RESEARCH ARTICLE

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Modelling the probability of meeting IUCN Red List criteria to

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Abstract

Comparative extinction risk analysis—which predicts species extinction risk from correlation with traits or geographical characteristics—has gained research attention as a promising tool to support extinction risk assessment in the IUCN Red List of Threatened Species. However, its uptake has been very limited so far, possibly because existing models only predict a species' Red List category, without indicating which Red List criteria may be triggered. This prevents such approaches to be integrated into Red List assessments. We overcome this implementation gap by developing models that predict the probability of species meeting individual Red List criteria. Using data on the world's birds, we evaluated the predictive performance of our criterionspecific models and compared it with the typical criterion-blind modelling approach. We compiled data on biological traits (e.g. range size, clutch size) and external drivers (e.g. change in canopy cover) often associated with extinction risk. For each specific criterion, we modelled the relationship between extinction risk predictors and species' Red List category under that criterion using ordinal regression models. We found criterion-specific models were better at identifying threatened species compared to a criterion-blind model (higher sensitivity), but less good at identifying not threatened species (lower specificity). As expected, different covariates were important for predicting extinction risk under different criteria. Change in annual temperature was important for criteria related to population trends, while high forest dependency was important for criteria related to restricted area of occupancy or small population size. Our criteria-specific method can support Red List assessors by producing outputs that identify species likely to meet specific criteria, and which are the most important predictors. These species can then be prioritised for re-evaluation. We expect this

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new approach to increase the uptake of extinction risk models in Red List assessments, bridging a long-standing research-implementation gap.

KEYWORDS

assessment, Aves, biodiversity conservation, birds, comparative analysis, extinction risk, functional traits

1 | INTRODUCTION

Over recent decades, the IUCN Red List of Threatened species (henceforth 'Red List') has become the global standard for species' extinction risk assessments (Betts et al., 2020; Mace et al., 2008; Rodrigues et al., 2006). A Red List assessment is based on at least one of five complementary criteria with quantitative thresholds relating to population and distribution size, structure and trends to assign species to categories of extinction risk (IUCN, 2012; Mace et al., 2008). The Red List now includes assessments for over 150,000 species of animals, fungi and plants (IUCN, 2022), but, despite its great importance for conservation action and policy (Betts et al., 2020; Hoffmann et al., 2010; Williams et al., 2021), it is insufficiently funded (Juffe-Bignoli et al., 2016). As a consequence, the Red List faces important challenges in keeping assessments up to date (i.e. <10 years old) and reducing the proportion of data deficient species (Cazalis et al., 2022; Rondinini et al., 2014).

Different methods have been developed to support Red List assessments and address the above challenges (e.g. Bachman et al., 2019; Buchanan et al., 2008; Cazalis et al., 2023; Santini et al., 2019; see Cazalis et al., 2022 for an overview). Among them, comparative extinction risk models link extinction risk (i.e. Red List categories) with species' biological traits (e.g. body mass, habitat specialisation, range size) and external drivers of risk (e.g. human density, land-use change, climate change; Chichorro et al., 2019, 2022; Purvis et al., 2000). The models are then used to predict the Red List categories of species that have not yet been assessed for the Red List (Darrah et al., 2017; Zizka et al., 2021), that are Data Deficient (Bland & Böhm, 2016; Luiz et al., 2016) or that need updating (Di Marco et al., 2014; Lucas et al., 2023), with the objective of accelerating and helping to prioritise the work of Red List assessors by providing additional information on species' extinction risk.

These comparative extinction risk models predict that Red List categories met under any of the five possible criteria (based on e.g. distribution, abundance, population trends), thus ignoring potential differences in their driving forces. This 'criterion-blind' approach assumes all criteria can be predicted from the same covariates, while in reality, the criteria address different sources of risk that are spatially structured (Figure S1), and some are likely easier to predict than others. For instance, predicting species threatened under criterion B1 (restricted extent of occurrence combined with some subcriteria) is relatively easy using range size, while it may be harder to find relevant covariates to predict species threatened under criterion A3 (future population decline). This suggests that species classified

under different criteria might have different risk correlates and face different prediction uncertainties, which might have contributed to the low performance of some criterion-blind models when tested on independent samples of species (Di Marco, 2022). In some cases, a covariate could even have opposite effects on different criteria. For instance, species with large body mass tend to have low population density (Santini et al., 2022; Silva & Downing, 1995) and might be more likely to trigger criterion C1 (small population size and decline), but such species tend to have large ranges (Newsome et al., 2020) hence are less likely to trigger criterion B. Importantly, ignoring the diversity of criteria limits the uptake of comparative extinction risk models by assessors, who need criteria-specific information (Cardillo & Meijaard, 2012; Cazalis et al., 2022).

