

## CONTRIBUTED PAPER

# Effects of anthropogenic landscapes on population maintenance of waterbirds

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**Article Impact Statement:** Protecting natural areas and improving the quality of anthropogenic landscapes as habitat are both needed to achieve effective conservation.

## Abstract

Anthropogenic impacts have reduced natural areas but increased the area of anthropogenic landscapes. There is debate about whether anthropogenic landscapes (e.g., farmlands, orchards, and fish ponds) provide alternatives to natural habitat and under what circumstances. We considered whether anthropogenic landscapes can mitigate population declines for waterbirds. We collected data on population trends and biological traits of 1203 populations of 579 species across the planet. Using Bayesian generalized linear mixed models, we tested whether the ability of a species to use an anthropogenic landscape can predict population trends of waterbird globally and of species of conservation concern. Anthropogenic landscapes benefited population maintenance of common but not less-common species. Conversely, the use of anthropogenic landscapes was associated with population declines for threatened species. Our findings delineate some limitations to the ability of anthropogenic landscapes to mitigate population declines, suggesting that the maintenance of global waterbird populations depends on protecting remaining natural areas and improving the habitat quality in anthropogenic landscapes.

## KEYWORDS

conservation, habitat management, natural habitat, population trends, threatened species, wetlands

Efectos de los Paisajes Antropogénicos sobre la Conservación de Poblaciones de Aves Acuáticas

**Resumen:** Los impactos antropogénicos han reducido las áreas naturales, pero han incrementado el área de los paisajes antropogénicos. Existe un debate sobre si los paisajes antropogénicos (p. ej.: campos de cultivo, huertos, estanques de peces) proporcionan alternativas al hábitat natural y bajo cuáles circunstancias. Consideramos si los paisajes antropogénicos pueden mitigar las declinaciones poblacionales de las aves acuáticas. Recolectamos datos sobre las tendencias poblacionales y las características biológicas de 1203 poblaciones de 579 especies de aves de todo el mundo. Mediante modelos bayesianos generalizados lineales mixtos, analizamos si la habilidad de una especie para usar un paisaje antropogénico puede pronosticar las tendencias poblacionales de las aves acuáticas a nivel mundial y de las especies de interés para la conservación. Los paisajes antropogénicos beneficiaron a la conservación de las poblaciones de especies comunes, pero no para las especies menos comunes. Por otro lado, el uso de paisajes antropogénicos estuvo asociado con las declinaciones poblacionales en las especies amenazadas. Nuestros descubrimientos delinean algunas limitaciones que tienen los paisajes antropogénicos para mitigar las declinaciones poblacionales, lo que sugiere que la conservación mundial de las poblaciones de aves acuáticas depende de la protección de las áreas naturales remanentes y del mejoramiento de la calidad del hábitat en los paisajes antropogénicos.

**Palabras Clave:**

conservación, especie amenazada, hábitat natural, humedales, manejo de hábitat, tendencias poblacionales

**人工景观对水鸟种群维持的影响**

人类活动导致自然景观的面积不断减少而人工景观的面积不断增加。关于人工景观(例如农田、果园、鱼塘)能否为野生生物提供替代自然景观的栖息地,以及在什么情况下可以提供适宜的栖息地,目前仍存在争论。我们收集了全球 579 种水鸟 1203 个种群的数量变化趋势和生物学特性数据,探讨了水鸟利用人工景观是否有助于其维持种群数量。利用贝叶斯广义线性混合模型,我们分别针对全球水鸟和受胁水鸟检验了物种是否利用人工景观与其种群趋势的关系。利用人工景观有助于数量较多的常见种的种群维持,但对数量较少的不常见种的种群维持没有显著影响。相反,利用人工景观的受胁物种更倾向于表现出种群下降的趋势。本研究结果指出了人工景观在减缓种群数量下降方面存在一定局限性,表明了维持全球水鸟种群稳定不仅需要保护自然景观,而且需要改善人工景观的栖息地质量。

**INTRODUCTION**

Human activities have dramatically changed the Earth's land surface, causing population declines and species extinctions that have escalated rapidly alongside natural habitat loss (Dirzo et al. 2014; Ceballos et al. 2015; Goncalves-Souza et al. 2020). At the same time, the number and area of anthropogenic landscapes, such as farmlands, orchards, and fish ponds, have continually increased. These areas are mainly used for commodity production, but can also be extensively used by wildlife (Ma et al. 2010; Oertli 2018; Sievers et al. 2018). Understanding the role of anthropogenic landscapes in wildlife conservation is important in light of the increasing scope and intensity of human activities worldwide (Dirzo et al. 2014).

