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RESEARCH ARTICLE

Bird species' tolerance to human pressures and associations with population change

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Abstract

Aim: Some species thrive in human-dominated environments, while others are highly sensitive to all human pressures. However, standardized estimates of species' tolerances to human pressures are lacking at large spatial extents and taxonomic breadth. Here, we quantify the world's bird species' tolerances to human pressures. The associated precision values can be applied to scientific research and conservation.

Location: Global.

Time Period: 2013–2021.

Major Taxa Studied: 6094 bird species.

Methods: We used binary observation data from eBird and modelled species' occurrences as a function of the Human Footprint Index (HFI). With these models, we predicted how likely each species was to occur under different levels of human pressures. Then, we calculated each species' Human Tolerance Index (HTI) as the level of the HFI where predicted occurrence probability was reduced to 50% of the maximum species' occurrence probability. We used resampling to obtain estimates of uncertainty of the Human Tolerance Indices. We also compared tolerances across species with increasing, stable, and decreasing population trends.

Results: We found that 22% of the bird species tolerated the most modified human-dominated environments, whereas 0.001% of species only occurred in the intact environments. We also found that HTI varied according to species' population trend categories, whereby species with decreasing population trends had a lower tolerance than species with increasing or stable population trends.

Main Conclusions: The estimated HTI indicates the potential of species to exist in a landscape of intensifying human pressures. It can identify species unable to tolerate these environments and inform subsequent conservation efforts. We found evidence that species' sensitivity to human-dominated environments may be driving birds' use of space. Bird species' tolerances are also linked to their population trends, making the tolerances a relevant addition to conservation planning.

KEYWORDS
Anthropocene, avian species, disturbance, eBird, functional trait, global change, Human Footprint Index, macroecology, synanthropy

1 | INTRODUCTION

Most of the terrestrial world has been modified by human actions, either through urbanization or through air pollution and climate change, which can have impacts on animal and plant populations far from human-occupied areas (Sanderson et al., 2002; Venter et al., 2016). All these changes can lead to myriad effects on ecological communities. Habitat loss and fragmentation are a common result of intense land use in forms of built infrastructure (e.g. urban areas and roads) and agriculture (e.g. crop areas); they influence population dynamics, dispersal, and ecological interactions, and thereby the occurrences and abundances of wildlife across space and time (Barlow et al., 2016; Cazalis et al., 2020; Fahrig, 2017; Gibson et al., 2011; Haddad et al., 2015; Horváth et al., 2019; McKinney, 2006). The Human Footprint Index (HFI) summarizes the various facets of human pressures by accounting simultaneously for built environments, human population density, night-time lights, crop lands, pasture lands, and accessibility via roads, railways, and navigable waterways (Sanderson et al., 2002; Venter et al., 2016). As human pressures are globally widespread, most species necessarily occur in impacted habitats. Some species even thrive in urban environments and depend on humans for resources, such as food or nesting sites (McKinney, 2006; Spotswood et al., 2021). Some species have high plasticity to survive both with and without intense human pressures (Ducatez et al., 2018; McKinney, 2006), whereas others are highly sensitive to even low levels of human pressure (Şekercioğlu et al., 2019), particularly during their breeding season. Sensitivity and tolerance of species to human pressures have been estimated for single and small groups of species (de Jonge et al., 2022; Gnass Giese et al., 2015; Guetté et al., 2017; Silva et al., 2016) but rarely with a global scope and for an entire, species-rich taxonomic group (but see, Cazalis et al., 2021; Neate-Clegg et al., 2023). To effectively conserve species, there is an urgent need to design conservation measures that are suitable for different species.

Currently, 13.5% of 10,994 recognized extant bird species are threatened with global extinction (Lees et al., 2022), which calls for effective tools for their conservation in the Anthropocene. A measure of species' maximum tolerance to human pressures can indicate the potential for species to exist in landscapes with different pressures and thereby inform conservation efforts. For the first time, we provide indices of species' tolerances to human pressures (Human Tolerance Index; HTI), with uncertainty estimates for the majority of bird species in each continent. Thus, we contribute to the increasingly available functional trait data of species. We also provide a means for use of regional species-specific tolerances while accounting for the spatial variation and the uncertainty in tolerance indices. As opposed to many earlier studies (Ducatez et al., 2018; Guetté et al., 2017; McKinney, 2006), our HTI goes beyond the synanthropy of species that describes species' sensitivity to urban settlements (Guetté et al., 2017). Although synanthropy can account for a species' ability to tolerate intense anthropogenic disturbances, a consistent index is lacking, and urban conditions are only one of the facets of human pressures on wildlife. Other facets, such as intensive agriculture, need to be included in a summary measure of human pressure tolerance of wildlife species. With a global index of human pressure tolerance of bird species, it will be possible to evaluate how the composition of tolerant and sensitive species is changing in ecological communities over time and how this change varies spatially in regions with intense human pressures.

Here, we quantify the HTI of bird species to human pressures with bird observation data from eBird complete lists collected from 2013 to 2021 (Sullivan et al., 2009) and HFI data from 2013 (Williams et al., 2020). In addition, we report variation in HTIs across continents and species. We hypothesized that there is high interspecific variation in the index. However, we expected that most extant species tolerate human pressures to some extent due to the pervasive nature of human influence globally. We also hypothesized that Europe has on average more species that are highly tolerant to human pressures than Africa and Latin America because of Europe's longer history of intense land use and human disturbance. We tested the potential link between HTI and population trends of species globally. We hypothesized that species with higher human tolerance are more likely to have positive population trends because they may benefit from the intensified land use, including urbanization, that has occurred in recent decades.

2 | METHODS

2.1 | Bird data

To link bird species' occurrences to human pressures across the world, we used data from eBird (Sullivan et al., 2009), an online community science platform containing over a billion bird observations globally (Appendix S1, Figure S1). We used eBird data as the source because it is the largest bird database, both spatially and taxonomically. In addition, many human pressures, such as urban areas, roads, and night lights, are only distinguishable at a fine spatial resolution, and eBird data allowed us to spatially link bird observations to these fine-resolution environmental characteristics.