Here, we aim to overcome this research-implementation gap by developing criterion-specific extinction risk models and comparing their performance and applicability to a classic criterion-blind model. While the latter estimates the probability of a species to be threatened under any criterion, our criterion-specific model estimates such a probability independently for each individual criterion (A1, A2, A3, etc). While benefiting from the power of the multi-species comparisons, this approach better encompasses the diversity of reasons that may qualify a species as threatened on the Red List and provides assessors with an output that is directly related to the information needed for assessments. We use birds as a study group to test our approach as they are the most consistently assessed group across Red List criteria (Cazalis et al., 2022), with very few data deficient species (0.4%), they have been used in many previous comparative extinction risk analyses (e.g. Olah et al., 2018; Richards et al., 2021; White & Bennett, 2015), and they present great variation in their response to human pressure (Cazalis, 2022; Lees et al., 2022).

2 | METHODS

We compiled data on avian biological traits associated with extinction risk (e.g. range size, clutch size) as well as external risk drivers operating within species ranges (e.g. change in forest canopy cover, distance to cities). We modelled the relationship between extinction risk predictors and each species' Red List category met under each specific criterion, using ordinal regression models that best match the ordinal structure of the Red List categories (Lucas et al., 2019, 2023; Luiz et al., 2016), and combined these models into a single final prediction. We then compared the performance of these criterion-specific models with a criterion-blind approach, as well as

the importance of different predictors in each approach. Finally, we evaluated the potential conservation applications of the criterionspecific approach. All analyses were conducted in R version 4.0.2 (R Core Team, 2020).

2.1 **Extinction risk predictors**

For each of the 11,162 bird species included in the Red List version 2021-3 (BirdLife International, 2022), we gathered information on species biological traits that are associated with extinction risk (e.g. Olah et al., 2018; Ripple et al., 2017; Tobias & Pigot, 2019), considering five types (see details and rationale in Table S1): morphological (body mass, beak length, hand-wing index), behavioural (nocturnality, migratory status), life history traits (clutch size, generation length), ecological (trophic niche, forest dependency, habitat breadth) and geographical (insularity, range size). However, species' intrinsic traits alone cannot predict extinction risk (Chichorro et al., 2022: González-Suárez et al., 2013), and it is key to include measurements of the impact of human activities within the species' range (Di Marco et al., 2014; Murray et al., 2014). We thus also included proxies for habitat alteration and degradation (extent and change of cropland and forest cover), human encroachment (human density and trends, proportion of rural population, travel time to the nearest city) and past and contemporary climate change (difference in precipitation and temperature) within each species range (see details in Table S1).

Species traits and characteristics

We used the distribution maps published in BirdLife International and Handbook of the Birds of the World (2021), filtering polygons with a high probability of presence ('extant') and of 'native' origin during the breeding season ('resident' and 'breeding season'), while removing polygons coded with other presence (e.g. extinct), origin (e.g. introduced, vagrant) and season (e.g. non-breeding, passage) attributes. As most of the available data on predictors of extinction risk are terrestrial, we removed marine species from our study (N=365, as defined by BirdLife International).

We calculated range size as the area of the filtered distribution map transformed into a Mollweide equal-area projection. In addition, four predictors were extracted from BirdLife International (2022): generation length, migratory status, forest dependency and habitat breadth (calculated as the number of major habitat types that are coded as suitable for each species).

Morphological traits relating to beak length (from tip to nares), body mass and hand-wing index were extracted from AVONET (Tobias et al., 2022), alongside ecological information on trophic niches (aggregated into four classes: herbivore, omnivore, invertivore and carnivore; Table S1). Insularity and clutch size were obtained from Tobias and Pigot (2019), and information on the diurnal/ nocturnal activity of birds was obtained from Wilman et al. (2014). To address taxonomic mismatches, we matched all taxa to the taxonomy used by BirdLife International, using the synonym table from Tobias et al. (2022). The remaining 200 taxonomic mismatches were then corrected manually using the synonyms documented in BirdLife International (2022). A table of these matches is included in the Extended Data \$1 provided with this article.