Although many species can use anthropogenic landscapes, whether this ability mitigates population declines is still largely unexplored. Given the large variation in life-history traits, habitat requirements, and responses to human activities among species, this ability may vary taxonomically (McKinney 1997; Newbold et al. 2013; Jackson et al. 2020). Anthropogenic landscapes are created and managed by humans, and the responses of species to habitat change and human disturbance are closely related to their population dynamics (Owens & Bennett 2000). Common species (i.e., those with a large population size) are usually widely distributed; are often habitat generalists; tend to be flexible in their habitat use (Gaston et al. 2000); and, relative to less common species (i.e., those with a small population size), are relatively tolerant of human disturbance and habitat change (McKinney 1997; La Sorte 2006; Clavel et al. 2011). One would predict that the use of anthropogenic landscapes may be beneficial, especially for common species.

The role of anthropogenic landscapes in wildlife conservation may also be linked to the quality of nearby natural landscapes. In regions where natural landscapes are well protected, the role of anthropogenic landscapes in population maintenance may be limited, whereas in regions with dramatic loss and degradation of natural landscapes, anthropogenic landscapes can contribute much to wildlife conservation because no better quality

habitat is available (Tourenq et al. 2001; Jackson et al. 2020). Previous studies show that population trends in some species vary by region. This variation is related to local or regional differences in habitat conservation and management efforts (e.g., Boere et al. 2006; Yu et al. 2017; Amano et al. 2018). Whether there are regional differences (e.g., among flyways) in the contribution of anthropogenic landscapes to the mitigation of population decline is unclear.

Wetlands are habitat for a great variety of species. Over the past century, more than half of the total area of wetlands has disappeared globally, mainly as a result of land conversion by humans (Ma et al. 2014; Davidson 2018; Xu et al. 2019). Wetland loss has caused population declines in many waterbird species (Studds et al. 2017). Many studies show that anthropogenic wetlands (e.g., irrigated land, aquaculture ponds, and salt pans) are used as habitat by diverse species of waterbirds (Amano et al. 2010; Jackson et al. 2020; Kasahara et al. 2020) and therefore contribute to waterbird conservation. However, most of these studies focused on a limited number of species and groups at a local or regional scale (e.g., Rendon et al. 2008; Almeida et al. 2020; Jackson et al. 2020). Moreover, it is unclear how the use of anthropogenic landscapes affects population dynamics.

Because human activities will likely drive further decreases in natural areas and further increases in anthropogenic landscapes (Davidson 2014), it is critical to clarify the potential role of anthropogenic landscapes in population maintenance to inform conservation policy and management (Ma et al. 2010; Oertli 2018; Sievers et al. 2018). We used an extensive data set on global waterbird populations to explore the relationship between anthropogenic landscape use and waterbird population trends. We divided waterbirds into two groups: those that use anthropogenic landscapes and those that do not (IUCN 2019) (see Methods). We tested three hypotheses: waterbirds that do not use anthropogenic landscapes are more likely to exhibit population declines than those that use anthropogenic landscapes (hypothesis 1); the effects of anthropogenic landscape use on population trends are related to population abundance such that the use of anthropogenic landscapes mitigates

population decline of common but not of uncommon species (hypothesis 2); and because natural wetlands have declined more rapidly in Asia than in Europe and North America over the past several decades (Davidson 2014), anthropogenic landscape use can mitigate the population decline of waterbirds to a greater extent in Asia (Asia-Pacific flyway) than in Europe (Europe-Africa flyway) or the Americas (America flyway) (hypothesis 3). Because species with high extinction risk are conservation priorities, we determined whether these hypotheses apply to all species or only to species of conservation concern (i.e., those listed as critically endangered, endangered, vulnerable, or near threatened [IUCN 2019]).