We used the eBird data released in 2022 (for continent-specific release months, see Appendix S1, Table S1) and used R package 'auk' (Strimas-Mackey et al., 2018) to filter the data following guidelines provided by the eBird team (Johnston et al., 2021; Strimas-Mackey et al., 2020; Sullivan et al., 2009). The process was similar to the data filtering process described by Cazalis et al. (2020, 2021). We only considered recent observations (01.01.2013–31.12.2021) to minimize the effect of possible temporal trends in the human pressure tolerances of bird species. To reduce the computational time for the large North American dataset, we selected only observations from odd years during the study period (2013, 2015, 2017, 2019, and 2021). We also only considered checklists compiled during stationary counts or transects (distance travelled <8 km and duration between 0.5 and 10 h) and complete checklists (for which observers had reported all species identified). Moreover, we included only the checklists from within each bird species' resident and breeding

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ranges (BirdLife distribution maps; BirdLife International, 2022). To link the taxonomies of eBird and BirdLife, we used the taxonomy crosswalk from AVONET (Tobias et al., 2022). In addition, similar to Santini et al. (2023), we excluded observations outside the principal breeding season months for coarse latitudinal bands within continents (Appendix S1, Table S2) because breeding and resident ranges also include habitats used by birds at other times of the year, such as during migration (La Sorte et al., 2022; Zuckerberg et al., 2016). Breeding-related demographic parameters are also often the most important determinants of species' population dynamics, especially for smaller, short-lived species, underscoring the relevance of studying pressures during the breeding season (Morrison et al., 2021). We determined the latitudinal bands that encompassed all bird species within them similarly to Santini et al. (2023) but increased the resolution by using continent-specific latitudinal bands. In addition, we considered the breeding season to last year-round in the tropics to encompass most bird species that breed at different times and generally do not migrate. Use of latitudinal band-specific definitions of the breeding season is clearly a simplification, but the method provides an estimate of human pressure conditions at the time of reproduction for the vast majority of species (Santini et al., 2023). Next, we filtered the eBird data to reduce spatial bias by balancing the number of checklists across 3×3km grid cells within each continent. We did this by using R package 'ebirdst' (Strimas-Mackey et al., 2021) to randomly select one checklist per week per grid cell across years. This allowed us to obtain a more uniform distribution of observations across space and to avoid strong bias towards easily accessible locations that usually attract more people to make bird observations and that are often highly human-modified. We used this same sample of checklists for the analyses of all species in the following steps.

We excluded oceanic species as defined by IUCN Red List (IUCN, 2022) from our study due to their incomplete and potentially biased overlap with the terrestrial HFI data. We included non-native species in our study. We calculated the HTI separately for each species within each continent (see Section 2.3) and did not include whether the species is native as an additional variable in the analyses. Our study design could reflect that species may have different tolerances to human pressures within their native and non-native ranges. Understanding the tolerances of non-native species in their native and non-native ranges can be particularly useful for studies in invasion biology.

We transformed both the counts and detections on checklists into binary occurrences, which reduced the potential bias related to the detection of large numbers of individuals during migration and allowed inclusion of eBird observations that do not specify the number of observed individuals, thus increasing the taxonomic coverage of our study. The data for our main analyses consisted of 84,763,985 binary species observations, structured into 4,429,380 checklists. We inferred non-detections of species by their omission from the complete checklists. However, we only included a checklist (with detection or non-detection) in a species' analysis if it was collected within its breeding and resident ranges and within the breeding period. We then used all selected checklists within the species' breeding and resident ranges.

To link HTI to species' population trends and threat category, we obtained data on bird species' population trends and Red List categories from IUCN Red List (www.iucn.org, downloaded 27.04.2023). Because global data on quantitative and continuous population trends of all bird species are not available, we followed the example set by Ceballos et al. (2017) and Finn et al. (2023) and used the categorical population trend measures of the IUCN Red List (i.e. declining, stable, or increasing).

2.2 | Human pressure data

We used the HFI from the year 2013 at a resolution of ~1 km as a measure of human pressure influence on wildlife (Williams et al., 2020). This index is updated and more complete compared to the 1993–2009 version by Venter et al. (2016). The HFI has been used to analyse species' responses to human pressures (Barnagaud et al., 2019; Cazalis et al., 2020; Di Marco et al., 2018). The HFI includes eight variables (built environments, human population density, night-time lights, crop lands, pasture lands, and accessibility via roads, railways, and navigable waterways), and it ranges from 0 (perfect intactness) to 50 (extremely high human pressure; Venter et al., 2016; Williams et al., 2020). Values between 0 and 1 are considered to represent areas free of mapped anthropogenic disturbance, values between 1 and 4 are considered to represent areas relatively free of anthropogenic disturbance, and values between 4 and 50 are considered to represent areas highly impacted by mapped anthropogenic disturbance (Williams et al., 2020). We assigned each eBird checklist a value of the HFI. To do so, we set a 1.5 km radius buffer around each eBird checklist and used the function 'extract' from R package 'raster' (Hijmans, 2023) to calculate the mean HFI within the buffer. We used the 1.5 km radius because such a buffer includes most of the bird observations in travelling counts <8 km and because the eBird team uses such a buffer in their Status and Trends work, allowing meaningful comparisons between this and earlier studies (Fink et al., 2022). There is good agreement and strong correlations among the different published Human Footprint Indices, which makes the selected measure highly suitable for our study (Kennedy et al., 2019; Mu et al., 2022). The HFI values across checklists covered the full extent of possible values, but the distribution was not uniform across or within continents (Appendix S2, Figure S1).

2.3 | Hierarchical organization of data

Human pressures are context-dependent and may vary due to factors related to administrative boundaries. For example, the influence of a road on species is likely different in different parts of the world because the road type and traffic intensity can differ greatly. Therefore, we considered the measure of human pressures (here, the HFI) within geographically consistent areas of continents and quantified the HTIs of all birds that were observed within the focal continent during their breeding season and within their breeding or resident range. That means that some bird species occurring on multiple continents were assigned multiple HTIs, one for each continent in which they occurred. We considered six continents (Africa, Asia, Europe, Latin America, North America, and Oceania) when quantifying HTIs (for lists of countries included in each continent, see Appendix S4). Calculating tolerance for each species in each continent where the species occurs allows comparisons of intraspecific variation in human pressure tolerance across continents and linking such variation to functional traits or other properties, such as whether species are native. Moreover, it enables high-resolution studies within continents.