Extrinsic factors 2.1.2

Similarly to the range size calculation, we only considered breeding range when measuring extrinsic variables for consistency among migratory and resident species. We used a raster layer of percentage tree canopy cover in 2018 and changes in cover during 2000-2018 at 300-m resolution from Remelgado and Meyer (2023; using Landsat data to correct some biases in global forest cover maps). We extracted the median value of these predictors within the range of each species. Similarly, we calculated the median value of rangewide cropland coverage (in 2019) and cropland changes from 2003 to 2019 obtained from Potapov et al. (2022).

We also calculated the median human population density within each species' range, and the difference between median density in 2015 versus 2000 (Global Human Settlement [GHS]; Schiavina et al., 2019), used as a proxy for human direct pressure, although some species are well adapted to it (Cazalis et al., 2021). To account for the direct pressures that species can face in the rural environment (as defined by the GHS product), we also calculated the proportion of the human population living in rural areas within each species' range (Schiavina et al., 2019). As human accessibility can also determine the level of disturbance to which species are exposed, we extracted data from the global map of travel time to cities (Weiss et al., 2018) and calculated the median value of pixels contained within each species' distribution. Finally, we extracted the countries of occurrence of each species from BirdLife International (2022) and calculated the resulting median gross domestic product (GDP) per capita from WorldBank data (Worldbank, 2021) as an index of human population development.

In order to account for climatic correlates of risk, we extracted the current value and difference between past and current values for two variables from the CHELSAcruts database version 1.0 (Karger et al., 2017; Karger & Zimmermann, 2018), choosing mean annual temperature and annual precipitation for their relevance in influencing species' distributions and their ease of interpretation (Supplementary Methods S1). Using data from another study predicting Red List categories (Lucas et al., 2023), we calculated the average value of both bioclimatic variables over two periods based on CHELSA data (Karger et al., 2017): 1965-1995, to represent the past climate, and 2005-2014, to represent the current climate. We then extracted the median value of each variable within the species' range at both periods. We finally calculated the difference between both time periods as a proxy of recent climate change experienced by the species within their geographic range.

We extracted raster values within species' distribution polygons using the R package 'exactextractr' (Baston & ISciences, LLC, 2022).

Polygons were reprojected according to each raster's original coordinate system before extraction in order to minimise raster reprojection. Variables that followed a skewed distribution were log-transformed, and all numeric variables were scaled (Table S1).

We removed 1864 species for which we could not extract and calculate all predictors (mainly due to gaps for clutch size, insularity [1400 species missing data] and diurnality [1183 species missing data]), leaving a final dataset composed of 8695 species. We ensured that the absence of 20% of the data did not introduce any bias into the distribution of species within the Red List categories (Figure S3).

2.2 | IUCN Red List framework

We extracted from BirdLife International (2022) the Red List category assigned to each species under each criterion (see below), as well as the final listed category (Figure 1; see Figure S1 for spatial distribution of these criteria). For birds, generally all Red List criteria have been evaluated for all species (with the exception of criterion E, which is excluded from our study). For threatened bird species (i.e. those qualifying as Critically Endangered, Endangered and Vulnerable), all criteria that qualify a species as threatened should be reported in BirdLife International (2022), not just the one resulting in the highest risk category, although this may be omitted in some specific cases. However, this is not the case for species qualifying as Near Threatened (e.g. data are not available on whether a species classified as Endangered under B1 qualifies as Near Threatened under B2). To account for this, we followed two approaches. In the first, we classified a criterion as 'missing data' if not explicitly listed; the results presented in the main text, Figure 1 and Table S2 correspond to that assumption. In the second. we assumed that the species was Least Concern under a criterion unless it was explicitly listed. As a consequence, all models were run on the same set of species. These results were qualitatively equivalent with those obtained from our original model (the performances of individual criterion-specific models were even slightly poorer; Table S4). This sensitivity analysis demonstrates the limited impact of sample size differences on our model outcomes.

Only three species qualified as threatened under A1, hence the criterion has been excluded from the analysis.