## METHODS

### Waterbird population trends

We defined *waterbirds* as all aquatic birds (waterfowl and waders [Wetlands International 2015; Appendix S1]). A waterbird species may have one or more populations. Here, a population refers to a biogeographical population identified by their breeding or nonbreeding range. It is an assemblage of individuals that does not experience significant emigration or immigration (Wetlands International 2015).

Systematic monitoring of waterbirds has a long history and thus provides a reliable global data set of population changes (Boere et al. 2006; Green & Elmberg 2014; Amano et al. 2018). Data on waterbird population trends were obtained from the database of Wetlands International (2015), which provides comprehensive information for 2304 populations of more than 800 species worldwide. We included those populations with declining, stable, and increasing trends and excluded populations with fluctuating and unknown trends (Appendix S1). For those species with a single population that had an unknown population trend in the database, we checked the International Union for Conservation of Nature (IUCN) Red List assessment (IUCN 2019), which evaluates population trends at the species level, and supplemented our data with this information when available. A total of 1203 populations of 579 waterbird species (36.1% in decline, 42.7% stable, and 21.2% increasing) were included in the data set, which represented 52.2% of the total number of waterbird populations (2304) and 85% of the total number of populations with known trends (1422) (Wetlands International 2015). The data set represented a comprehensive collection of all available data.

### Predictor variables

To test whether populations of waterbirds that do not use anthropogenic landscapes are more likely to decrease than those of species that use anthropogenic landscapes, we used the variable anthropogenic landscape use. For this, we determined habitat categories of waterbirds according to the IUCN Habitats Classification Scheme, which categorizes important habitat types for each species (IUCN 2019). Because waterbirds can use both terrestrial and aquatic habitats, we included terrestrial

and aquatic anthropogenic landscapes created or managed by humans (type 14 and 15 in IUCN Habitat Classification Scheme [IUCN 2019]) (Appendix S2). A population was considered to have the ability to use anthropogenic landscapes if one or more anthropogenic landscapes are regularly or frequently used by the species (considered “suitable” by IUCN [2019]).

To test whether the effects of anthropogenic landscape use on population trends are related to population abundance, we collected data for population size from Wetlands International (2015). If the report presented population size as a range, we calculated the geometric mean of the minimum and maximum estimate. To test whether the mitigation of population decline by anthropogenic landscape use varied among geographic regions, we classified the distribution of populations into three regions according to the zones of Wetlands International (2015): Asia-Pacific, the Americas, and Africa-Eurasia. Although we recognize that population size is only one measure of abundance or commonness, others include range size and diversity of habitat types, we selected population size because range size at a population level is unknown for many species and habitat diversity is somewhat subjective. Further, we expected there to be a significant correlation between these variables. To test the relationship between population size and range size and habitat diversity of waterbirds, we extracted the range size of waterbirds according to extent of occurrence at species level (IUCN 2021) and found that there was significant correlation between population size and range size ( $r = 0.67, p < 0.001, n = 311$ ) (Appendix S3a). In addition, we extracted the number of habitat types at species level (IUCN 2021) as representative of habitat diversity and found that population size was significantly related to habitat diversity ( $r = 0.28, p < 0.001, n = 311$ ) (Appendix S3b). Based on these results, we retained population size as the most appropriate measure of abundance in our models.

We also included body size and migration distance, which previously have been determined to predict population trends (Vickery et al. 2014; Barnes et al. 2016; Amano et al. 2018), in the models. We used the mean body mass of the population as a representation of body size whenever possible (Dunning Jr 2008; del Hoyo et al. 2014). When data at the population level were absent (which was the case for 1076 of 1203 populations), we defined the mean body mass of the population as the mean body mass of the species. The migration distance of a resident population was set at 0. For a migratory population, we extracted the global distribution map of the species in vector format from the database of BirdLife International and NatureServe (BirdLife International and NatureServe 2015). According to the description in Wetlands International (2015), regional distribution of each population was digitized on a global map. Migration distance was measured as the spherical distance between the geometric center of breeding and nonbreeding sites in the `rdist.earth` function in the R package `fields` (Nychka et al. 2017).