2.4 | Calculating species-specific human tolerance indices

To estimate HTI, we conducted separate analyses for each species in each continent. In preparation, we performed several further data manipulation steps to aid statistical inference and estimate the uncertainty. We repeated the modelling and predictions 50 times for each species within each continent to estimate uncertainty. For each model, we randomly sampled 75% of the checklists within the species' breeding and resident range after the spatial subsampling described above. Then, we divided eBird checklists into categories based on their HFI values and sampled each category according to assigned target numbers of detections and non-detections to both maintain the relationship with the HFI and balance classes across the range of the HFI (for details, see Appendix S1, Section S1).

In each of the 50 resampling replicates, we quantified three measures of the HTI of each bird species in each continent (Peak HTI, Conservative HTI, and Maximum HTI) on the basis of species' occurrences across the range of HFI values (Figure 1). To do this, we modelled and predicted species' occurrences as a function of the HFI in each continent. We did this because a species may not be observed throughout the human pressure gradient due to either their actual human pressure tolerance or bias in observations towards certain parts of the HFI gradient. We used generalized additive models (GAMs) to model the relationship between the HFI and occurrence of each species on checklists. These models allow non-parametric relationships and thus high flexibility in the occurrence probability—HFI relationships compared to linear relationships. However, we also wanted to remove the possibility of unrealistically complex relationships, so we used R package 'scam' (Pya, 2021; R Core Team, 2022) to constrain the possible relationship shapes to be unimodal with monotonic increase and decrease on each side of a peak (bs = 'cv'). We used the shape-constrained GAMs to allow non-linear relationships between species' occurrences and the HFI because most species are assumed to have a trait optimum, or an optimal HFI value, rather than a simple positive or negative linear relationship with the HFI. We considered the binary occurrence on a checklist as the response variable.

We included as the main predictor in the models the HFI within the 1.5 km radius buffer of each checklist with maximum smoothing degrees of freedom set to $k = 9$. We also included the following variables as predictors in the models: latitude, longitude, survey protocol (stationary, travelling), survey duration (min), survey distance travelled (km), continuous survey year, and number of observers. We did not include these variables as splines due to model run-time limitations. In addition, we included the time of the day of the survey as a cyclic spline (bs = 'cc') with maximum smoothing degrees of freedom set to $k = 9$. These additional predictor variables allowed us to account for the observation process in the model fitting, mitigating the effects of heterogeneous detectability. We used a binomial error distribution for the binary occurrence data response. After the model fitting, we excluded species that had >10 missing resampling replicates to ensure reliable HTI estimation. Species may lack resampling replicates due to failed model convergence or detections that are not well distributed throughout the HFI continuum. This process yielded 6094 of the roughly 11,000 bird species across continents and 7317 species-continent combinations. In the results, we averaged values within species across continents when the species occurred on multiple continents.

On the basis of the model fit, we predicted how likely each species was to occur across the full gradient of the HFI. We did this by setting the other predictor variables as fixed (for exact values, see Appendix S1, Section S1) and using the GAM model fit to predict occurrences across the full range (0–50) of HFI values. From these predictions, we obtained the predicted occurrence probabilities across the range of HFI values and calculated the following values for each species within each continent: (1) Peak Occurrence Human Tolerance Index (Peak HTI), the level of the HFI with maximum occurrence probability; (2) Conservative Human Tolerance Index (Conservative HTI), the level of the HFI above the majority tolerance where predicted occurrence probability is 50% of the maximum predicted occurrence probability; and (3) Maximum Human Tolerance Index (Maximum HTI), the level of the HFI where predicted occurrence probability is 10% of the maximum predicted occurrence probability (Figure 1). We calculated these HTIs as the mean of each metric across the 50 resampling replicates. We quantified these three indices rather than a simple mean tolerance because the mean does not indicate as clearly the potential (upper limit of tolerance) of the species to adapt to greater human pressures in the future. That is, two species can have a similar tolerance mean, but one can have a narrower range of tolerance, so it is more sensitive to human pressures. For example, urban birds have wider environmental tolerance than their rural relatives (Bonier et al., 2007). The Conservative and Maximum HTIs show the species' upper limits of tolerance to human disturbance, which is critical in understanding the potential impact of any intensification or expansion of human pressures. In addition to the HTI estimates, we calculated the associated 80% confidence intervals for each of the three metrics on the basis of the 50 bootstrap resampling replicates. We chose 80% intervals to optimize computational requirements of the model fitting analysis step, as