2.3 | Extinction risk modelling

We developed a 'criterion-specific' modelling approach in which we fitted a separate model for each Red List criterion. Each criterion is thus considered independently, and the Red List category met under that criterion is contrasted with the same set of extinction predictors. For comparison, we also fitted a 'criterion-blind' model, as typically done in comparative extinction risk analyses, using the single listed species' Red List category as the response variable.

To investigate the relationship between species traits, extrinsic factors and extinction risk, we used cumulative link models (CLM, also known as ordinal regression models) from the R package 'ordinal' (Christensen, 2019), which allow preservation of the ordinal structure of the Red List categories (Lucas et al., 2019, 2023; Luiz et al., 2016). Moreover, CLMs have been demonstrated to be the best algorithms to deal with the ordinal structure of Red List categories when compared to other algorithms traditionally used in comparative models of extinction risk, such as Random Forest, Neural networks or Phylogenetic Generalised Linear Models (PGLS) (Lucas et al., 2023). CLM does not allow to include phylogenetic information in a way as PGLS does to account for potential non-independence in species extinction risk, but overall CLM has demonstrated to predict significantly better than PGLS, possibly due to the necessity of PGLS to transform Red List categories into a binary or discrete variable, losing important information from the original ordinal variable (Lucas et al., 2023). We therefore considered the Red List category as an ordered categorical factor (LC<NT<VU<EN<CR; excluding all species with categories EX, EW and DD), used it as the response variable and contrasted this with the predictors.

Models varied from n=7060 for criterion B2 to n=7702 for criterion C2, with a total of 8695 species included in the analysis. We checked that predictors were not highly correlated (Pearson

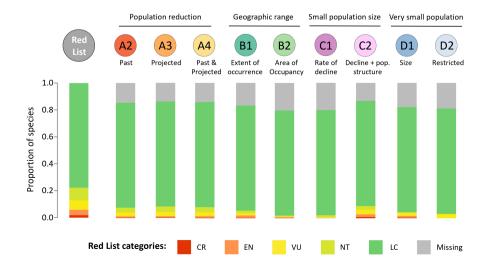


FIGURE 1 Proportion of the 8695 bird species included in our analysis currently qualifying in each Red List category for each criterion. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern. 'Missing' applies to species qualifying as threatened for which the given criterion is not explicitly listed. The number of species per criterion is given in Table S2.

correlation or Kruskal-gamma coefficients > |0.70|; Figure S2). To adjust for unbalanced data (Figure 1), we calculated the proportion of threatened and not threatened species under each criterion and weighted our models by the proportion of species in the opposite category (i.e. species with categories VU, EN or CR were weighted by the proportion of not threatened species, and species with categories LC or NT were weighted by the proportion of threatened species). A backward stepwise model selection was performed using the step function from the R package 'stats' (R Core Team, 2020) in order to find the subset of variables that minimise the Akaike Information Criterion for each criterion. The proportional odds assumption of a linear relationship was not always met, but this should not impact our results substantially (see Supplementary Methods S2).

As the number of species listed in EN and CR categories was very small for some criteria (Figure 1), we anticipated predicting specific categories could be challenging (Table S5); thus, for validation, we focused on a simplified prediction: whether a species was classified as threatened or not. We used a method of taxonomic block validation in which we iteratively excluded one taxonomic family from the data used to train the model and then used the model to predict the Red List binary threat level of the species in the left-out family. A species was predicted as threatened under a given criterion if the sum of the probabilities to be CR, EN and VU was >0.5 and predicted as not threatened otherwise. We then compared the predictions with the actual Red List categorisation under that specific criterion (assuming that the current Red List category of each species is correct for each criterion). Specificity and sensitivity were defined, respectively, as the percentage of not threatened species (LC, NT) correctly classified as such and the percentage of threatened species (VU. EN. CR) correctly classified as such. Following Red List guidelines (IUCN Standards and Petitions Committee, 2022), we assigned a 'combined' category to each species based on the nine criterion-specific models as the highest category predicted among models; consequently, a species was classified as not threatened only because it was not predicted as threatened in any of the criterion-specific models. We also report the models' performance in predicting the specific Red List category for each species (assigning to each species the category with the highest probability; Table S5).