### Statistical analyses

Because we were concerned about factors related to population decline, population trends were classified as declining or not declining (the latter included increasing and stable populations).

Using Bayesian generalized linear mixed models (GLMMs), we tested whether the ability of a species to use an anthropogenic landscape (binary variable, use or no use) can predict trends (binary variable, declining or not declining) of waterbird populations globally and for species of conservation concern (hypothesis 1). To determine whether the effects of anthropogenic landscape use on population trends were related to population size, the interaction between anthropogenic landscape use and population size was included in the models (hypothesis 2). To test whether the benefit of anthropogenic landscape use differed markedly among regions, regional distribution and the interaction between regional distribution and anthropogenic landscape use was included in the models (hypothesis 3). Body size and migration distance were included in the models as covariables. We performed analyses for the entire data set and for the set of species of conservation concern (threatened and near threatened species).

To regularize inference, we used weakly informative priors. Based on the model with Bernoulli distribution, Student's  $t$  distribution (6, 0, 2.5) was set for slope, and Student's  $t$  distribution (6, 0, 10) was set for variance of the phylogeny. We ran four Markov chains with 10,000 iterations per chain. We discarded the first 5000 iterations as burn-in. Rubin–Gelman statistics ( $<1.1$ ) for each parameter were used to assess convergence (Brooks & Gelman 1998). We used the year in which the population trend was estimated as a random effect to control its potential effect on population trends (Appendix S4). Analyses were conducted with the *brms* package of R (Buerkner 2017).

To control the potential effects of phylogeny, we built a maximum clade credibility tree derived from the phylogenetic tree distributions (Hackett et al. 2008). We pruned the global phylogenetic tree of birds from BirdTree.org under the option “Hackett All Species: a set of 10 000 trees with 9993 OTUs each” to download waterbird species data sets (Jetz et al. 2012). We randomly sampled 1000 pseudo-posterior distributions and then constructed the maximum clade credibility tree with common ancestor node heights in TreeAnnotator software of the BEAST package (Drummond & Rambaut 2007; Rubolini et al. 2015). We calculated the phylogenetic similarity at the species level with a variance-covariance matrix and included species as a random effect in these models to account for repeated measures of species at the population level.

All of the predictor variables were standardized to ensure commonality of scale. The variance inflation factor (VIF) was used to test for multicollinearity among predictor variables, including the mixed effects and interaction items in the *vif* function in the R package *car* (Fox & Weisberg 2019). The VIF values of all of the variables were  $<1.6$  (Appendix S5).

## RESULTS

### Global waterbird populations

Of the 579 species and 1203 populations in the data set, anthropogenic landscapes were regularly used by 359 (62.0%) species and 815 (67.7%) populations. The GLMMs indicated that anthropogenic landscape use was not significantly related

to waterbird population trends (Figure 1a), which is inconsistent with our first hypothesis. Moreover, population size was closely related to population trends; less abundant populations exhibited a relatively high probability of decline. Consistent with our second hypothesis, the interaction between population size and the anthropogenic landscape use was significantly associated with population trends (Figure 1a) in that anthropogenic landscape use reduced the probability of decline in abundant but not in less abundant populations (Figure 2a).