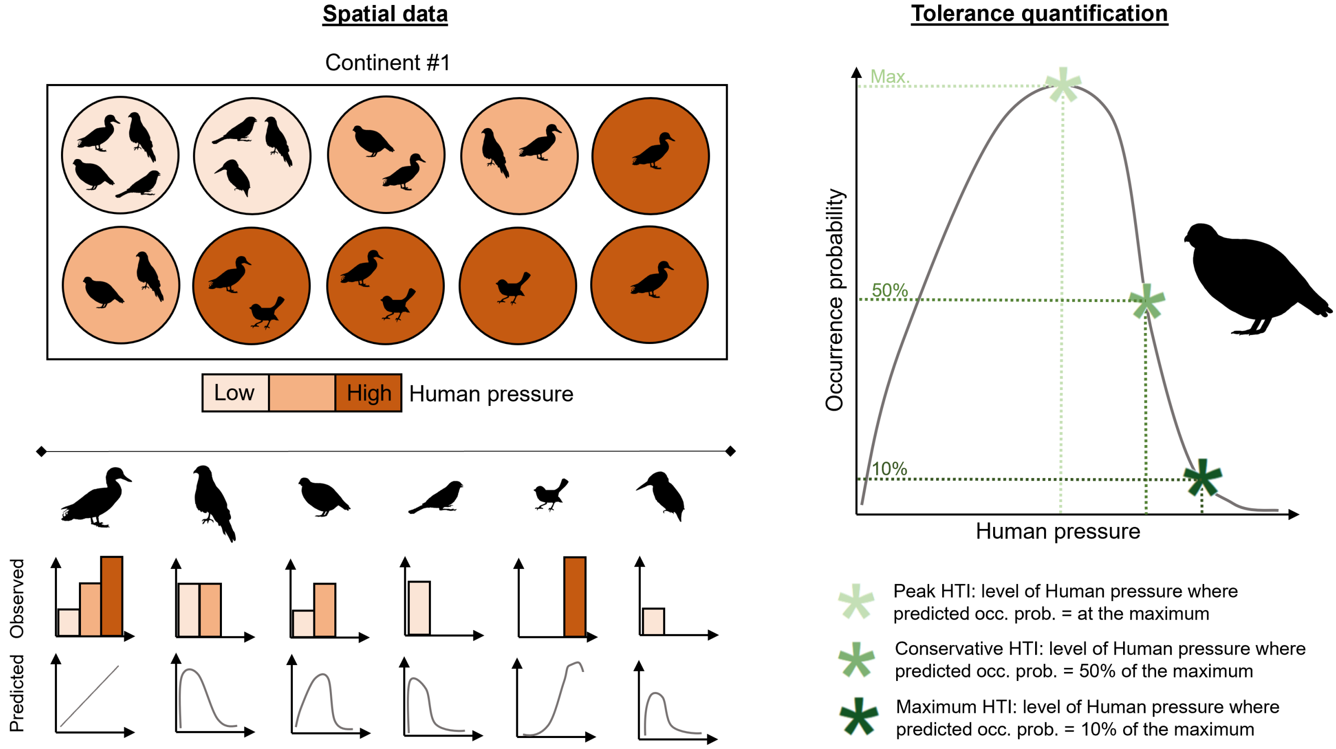

FIGURE 1 Schematic illustration of the quantification of bird species' tolerances to human pressures globally. The circles within a box in the left panel illustrate the spatial hierarchy in the bird occurrences across the gradient of human pressures. Hypothetical bird species are illustrated with silhouettes. The lower row illustrates the modelling and prediction steps of the analyses; the observed occurrences of each bird species across observed human pressures (coloured bars) are used as the basis for the prediction of occurrence probability across the full gradient of human pressures (grey lines). The panel on the right illustrates the predicted relationship between the occurrence probability and human pressure that was then used to calculate three Human Tolerance Indices (HTIs) for an example species (represented with a large silhouette). The three HTIs are shown as green stars and coloured dashed lines on the graph (see legend). These modelling and prediction steps were repeated 50 times for each species to calculate mean HTIs and 80% confidence intervals for each species.

fewer bootstrap resampling replicates are required for a robust estimate of the uncertainty. We calculated the confidence intervals to allow future applications to account for uncertainty when using the species' tolerances.

We compared Conservative HTI values of bird species among IUCN Red List population trend and threat categories with one-way ANOVA. We excluded the Data-Deficient category of threat because only two bird species were in that category. We confirmed the robustness of the results of the above models to any phylogenetic correlation between the studied species. To do so, we ran a sensitivity analysis on the potential effect of phylogenetic relations to the Conservative HTI ~ population trend category and Conservative HTI ~ threat category relationships with function phylANOVA from the R package 'phytools' (Revell, 2012). We obtained 100 phylogenetic trees from birdtree.org (Ericson All Species trees with 9993 OTUs each; Jetz et al., 2012). We then randomly selected 10 of the trees and repeated the phylANOVA test 10 times. We averaged the modelled results across the trees to obtain an average phylogenetic effect of the modelled relationships. For each phylANOVA, we also tested whether the pairwise differences were significant and applied a Bonferroni correction to the *p*-values. As another sensitivity analysis, for a subset of 155 European bird species (see Appendix S2, Table S7 for the full species list) with available continuous population trend estimates (Brlík et al., 2021), we fitted a linear regression model with the Conservative HTI as the response and continuous per-year population trend estimate for years 2012–2021 as the predictor variable.

3 | RESULTS

We modelled and predicted HTIs for 6094 bird species (Figures 2 and S2; Appendix S2), which we included in the final dataset (Appendix S3) with the numbers of missing resampling replicates as an additional variable. All 50 resampling replicates were completed for 5090 species. The models could not be fitted for all resampling replicates for all species due to insufficient data. On average, species had a Peak HTI of 13.7 (SD = 14.1), whereas the Conservative HTI and Maximum HTI were at 29.1 (SD = 13.5) and 37.7 (SD = 11.6), respectively (Figure 3). These averages correspond to HFI values of highly impacted areas (Williams et al., 2020). The mean 80% confidence interval widths across all species were less than two units of the HFI for all HTIs (CI widths: Peak HTI = 1.43; Conservative HTI = 1.00; Maximum HTI = 0.76).

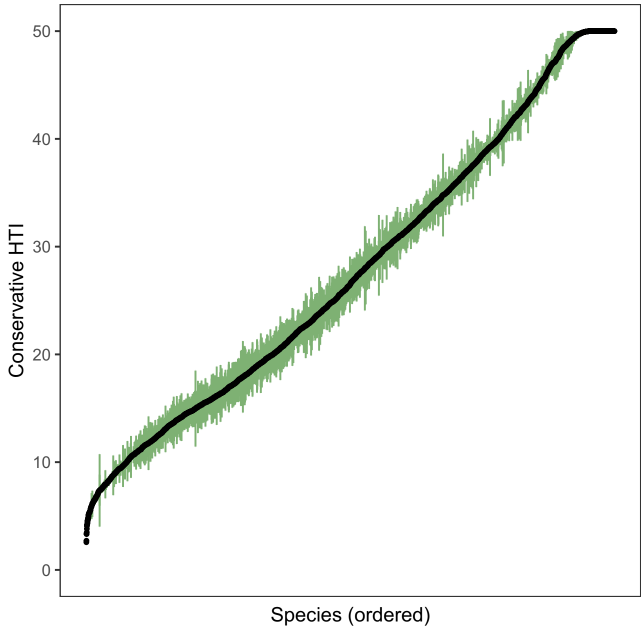

FIGURE 2 Estimated Conservative HTIs (black dots) with confidence intervals (green error bars) for all 6094 bird species globally. Species were ordered by HTI values. For those species with different tolerance values on different continents, we averaged the tolerances and lower and upper confidence interval limits across continents ($N=830$).