To measure and compare the overall performance of both modelling approaches, we used the True Skill Statistic (TSS), defined as: sensitivity + specificity - 1. TSS takes into account both omission and commission errors and ranges from -1 to +1, where +1 indicates perfect agreement, values greater than 0.5 indicate a good performance and values of 0 (or less) indicate a performance no better (or worse) than random (Allouche et al., 2006).

Finally, our models were employed to predict the most probable Red List category for all species, which was then transformed into a binary prediction (threatened/not threatened) and compared with the actual Red List category. The mismatches thus identified serve as flags for prioritising reassessments of a specific list of species, as classically done in comparative extinction risk analyses (Di Marco et al., 2014; Lucas et al., 2023).

RESULTS 3 |

3.1 Model performance

Models' performance in predicting extinction risk greatly varies among criteria (Figure 2). The model predicting criterion D2, related to population structure, had the highest TSS score (0.91), followed by criteria B1, D1, B2, C2 and C1 (0.88-0.69). All these models had TSS scores higher than the criterion-blind approach (0.61), meaning that models are better at predicting extinction risk for single criteria than for the overall categories. For most criteria, these high TSS scores were the result of both higher specificity and higher sensitivity (Figure 2). Conversely, models predicting criteria A2-A4, related to population declines, showed the lowest TSS scores among all criteria (0.52-0.59), and they were slightly lower than the criterionblind model

Following Red List guidelines, we assigned a 'combined' category to each species as the highest extinction risk category from any of the nine individual criterion-specific models and found that this substantially reduced the TSS (0.52) compared with applying the models individually for each criterion (average model TSS=0.72; Figure 2a). This is largely due to lower specificity compared to the criterionblind approach (0.68 vs. 0.83 probability of correctly classifying a not threatened species. Figure 2c; Table S2), this is partly explained because a species had to be classified as not threatened under each of the nine applied criterion-explicit models in order to fall in this group overall. In contrast, using a criterion-specific approach resulted in a 0.84 probability of correctly classifying threatened species, compared with 0.79 for the criterion-blind approach (Figure 2b; Table S2).

Considering 'missing' criterion-specific categories as LC (Table S4) or predicting at the category level rather than binarily contrasting threatened versus not threatened (Table S5) resulted in respectively equivalent or lower performances.

Drivers of extinction risk

The criterion-blind approach showed positive relationships between extinction risk and body mass, carnivore trophic niche, high forest dependency and cropland cover, while showing negative relationships with insularity, range size or percentage canopy cover (Figure 3). Some of these relationships were also detected by criteria-specific models. For instance, carnivorous species were generally associated with higher levels of extinction risk, while species with a larger range size or with distributions that had a high tree canopy coverage were less at risk on average.

In contrast, the importance and significance of other predictors were idiosyncratic between criteria. For instance, body mass generally correlated positively with extinction risk for criteria related to rapid population declines or small population size (A2, A3, A4, C1, C2, D1), while it had no influence on criteria related to restricted geographic range (criteria B1, B2, D2). Conversely, high forest

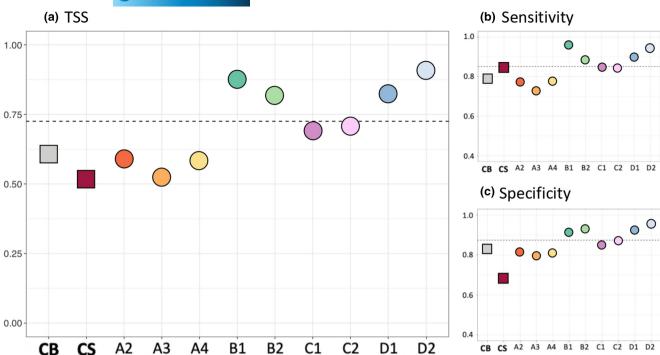


FIGURE 2 Comparison of model performances. The left-hand side of each plot compares the performance of the combined criterion-specific models (referred to as 'CS') with that of the criterion-blind approach to comparative extinction risk modelling (referred to as 'CB'), while the right-hand side presents the performance of each criterion-specific model. (a) True Skill Statistic [-1,1]; (b) sensitivity [0,1], proportion of threatened species correctly classified; (c) specificity [0,1], proportion of not threatened species correctly classified. Dotted lines represent the mean value obtained from the nine independent criteria-specific models.

dependency was associated with increased extinction risk for criteria B1, B2 and C2, all relating to small population size, restricted area of occupancy and subpopulation structure, but did not, or slightly negatively, influence criteria based on rates of decline alone. Extrinsic factors were mainly important to predict criteria related to population reductions (A2, A3 and A4); for instance, change in annual temperature correlating positively with extinction risk for criteria A2–A4 and C2, and GDP per capita correlating positively with criteria A2–A4, B2 and C1.