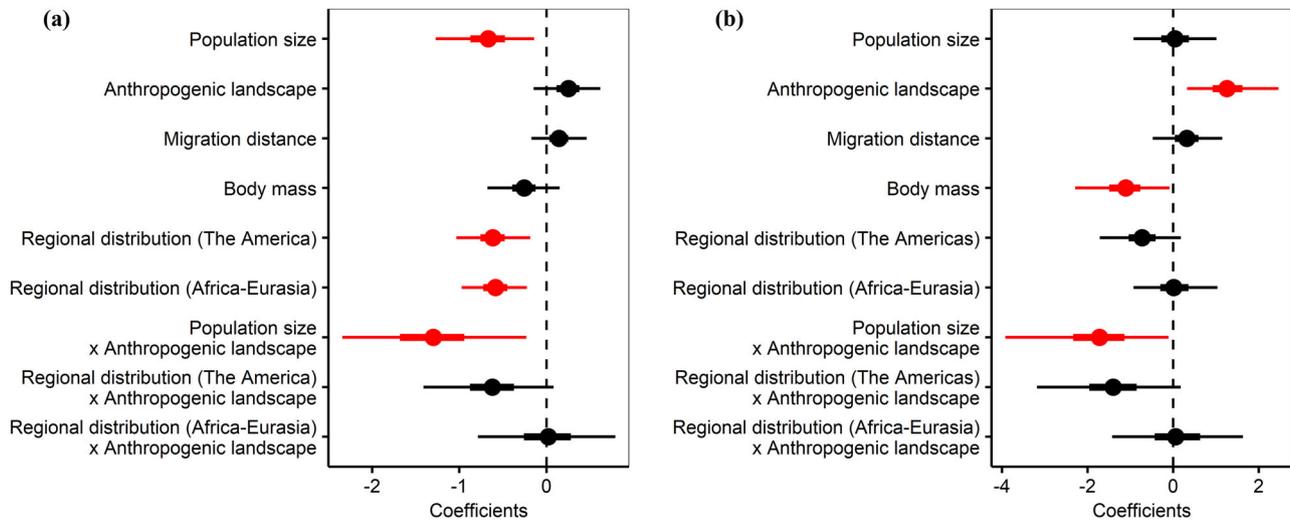
Compared with populations in the Americas and Africa-Eurasian region, populations in the Asia-Pacific region exhibited a higher probability of decline. The interaction between regional distribution and anthropogenic landscape use, however, was not significantly associated with population trends (Figures 1a & 2b). This suggests that the relationship between anthropogenic landscape use and population trend did not differ significantly among regions, which is inconsistent with our third hypothesis. Moreover, body mass and migration distance were not significantly related to population trends (Figure 1a).

### Waterbirds of conservation concern

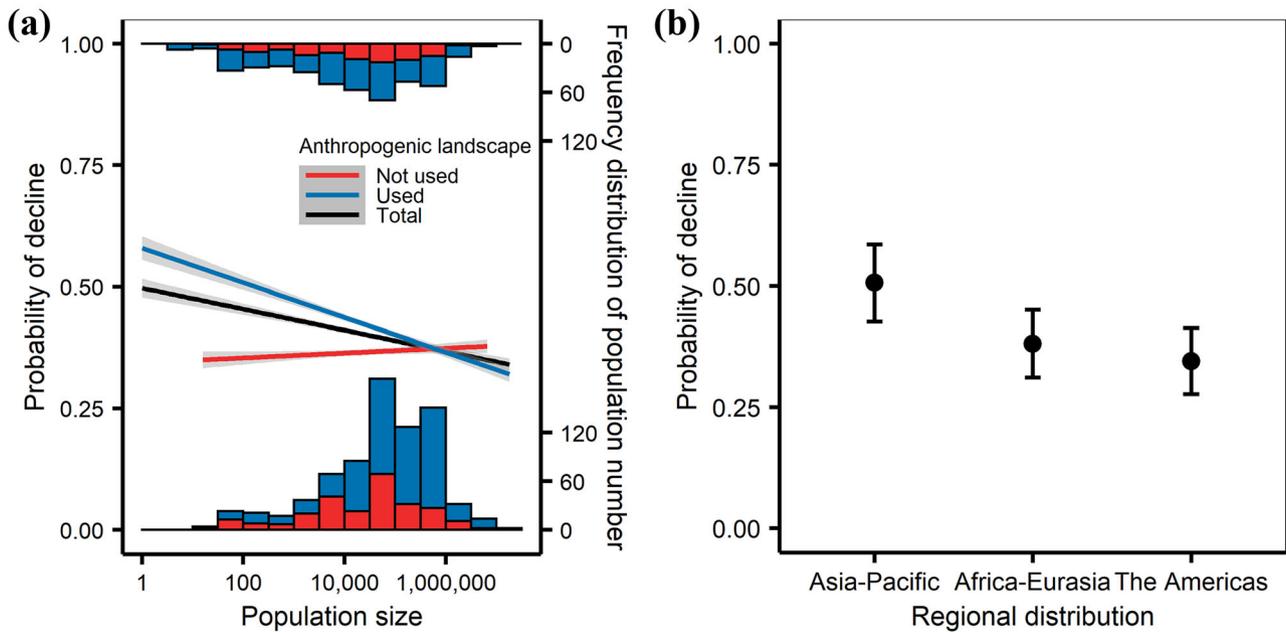
Among the 263 populations of 162 species of conservation concern, anthropogenic landscapes were regularly used by 85 (52.5%) species and 143 (54.4%) populations. Populations that use anthropogenic landscapes were much more likely to be declining than those that do not use anthropogenic landscapes (Figures 1b & 3a). This is the opposite of our first hypothesis. Because the population size of threatened species is generally smaller than that of nonthreatened species (Wilcoxon rank sum test,  $Z = 10.2$ ,  $W = 72818$ ,  $p < 0.001$ ), this result is consistent with the earlier analysis of all species, indicating that the role of anthropogenic landscapes in mitigating population decline diminishes as population size decreases. The interaction between population size and anthropogenic landscape use had significant effects on the population trends (Figure 1b); anthropogenic landscape use was associated with population decline of small populations (Figure 3a). There was no significant difference in the probability of population declines among geographical regions. Moreover, populations of species with a small body size had a higher probability of decline than those with a large body size (Figures 1b & 3b).