We also found that the three HTIs were strongly positively correlated (Pearson $r_{\text{Peak–Conservative}}=0.81$; $r_{\text{Peak–Maximum}}=0.58$; $r_{\text{Conservative–Maximum}}=0.89$; Appendix S2, Figure S9). For simplicity, from here onward, we present results for Conservative HTI in the main text and for Peak and Maximum HTI in the supplementary material (Appendix S2). Conservative HTI showcases the potential upper limit of species' tolerances to human pressures in the future while maintaining a large variation in values to allow across-species comparisons.

Many species were able to tolerate extremely high levels of human pressures (here, HFI >40). Roughly 22% (1336 of the 6094 species) tolerated such intense human pressures when tolerances were quantified as Conservative HTI. For example, an urbanized common swift (*Apus apus*) tolerated the most extreme values of human pressures within its breeding range (Figure 4). Of the 6094 species, 830 (13.6%) occurred in more than one continent, also outside their native ranges. On average, these species had a Conservative HTI of 35.5, higher than that of all the species. For example, both within its native range in Eurasia and non-native range in North America, common starling had a Conservative HTI of 50. Similarly, within its native range in Asia and non-native range in Europe, rose-ringed parakeet had a Conservative HTI of 49.5 and 50, respectively.

Within each continent, we looked at the proportion of species that occurred in highly modified environments (HFI > 40). Europe had a higher percentage of highly human-tolerant species, 42%, than North America (36%), Oceania (32%), Asia (32%), Africa (24%), and Latin America (19%). On the other end of the spectrum, we assessed the species that were strongly associated with intact areas for their breeding (here, HFI < 4; Williams et al., 2020). Seven (~0.001%) of the 6094 species had a low Conservative HTI and were associated with intact areas. The species with the lowest estimated Conservative HTI of 2.57, broad-billed sapayoa (*Sapayoa aenigma*), occurs in humid forests in Colombia, Ecuador, and Panama.

The Conservative HTI differed significantly among population trend categories (one-way ANOVA: $F=163.7$, $df=3$, $p<0.001$; Figure 5a). Pairwise comparisons showed that all population trend categories differed significantly from each other: increasing species had the highest HTI and decreasing the lowest (Bonferroni-corrected $p<0.01$). Conservative HTI differed significantly among Red List threat categories (one-way ANOVA: $F=23.1$, $df=4$, $p<0.001$; Figure 5b). Pairwise comparisons showed that species in the Least Concern category had a significantly higher Conservative HTI than species in the Near-Threatened and Vulnerable categories (Bonferroni-corrected $p<0.001$), but other categories did not significantly differ from each other. For exact pairwise p-values, see Tables S3 and S4 in Appendix S2. The phylogenetic effect on the HTI ~ population trend category and HTI ~ threat category was consistent and significant (phylANOVA for population trend category: $F=162.14$, $p<0.001$; phylANOVA for threat category: $F=22.76$, $p=0.003$; Appendix S2, Tables S5 and S6). In the second sensitivity analysis with continuous population trend estimates, we found that species with higher tolerance had significantly larger positive population trend slope estimates ($R^2=0.04$, $F=7.45$, $df=153$, $p=0.007$).

The Conservative HTI of threatened species varied from very low values to the maximum. For example, the endangered fern-wren (*Oreoscopus gutturalis*) had a low Conservative HTI of 3.33, whereas the vulnerable Javan myna (*Acridotheres javanicus*) had a high Conservative HTI of 50. Similarly, the Conservative HTI of non-threatened species varied greatly. For example, two species of least concern, broad-billed sapayoa (*Sapayoa aenigma*) and common redpoll (*Acanthis flammea*), represented the opposite ends of the Conservative HTI spectrum at 2.57 and 50, respectively. However, all four example species are reported to have a decreasing population trend.

4 | DISCUSSION

We quantified human pressure tolerances of over 6000 bird species on six continents and provided the tolerance values and uncertainty estimates. We found that bird species' tolerances to human pressures were high across continents regardless of the tolerance metric. Even species' peak occurrences were, on average, observed at locations with high HFI values, corresponding to intermediate and highly impacted areas. Consequently, high tolerances are inevitable in the Anthropocene as most species necessarily occur in areas under strong human pressures, which cover 58% of the terrestrial world (Williams et al., 2020). Our results also show that HTI is associated with bird species' population trends and IUCN threat categories.