3.3 | Criterion-specific approach to prioritise reassessments

The criterion-blind model predicts that 15% of species currently classified as not threatened (N=1337) may be threatened (Table 1), but this percentage almost doubled (to 28%, N=2467) under the criterion-specific model. Conversely, we predicted 104 threatened species as not threatened (199 with the criterion-blind model).

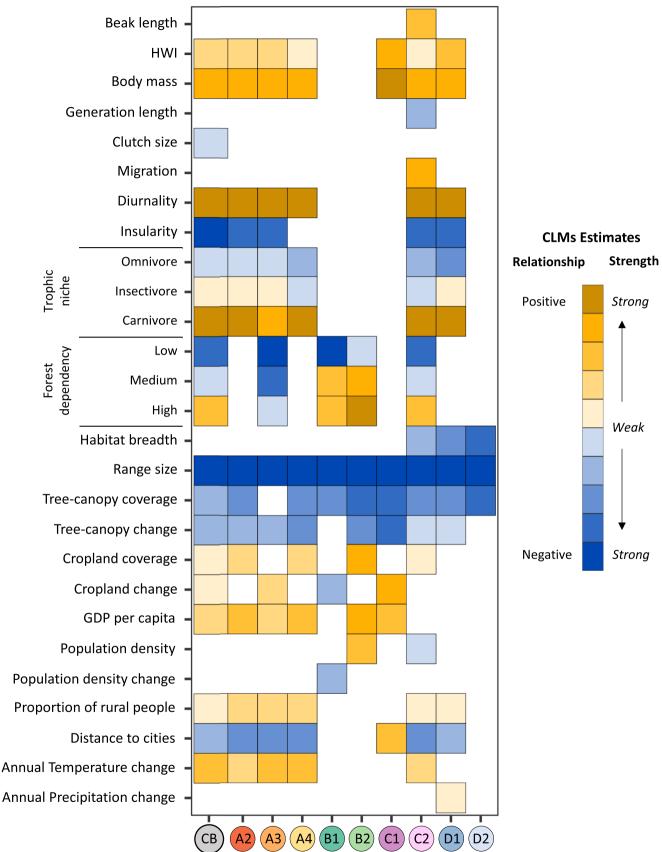
Predictions for all models and all species are provided in Extended Data S2.

4 | DISCUSSION

In this study, we developed a modelling approach that partitions extinction risk according to individual Red List criteria and compared it with a criterion-blind approach. On average, modelling individual criteria performed better than the criterion-blind approach, with higher performance for six criteria (especially criteria B1 and D2), while three provided similar or marginally lower performance (criteria A2–A4). This result highlights that predicting extinction risk under some criteria may be intrinsically difficult, at least using the predictors considered here. In particular, criteria related to population trends (especially A3 related to future trends) are more difficult to predict. With these models, we can enhance our understanding of the mechanisms underlying observed correlations and, ultimately, point to distinct drivers of risk.

FIGURE 3 Heatmap of predictor importance associated with extinction risk under each criterion. Rows indicate predictors of extinction risk, and columns relate to criterion-specific models. The 'CB' model describes the criterion-blind approach to extinction risk modelling. Colour indicates the sign (blue for negative and orange for positive), with darker tones indicating stronger relationships. Both positive and negative values were divided into five equal groups according to the intervals: -3.71, -0.97, -0.46, -0.27, -0.15 and 0 for negative estimates and 0, 0.16, 0.24, 0.42, 0.89 and 1.76 for positive estimates (blanks indicate that the predictor has not been retained in the optimal model after predictor selection; see Section 2.3; estimates are detailed in Table S3). CLM, cumulative link models; GDP, gross domestic product.