## DISCUSSION

Our results indicate that population size affects the relationship between anthropogenic landscape use and population trends, that is, anthropogenic landscape use may mitigate waterbird population decline for abundant but not for less-abundant populations. Although some rare species regularly and frequently use anthropogenic landscapes (Ma et al. 2010), our results suggest that many rare species are unlikely to benefit at a population level from these landscapes. This is likely because most rare species are sensitive to human activities and habitat modification associated with anthropogenic landscapes (Kokko & Sutherland 2001; Sorte 2006; Jackson et al. 2020). Although



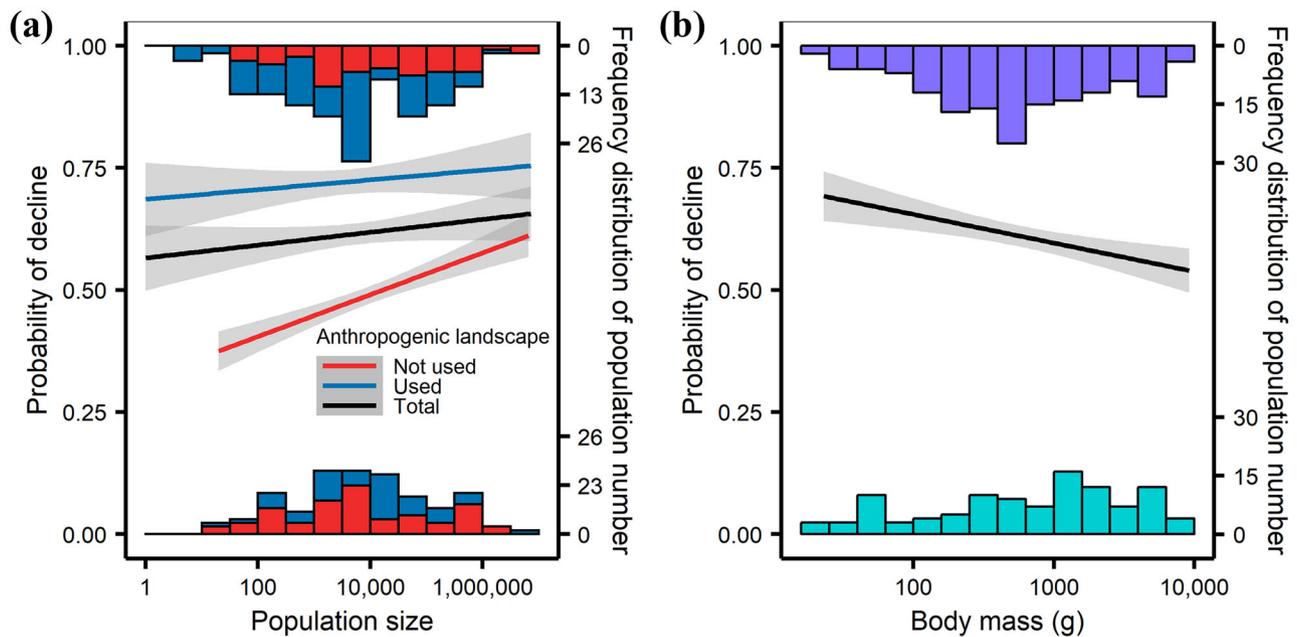
**FIGURE 1** Performance of candidate variables in predicting waterbird population trends. Coefficient estimates with 95% (fine line) and 50% (thick line) credible intervals for (a) 1203 populations of 579 waterbird species and (b) 263 populations of 162 threatened waterbird species (coefficients, effect size of the standardized variables; red, confidence intervals that exclude 0 [i.e., significantly associated with population trends])



