al., 2004; Colles et al., 2009).

4.1.2 Anthropogenic drivers

Not surprisingly, our analysis points to alien invasive species as an important factor affecting the risk of extinction of columbid species (Walker, 2007). Exotic species are indeed a major threat to biodiversity, as a result of predation, parasitism, competition, hybridization with native species and the disturbance of native ecosystems (Mack et al., 2000; Sax and Gaines, 2008; Walsh et al., 2012). Invasive mammals, especially rodents (e.g., rats *Rattus* sp.) and cats (*Felis catus*), are the most damaging group of alien species across all ecosystems. Both are responsible of more than 30% of all known contemporary extinctions, especially on islands (Doherty et al., 2016). Invasive species can predate native columbid species (Rodriguez-Estrella et al., 1991; Tidemann et al., 1994; Zarzoso-Lacoste et al., 2016; Lamelas-López et al., 2020), compete with them for resources (James and Clout, 1996; Bond et al., 2019), or transmit pathogens (Stimmelmayr et al., 2012). Based on IUCN data, 9% of

all columbid species have been reported to be exposed to invasive rats, 8% to cats, and 12% to other mammals (IUCN, 2021). Among non-threatened species, 3% of species have been reported to be exposed to invasive mammals, compared to 35% for threatened species and 77% for extinct species. However, the precise impact of invasive mammal species on the demography of columbid species of patrimonial interest in the wild remains to be quantitatively assessed in order to assess to what extent it compares in importance with hunting pressure or habitat loss and thus provide a more comprehensive and integrative approach to the management of species/populations.

Although global warming is supposed to increase extinction risk among species living at high altitude (Williams et al., 2003; Shoo et al., 2005; Sekercioglu et al., 2008; Bässler et al., 2010; La Sorte and Jetz, 2010), we found no evidence for a positive relationship between extinction risk and elevation in columbids. The consequences of global warming on extinction risk at higher elevation might not be felt yet (Bellard et al., 2012) in columbid species, or might have been hidden in our analysis by variation in habitat breadth and more intense human activities at lower elevations. Indeed, landscape heterogeneity tends to decrease with increased elevation, and species found at elevation tend to have a higher degree of ecological specialization than those found at lower elevation (Reif et al., 2013; Rivas-Salvador et al., 2019). Lower elevations are also associated with higher anthropogenic transformation, inducing various negative effects on local biodiversity (Ellis et al., 2010; Reif et al., 2013; White and Bennett, 2015; Smith et al., 2019). Further attention should then be given to the influence of elevation on the demographic trends of columbid species in relation to climate change and habitat modification.

Several other drivers of anthropogenic origin appeared to contribute, directly or indirectly, to increase the extinction risk of columbid species, such as low levels of governmental stability and poor socioeconomics and/or the loss and disturbance of natural habitats through the development of HFP. HFP provides an index of human conversion of natural terrestrial ecosystems based on the measure of eight different anthropogenic pressures related to urbanization, agriculture and human density (Venter et al., 2016), and can therefore be regarded as a proxy of habitat degradation or loss. Yearly variations in HFP have been found to be a good predictor of extinction risk in terrestrial mammals (Di Marco et al., 2018). Although some columbid species flourish in landscapes modified by humans, such as the widespread Feral Pigeon, *Columba livia domestica* (Carlen et al., 2021), the Zenaida Dove, *Zenaida aurita* (Wolff et al., 2018), or the invasive Eurasian Collared-Dove, *Streptopelia decaocto* (Luna et al., 2018), most species rely on their natural habitats to persist. For instance, the occupancy of the Kereru, *Hemiphaga novaeseelandiae*, an endemic New Zealand Pigeon, has been affected by habitat loss resulting from European settlement in New Zealand (Carpenter et al., 2021). Following Walker (2007), the present study confirms that the loss of natural habitat is the greatest cause of extinction and populations decline in columbid species.

Governmental and socioeconomic factors were also found to affect the extinction risk of columbid species, with species inhabiting in developing countries being more exposed to

extinction risk. Public policies can have negative or positive influences on biodiversity, through supporting or not reliable environmental and conservation projects and by protecting or not most vulnerable species and/or sensitive ecosystems (Chapron, 2014; Ripple et al., 2016). For instance, the Pink Pigeon, *Nesoenas mayeri*, have been downlisted twice, in the IUCN red list, from critically-endangered to vulnerable thanks to conservation projects lead by conservationists, private foundations and the Mauritian government (Tatayah, 2019). Globally, the socioeconomic level of countries tends to influence positively the persistence of species (Forester and Machlist, 1996; Dietz and Adger, 2003). For instance, Bösch (2021) showed that the level and speed of countries' economic-institutional development tend to be negatively associated with illegal logging, and hence, with habitat loss and biodiversity decline. The same is true for wildlife trafficking and hunting pressure, especially in developing countries where wildlife can be the sole source of proteins for isolated and/or low-income communities (Robinson and Bennett, 2002; Fa et al., 2003; Fa et al., 2009; Borgerson et al., 2016; Lescuyer and Nasi, 2016). Legal and illegal hunting can be practiced to obtain food or increased social status, or as a recreational or traditional activity (Phelps et al., 2016; Stirnemann et al., 2018). Indeed, wildlife meat consumption is not always associated with poverty and can also be a sign of wealth (Fa et al., 2009). This is for instance the case in the Pacific islands where poor people hunt both the Pacific Pigeon, *Ducula pacifica*, and the Tooth-billed Pigeon, *Didunculus strigiristris*, to sell their meat to high-income populations (Phelps et al., 2016; Stirnemann et al., 2018).