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Combining the nine criteria-specific models to obtain a single prediction per species led to substantially greater sensitivity (i.e. more likely identification of threatened species as threatened,

Figure 2b) but lower specificity than the classical criterion-blind approach (see, for example, Orange-fronted Parakeet *Eupsittula canicularis* in Figure 4a). Because one of the primary goals of automated

combining results from the nine individual criterion models.

	Prediction criterion-blind		Prediction criterion-specific	
IUCN Red List	Not threatened	Threatened	Not threatened	Threatened
Not threatened	6380 (73%)	1337 (15%)	5250 (60%)	2467 (28%)
Threatened	199 (2%)	779 (9%)	104 (1%)	874 (10%)

Note: The prediction for the criterion-specific method corresponds to the prediction after

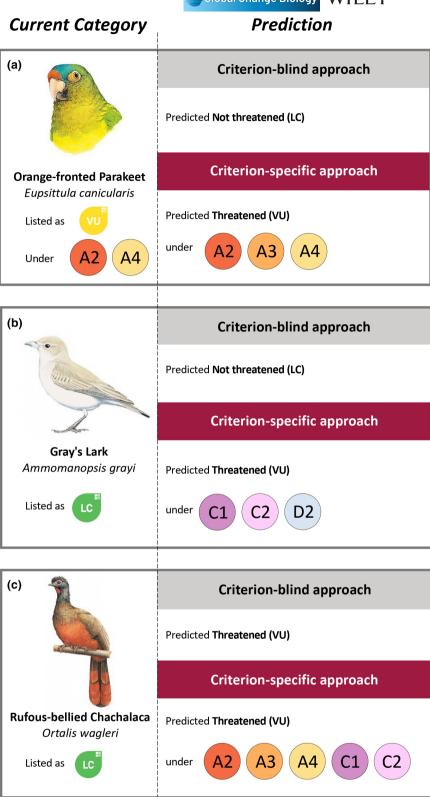
TABLE 1 Red List category prediction of criterion-blind and criterion-specific models compared with the current binarised category (Threatened for Vulnerable, Endangered and Critically Endangered: Not threatened for Least Concern; and Near Threatened).

extinction risk methods is to identify species likely to be at risk of extinction (but not currently recognised as such) to prioritise their reassessment (Cardillo & Meijaard, 2012), a model with high sensitivity will be more valuable than a model with similar TSS and higher specificity (Cazalis et al., 2022). Previous extinction risk models have typically predicted threatened species less accurately than not threatened species (Di Marco, 2022; Murray et al., 2014). Our results show that a reason behind this observation may be the omission of the diversity of reasons why a species is considered threatened on the Red List, which is represented by the multiple Red List criteria. However, combining nine criterion-specific models decreased the overall specificity of the prediction (see, for example, Gray's Lark Ammomanopsis grayi in Figure 4b), resulting in an overestimation of the proportion of threatened species and a slightly lower TSS in comparison with the criterion-blind approach (Figure 2a). This result is explained by the fact that, following Red List guidelines, a species was classified as not threatened only if predicted as such by all nine criterion-specific models. This is well aligned with the Red List process and a precautionary approach, but it makes our approach sensitive to misclassification. Hence, increasing the specificity of criterion-specific models is a priority for the future. Possible ways of achieving this include improving the performance of the individual models with additional covariates (for example, relating to hunting/ trapping pressure for criteria A2-A4), accounting for shared evolutionary history using phylogenetic models (Purvis, 2008) or developing an approach to combine individual models that accumulates fewer errors from individual models that misclassify a species as threatened under a given criterion.

In accordance with previous studies, our criterion-blind model identified extinction risk as correlating positively with for example, body mass, carnivorous niche, high forest dependency and lower tree canopy cover, and negatively with for example, clutch size, range size and distance to cities (Gaston & Blackburn, 1995; Olah et al., 2018; Richards et al., 2021; Ripple et al., 2017; Tobias & Pigot, 2019; White & Bennett, 2015). Our findings highlight the importance of considering separately the multiple processes underlying patterns of extinction (Figure 3; Figure S1). They reveal that increases in annual temperature across species' ranges are of particular importance for criteria related to population decline (A2-A4, and to some extent C2), consistently with the predicted role of climate change in driving declines in abundance and increases in species' extinction risk (Şekercioğlu et al., 2012; Mancini et al., 2023). Additionally, body mass is of particular importance for criteria related to population trends and population sizes (A1-A4, C1-C2, D1), suggesting that species with high body mass are more likely to be declining and to have small population sizes (Carvajal-Quintero et al., 2023). The diversity of relationships between predictors and criteria, along with their ecological meaning, emphasises the importance of accounting for heterogeneity in the predictability of Red List criteria, rather than considering them as equally predictable as assumed in criterion-blind comparative extinction risk analyses. They also highlight that our criterion-specific approach can help better understand the diverse mechanisms associated with extinction risk. Further, a better approximation of the causal relationships underlying species classification under different Red List categories can improve our ability to forecast status change based on changes in the drivers.