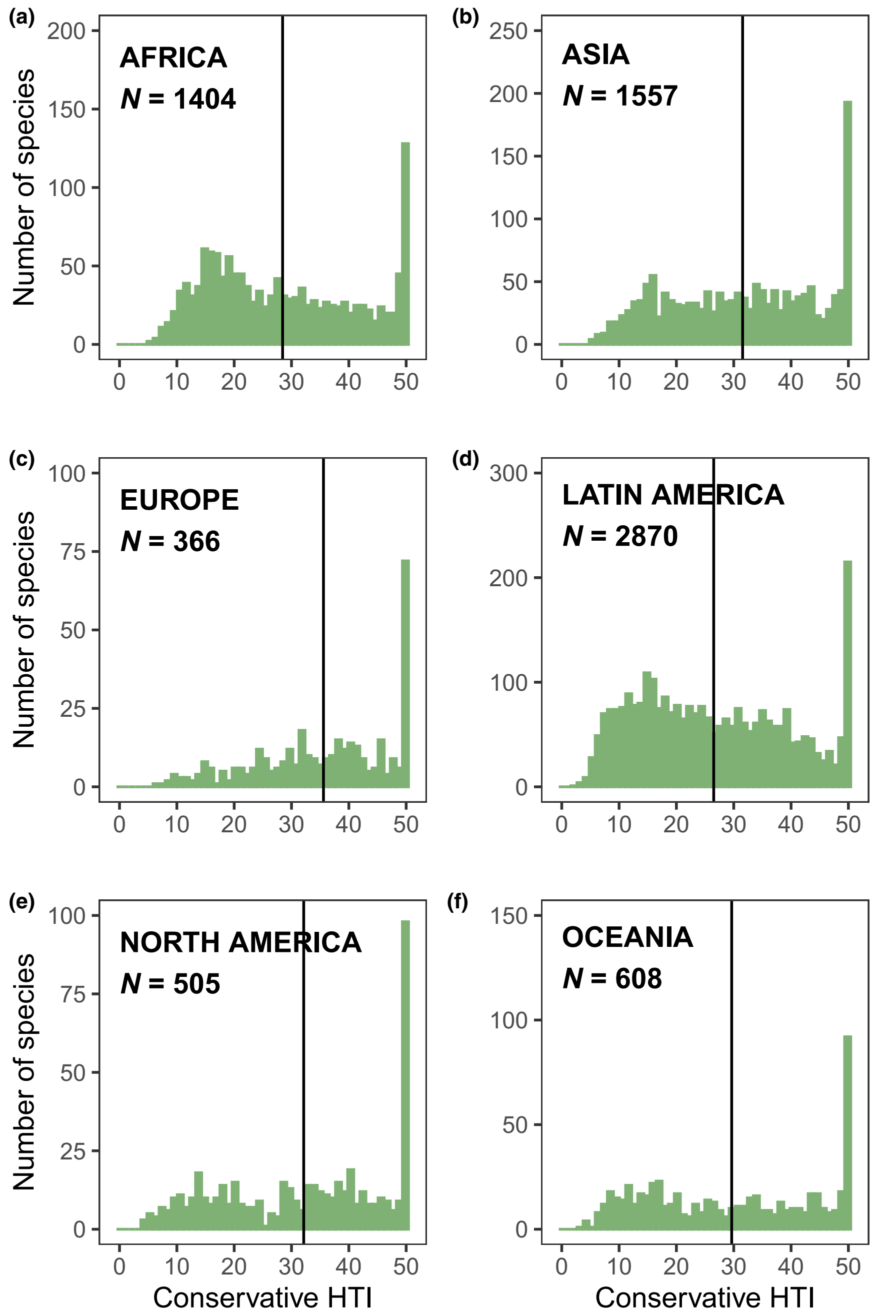

FIGURE 3 Distribution of Human Tolerance Indices (HTI; ranging from tolerance to perfect intactness [0] to extremely high human pressure [50]) across bird species measured as Conservative HTI. Panels illustrate Conservative HTI for (a) Africa, (b) Asia, (c) Europe, (d) Latin America, (e) North America, and (f) Oceania, respectively. The vertical lines illustrate the median HTIs across all species within the continent. Note the different scales on the *y*-axes.

4.1 | Spatial variation in human tolerance indices

Bird species' tolerances to human pressures varied across continents, such that larger proportions of species in Europe and North America than Latin America and Africa tended to tolerate highly modified environments (HFI > 40 of the maximum 50). The variation across continents can arise from two sources: variation in individual species' tolerances or in the ecological conditions caused by the human pressures (measured here with the HFI). Indeed, much larger proportions of Europe and North America are modified and on average have higher HFI values than other continents (Williams et al., 2020). Without studying the past distributions and more detailed ecology of each species, we cannot determine whether the high average tolerances in the highly human-modified continents stem from disappearance of sensitive species or adaptation of species.

4.2 | Species-specific variation in human tolerance indices

Few species (~0.001% of 6094) had a low Conservative HTI and were associated with intact areas. The low percentage is likely due to the fact that the most comprehensive data are associated with abundant and broad-ranged species and from areas that are uniformly under strong human pressures. The data for rare species or species with small distribution ranges are likely scarce, and such

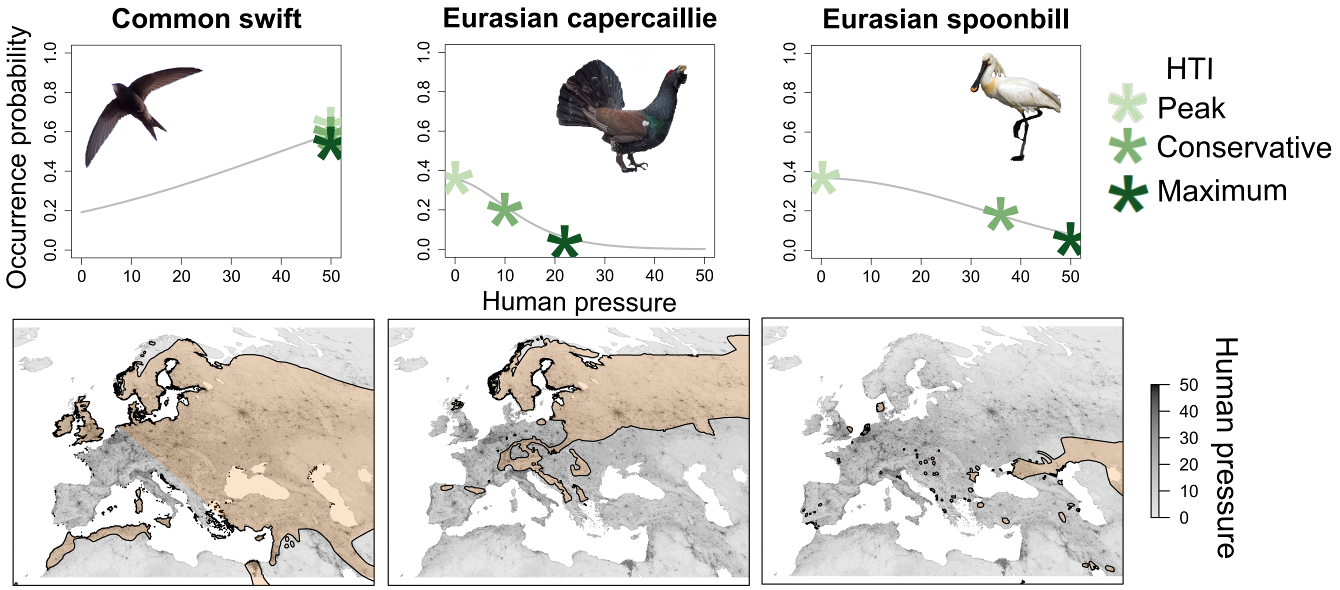

FIGURE 4 Examples of modelled Human Tolerance Indices for common swift (*Apus apus*), Eurasian capercaillie (*Tetrao urogallus*), and Eurasian spoonbill (*Platalea leucorodia*) in Europe. The upper panels illustrate the predicted relationships from one resampling replicate model between species' occurrence probabilities and the HFI when other variables were held constant. The green stars illustrate the three HTIs calculated from these predicted relationships. In the lower panels, the grey background map illustrates the spatial variation in human pressures across Europe, measured as the HFI (0 = perfectly intact, 50 = extremely high human pressure). The coloured transparent polygons represent the breeding or resident ranges of the three species.