4.2 Scientific attention

In strong contrast with the ubiquity of the family Columbidae throughout the world, the order Columbiformes is among the least studied orders in the Aves class (8th/25, Ducatez and Lefebvre, 2014). The same trend has been observed, at a lower geographical scale, in the Caribbean region (Devenish-Nelson et al., 2019). One reason for the low attention given to columbids could be that this family does not include any charismatic species (Seddon et al., 2005; Devenish-Nelson et al., 2019), excepted for the iconic Dodo and Passenger Pigeon that became textbook cases due to their extinction history (Kyne and Adams, 2017).

Scientific attention on columbid species appeared to be geographically biased and independent of species extinction risk, as shown by the negative association between scientific attention, the proportion of species in biodiversity hotspots and the influence of both HDI and GSI (Livingston et al., 2016; Tydecks et al., 2018; Melles et al., 2019). In addition, we found that island-endemic columbid species were on average less studied than continental species, and even more so the farther they are from mainland (see also Brooks et al., 2008). Contrary to Ducatez and Lefebvre (2014), we did not find any association between scientific attention and clutch size or generation time, probably due to low variability in these two variables among columbids.

Most of the research on columbid species is actually done by North-American and European researchers working on local

species, accounting, respectively, for about 43% and 32% of all articles published in peer-reviewed journals, whereas species living between Fiji and Indonesia, the most important hotspot for threatened columbid species and diversity (Walker, 2007), are among the least studied ones. The same geographical bias has been found in several studies focusing on diverse taxa (Ducatez and Lefebvre, 2014; Tydecks et al., 2018; Melles et al., 2019). It can be partly explained by logistic constraints, local poverty, political instability, geographic isolation and lack of local expertise in developing countries (Clark, 1985; de Lima et al., 2011; Amano and Sutherland, 2013; Wilson et al., 2016; Reboredo Segovia et al., 2020; Vallès et al., 2021).

Widespread columbids, in terms of geographic distribution or in terms of number of different habitats used, and relatively large-bodied species (>100g according to Figure 4) seemed more studied than others, as highlighted by Ducatez and Lefebvre (2014), who focused their research on bird Orders. More widespread species are presumably more accessible and have thus more chance to be studied than less widespread ones (Morales and Traba, 2016; Yarwood et al., 2019), while large species are usually easier to locate and observe than more discrete and smaller species (Ripple et al., 2017; Yarwood et al., 2019). Furthermore, we found that scientific attention on columbid species was positively associated with human density and human footprint, suggesting that columbid species inhabiting areas with high human density and highly urbanized were preferentially studied. As explained by Ibáñez-Álamo et al. (2017), species living close to humans, such as feral pigeons (e.g., Perez-Sancho et al., 2020), may receive more attention because of economic and public health issues (Lindahl and Magnusson, 2020) and/or because they are easier to study. Similarly, some applied research has been conducted on columbid species living close to humans in relation to negative impacts on crops (e.g, Murton and Jones, 1973; van Niekerk and van Ginkel, 2009; Firake et al., 2016; Verga et al., 2021). However, columbid species causing damages on crops may also experience higher extinction risk due retaliatory actions, including hunting and poisoning, by farmers (Marrero et al., 2004; Cuesta Hermira and Michalski, 2022).

5 Conclusion and perspectives

Our results quantitatively confirmed earlier findings on the main factors influencing extinction risk and population decline in columbids (Walker, 2007) and revealed large disparity in scientific attention given to columbid species, with the most threatened ones being the least studied. In this respect, species for which predicted extinction risk status were inconsistent with actual status were also the least studied. We therefore recommend to pay more attention to these species, and more generally to specialist species, restricted-range species, particularly insular ones, and/or large species, in relation to habitat disturbance and loss, in order to better estimate direct and specific extinction risk. In addition, investigations on urban populations of columbid species may help understanding interspecific variation in adaptive potential in relation to urbanization and global change.

Secondly, we strongly recommend to investigate the relative importance of sources of mortality of pigeons and doves in the wild in order to gain a more complete picture of the threats weighing on them. In this respect, it would be of interest to assess the relative importance of legal and illegal hunting compared to that of predation by exotic invasive predators in the decline of species. Columbids are indeed particularly appreciated by hunters, but are also exposed to various introduced potential predators in various regions. Although the impact of invasive mammal predators is widely acknowledged as an important threat to native wildlife, precise quantitative assessment is often lacking, particularly for columbid species. To that end, cooperation among hunters, scientists, wildlife officers and agencies should be encouraged, particularly where hunting traditions are an important part of local culture. Although difficult to implement, the regulation of invasive predators or their total eradication may have immediate positive impacts on native populations and ecosystems (Le Corre et al., 2015, Miller-ter Kuile et al., 2020).

Based on the influence of socioeconomic factors revealed here, we also recommend to develop coordinated efforts to better inform governments, public agencies and the general public of the key ecological role played by columbids and of the importance of conserving populations and associated habitats. In that respect, both extinct and extant columbid species could be used more widely in education programs about the erosion of biodiversity. Finally, fair transnational cooperation and capacity building in conservation-oriented research on columbids should be encouraged, especially between small island developing states and developed countries.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: caribaea.org.

Author contributions

CC: Conceptualization, methodology, formal analysis, data collection, data curation, writing – original draft, visualization. AJ-P: Data collection. EB: Conceptualization, supervision, resources, project administration. FC: Conceptualization,

validation, writing – original draft, supervision, project administration. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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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.2023.1141072/full#supplementary-material

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