By modelling criteria separately, we increase the applicability of comparative extinction risk models (Cazalis et al., 2022; Owens & Bennett, 2000; Ripple et al., 2017). Red List assessors are required to assess each species against all criteria for which there is sufficient information (IUCN Standards and Petitions Committee, 2022). Therefore, while our models' outputs do not fundamentally change the red-listing process, they allow for various sources of information to be considered by assessors. As these models are contingent on the availability of life history and distributional data, their use for helping reassess data deficient species-for which these are often unavailable-is likely to be limited. We contend them to be most suited to help prioritise efforts to reassess threatened and non-threatened species for which underlying data are available and to identify knowledge gaps and opportunities for future research. For instance, the Least Concern Rufous-bellied Chachalaca Ortalis wagleri (Figure 4c) is predicted to be threatened (VU) by both the criterion-blind and the criterion-specific approaches. However, while the criterionblind model offers no additional insight, our criterion-specific approach provides assessors with relevant information about why this species might be VU-namely, that it might meet criteria A2, A3, A4, C1 and C2. Assessors could use this information to focus efforts on investigating past and future population trends to assess criteria A2-A4 and population size and structure to assess criteria C1 and C2, which could be complemented with the specific contributions of different covariates that led to this prediction. If these data are not available, determining values for these parameters may be considered a priority for fieldwork and research.

Comparative extinction risk models have often been promoted as useful tools to provide a first prediction of extinction risk for



species not yet included in the Red List (Darrah et al., 2017; Zizka, Andermann, et al., 2022; Zizka, Barratt, et al., 2022), for data deficient species (Bland & Böhm, 2016; Borgelt et al., 2022; Cazalis et al., 2023; He et al., 2021; Luiz et al., 2016) or to prioritise reassessments (Di Marco et al., 2014; Lucas et al., 2023). But so far, these have remained largely unmet promises, with hardly any uptake of

these modelling approaches in the Red List (Cazalis et al., 2022). By focusing on reassessments and informing the assessors about the specific criteria under which a species is likely to qualify, criterion-specific models could help accelerate the rate of Red List assessments, guide data collection efforts and facilitate the growth and update of the Red List so that it can best inform conservation

policies. Although it may need further developments and be currently too data-demanding for some taxa, we believe this is a promising avenue to reduce the historical research-implementation gap between the comparative extinction risk model and the Red List assessment process.

AUTHOR CONTRIBUTIONS

Etienne G. Henry: Data curation; formal analysis; investigation; methodology; visualization; writing - original draft; writing - review and editing. Luca Santini: Conceptualization; formal analysis; methodology; supervision; writing - original draft; writing - review and editing. Stuart H. M. Butchart: Conceptualization; writing - original draft; writing review and editing. Manuela González-Suárez: Conceptualization; formal analysis; methodology; writing - review and editing. Pablo M. Lucas: Conceptualization; methodology; writing - review and editing. Ana Benítez-López: Conceptualization; writing - review and editing. Giordano Mancini: Conceptualization; writing - review and editing. Martin Jung: Conceptualization; writing - review and editing. Pedro Cardoso: Conceptualization; writing - review and editing. Alexander Zizka: Conceptualization; writing - review and editing. Carsten Meyer: Conceptualization; methodology; writing - review and editing. H. Reşit Akçakaya: Conceptualization; writing - review and editing. Alex Berryman: Methodology; writing - review and editing. Victor Cazalis: Conceptualization; formal analysis; methodology; resources; supervision; writing - original draft; writing - review and editing. Moreno Di Marco: Conceptualization; formal analysis; methodology; supervision; writing - original draft; writing - review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/doi/10.5281/zenodo.10392980.

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SUPPORTING INFORMATION

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

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