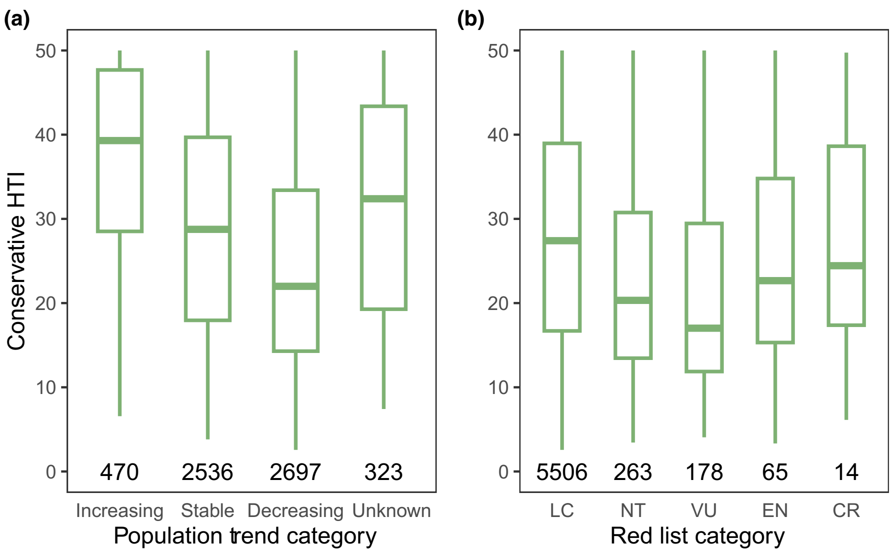

FIGURE 5 Conservative HTI of the world's bird species across continents depending on (a) the IUCN population trend category and (b) the IUCN Red List category. The boxplots illustrate the median and the first and third quartiles, and the whiskers show the largest and smallest values no further than 1.5*inter-quartile ranges from these quartiles, respectively. For species with different tolerance values in different continents (*N* = 830), we averaged the tolerances across continents. We excluded the Unknown population trend category (*N* = 323 species) from the visualization. Red List categories: CR, critically endangered; EN, endangered; LC, least concern; NT, near-threatened; VU; vulnerable. We excluded the DD (Data-Deficient) category because it included only two observations.

species have a higher chance of being excluded from the analyses. Moreover, the low number of species occurring only in intact areas and with low Conservative HTI values may be because areas with very low human influence are limited, and largely biased towards high latitudes (e.g. boreal zone) where species richness is lowest (Riggio et al., 2020). Perhaps the only exception to this is

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the Amazon, where large areas of low human pressures and high numbers of species exist. The species with HTI < 10 are most numerous in South America, although the sampling effort is not as high as in many other continents (Figure 3). This suggests that the distribution of Conservative HTI values across the ~6000 bird species may be driven more by the spatial distribution of human pressures than sampling bias.

We found non-random variation in bird species tolerances to human pressures across categories of IUCN population trend and Red List threat status. This implies that species with high and low tolerances to human pressures are characterized by different population attributes. Tolerances were strongly linked to species' population trends, such that the species with low tolerance had declining populations. This means that populations are affected by direct human pressures, such as land use changes, although population trends also could be driven by global drivers such as climate change. For instance, in Europe, climate change does not explain the colonizations and extinctions of species well, which suggests that other drivers, including habitat quality, play a role (Howard et al., 2023). The tolerances were also linked to species' threat status, such that species of least concern had higher tolerances than near-threatened and vulnerable species. However, the tolerances of the most threatened species (endangered and critically endangered) did not differ from those of the less threatened species. This is likely due to the low number of species in the highest threat categories for which we could estimate tolerances.

The observed increase in tolerance of threatened species (Appendix S2, Figure S9) may have ecological relevance in the form of extinction debt (Hanski & Ovaskainen, 2002). When using the maximum and the conservative human tolerance indices, one should be aware of the uncertainty stemming from the current extinction debt experienced by species in poor-quality habitats. Species may persist in lower quality and highly modified habitats but become extinct in the near future without quick adaptation to increasing human pressures. Therefore, the tolerance values may not accurately represent their future potential to tolerate intensifying human pressures. Our analyses partly account for the potential extinction debt given that the HFI is from 2013 and the eBird data from later years. Accordingly, if the environment was already degraded in 2013, the tolerances reflect birds that persisted in the degraded environment at least for some years. It is also possible that a species may have started to become more urbanized, but the process is not yet complete, and the species' current range does not fully represent its potential to tolerate intensifying human pressures. Our results make it possible to identify those threatened species that are tolerant to human pressures, which supports the approach of conserving them also in the highly modified environments. The link between human pressure tolerance and population trend was stronger than the link between human pressure and Red List threat status, likely because more species are declining than are threatened (Finn et al., 2023).

4.3 | Limitations and future research opportunities

Although our quantification of species' tolerances to human pressures is unprecedented at both spatial and taxonomic levels, further attempts to understand the underlying mechanisms are needed. Most importantly, future studies and conservation planning could investigate species' tolerances to specific human pressure variables (Mu et al., 2022) to gain a more detailed understanding of which human pressures each species can tolerate. For example, linear infrastructures such as roads may affect some species more strongly than others via anthropogenic sound and direct mortality, but this likely depends on species' ecological traits, such as diet (Cooke, Balmford, Donald, et al., 2020; de Jonge et al., 2022). Similarly, the HFI we used does not fully capture (but likely is a proxy for) other sources of human pressure, such as air pollution, anthropogenic sound, and climate change. Anthropogenic sound and air pollution, and to a lesser extent climate change, may be strongly associated at local to regional extents with human activities. HFI captures well the direct human pressures (especially those driven by land use) but not necessarily the indirect pressures, such as air pollution or climate change (which is also caused partly by air pollution).

We acknowledge that bird species' detectability in different vegetation types may affect the quantified tolerances to human pressures. However, we believe that the magnitude of variation in detectability is small relative to the variation in occurrences depending on the HFI (Anderson et al., 2015; Cooke, Balmford, Johnston, et al., 2020; Johnston et al., 2014). This is partially because most values of the HFI encompass a range of vegetation and land use types that likely influence bird detectability in different ways. For example, intact vegetation types with low HFI values include forest, wetland, and shrubland; and locations with high HFI could be urban or under intense agriculture.

As more eBird observation data accumulate quickly, the tolerance quantification could be repeated in the future. It is likely that the taxonomic coverage will increase in the future repetition because some species will exceed the occurrence threshold set in our study. When more abundance data accumulate, it will be possible to repeat the tolerance quantification with abundance data, giving a more detailed picture of the gradual response of species to human pressures. Poor-quality habitats (with a high HFI) may only support a small number of individuals, whereas high-quality habitats (with a low HFI) may support most of the individuals, but both areas could have a similar number of recorded occurrences of the species. A potential solution is to assess the local tolerances across a species' range against its population trends (when available) or abundances in those same parts of the range.

Species' migratory behaviour may also affect the quantification of the tolerances as the human pressure tolerance of migratory species may include some data that are outside the species' breeding season. We could not consider the species-specific breeding season months due to lack of systematic knowledge but used region-specific breeding months to filter the eBird observations. During migration, species may use suboptimal habitats that do not represent their actual tolerance to human pressures during their breeding (La Sorte et al., 2022; Newton, 2008; Zuckerberg et al., 2016). We mitigated the effect of this on our results by spatial and temporal filtering, which means that observations outside the species' actual breeding season are still likely to be close in time to its breeding season and within its known breeding range.

We used eBird data from COVID-19 lockdown years, among all years used, but we do not believe COVID-19 lockdowns introduced a significant bias in the eBird observations in our data as we strived to obtain observations from the full range of human pressure environments in the models. We did not use eBird data from North America in 2020 due to the filtering procedure (see Section 2), which likely mitigated any effects of bird behaviour changes during lockdowns. Moreover, the differences in pre-COVID-19 and during-COVID-19 eBird data were negligible (Hochachka et al., 2021). However, COVID-19 lockdowns may have affected bird behaviour, such that some species may have used more human-modified areas due to a lower degree of direct disturbance by humans (Gordo et al., 2021; Sanderfoot et al., 2022; Schrimpf et al., 2021; Warrington et al., 2022).

4.4 | Applications of human tolerance indices

We envision that the quantified HTIs of the world's birds can be applied to both ecological and evolutionary research and conservation. We recommend using maximum and conservative tolerances when predicting future species' distributions under intensifying human pressures as they best describe species' potential to respond to the pressures. Peak HTI values are best suited to understanding the contemporary situation and to assessing the human pressure optima of the species. Further studies on the characteristics of bird species with high and low tolerances to human pressures could link the tolerance indices to species' traits, such as generation lengths (Bird et al., 2020), diet and habitat specialization (Wilman et al., 2014), or temperature niche (Devictor et al., 2008). Given that increasing contact between wildlife and humans, especially in urban environments, increases the risk of spreading wildlife diseases, the HTI could be used as an additional tool to predict species potential as pathogen vectors in the future. To understand community-level changes in the composition of human pressure-tolerant and pressure-sensitive species, HTIs can be applied to calculate community-weighted means of the tolerances over time and space. Suitable, independent, and spatially extensive data on bird occurrences already exist in Europe (Keller et al., 2020) and North America (Meehan et al., 2019; Sauer et al., 2017).

Our approach for quantifying species' standardized tolerances to human pressures could be applied to taxa other than birds at different spatial scales, and for different pressures. Data on species occurrences at high spatial resolution are accumulating rapidly at regional and national levels (e.g. the Global Biodiversity Information Facility, Fink et al., 2022), which allows the application of our methods and the accompanying code for management and conservation purposes. For species-based conservation of other taxonomic groups, for example, camera trap occurrences of a threatened mammal species could be used to quantify its occurrence probabilities across the HFI gradient to assess the maximum tolerance to human pressures within the remaining range. For area-based conservation, HTIs could be used to identify areas where species with high human pressure tolerance and humans can co-exist. For example, there is a global target of protecting 30% of terrestrial Earth, but likely not all of that can be strictly protected (CBD/COP/15/L.25; CBD, 2022). HTIs of bird species could be used to identify candidate species and areas for protection that tolerate some levels of human pressures. The data also allow identification of priority areas for low human tolerance species, where human access could be restricted, at least during sensitive periods (e.g. breeding). In practice, this could guide the expansion of the current network of protected areas, and especially the identification of sensitive areas where strict nature reserves (IUCN protected area category Ia) might need to be designated.

AUTHOR CONTRIBUTIONS

All authors conceived the idea, E.-L.M. conducted the analyses with A.J., E.-L.M. wrote the first draft of the paper, and all authors contributed significantly to the later versions.

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CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are freely available. Bird species checklists (eBird version list in Appendix S1, Table S1) are available at http://ebird.org. Bird species' distribution maps (BirdLife International, 2022) are available at http://datazone.birdlife.org. Bird species' IUCN Red List statuses and population trend categories (IUCN Red List of Threatened Species, downloaded 24.04.2023) are available at http://iucnredlist.org. The calculated tolerances are provided as supplementary material (Appendix S3) and stored in Dryad (https://doi.org/10.5061/dryad.83bk3jb08). The codes used to quantify tolerances are also provided as supplementary material and stored in Dryad.

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BIOSKETCH

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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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