**FIGURE 2** Probability of waterbird population decline in relation to (a) the interaction between population size and use of anthropogenic landscapes and (b) regional distribution for 1203 populations of 579 waterbird species (lines, slope; shading, 95% credible intervals; upper bars, number of declining populations; lower bars, nondeclining populations; whiskers in [b], 1 SD)

in many cases, habitat in anthropogenic landscapes constitute an alternative to natural areas and thus reduce the consequences of habitat loss, our results suggest that this is true for abundant, common species. The beneficial effects of anthropogenic landscapes on common but not uncommon species may lead to a shift in community composition and increased homogenization because some species may be extirpated, whereas others may become more abundant (Oliver et al. 2015). It can also lead to changes in functional diversity of the community (Almeida et al. 2020).

Although species richness and individual abundance can sometimes be extremely high in anthropogenic landscapes (Rendon et al. 2008; Green et al. 2015; Jackson et al. 2020), these landscapes may not provide optimal conditions, as might be present in nearby natural areas. Some anthropogenic landscapes may have negative effects (e.g., disturbance and pollution) and may even become ecological traps that attract wildlife without adequately supporting their reproduction and survival (Appendix S6). Large populations, which typically experience strong intraspecific competition for habitat, are likely to use



**FIGURE 3** Probability of waterbird population decline in relation to (a) the interaction between population size and use of anthropogenic landscapes and (b) body size (i.e., body mass) for 263 populations of 162 threatened waterbird species (lines, slope; shading, 95% credible intervals; upper bars, number of declining populations; lower bars, nondeclining populations)

diverse habitat types for reproduction and survival and are therefore unlikely to be trapped in anthropogenic landscapes. In contrast, small populations, which typically experience weak intraspecific competition for habitat, are likely to be highly affected by the negative effects of anthropogenic landscapes (Kristan 2003). We found that anthropogenic landscape use was related to a high probability of population decline in species of conservation concern, which generally have a small population size. In addition, anthropogenic landscapes are not suitable for over 30% of the total populations. These factors highlight that protection of natural areas is critical for the conservation of threatened waterbirds and those highly dependent on natural habitats.

The expansion of anthropogenic landscapes has had profound effects on wildlife globally. Although some waterbirds can use habitats other than wetlands, wetlands are absolutely critical for their survival and reproduction (Boere et al. 2006). Many studies show that loss of wetlands (both decline in quality and quantity) is the major threat to waterbirds (e.g., Kirby et al. 2008; Studts et al. 2017; Wang et al. 2018). Consequently, waterbirds that adapt to anthropogenic landscapes and benefit from shelter or food from anthropogenic wetlands tend to maintain a stable and even flourishing population (e.g., Fleury & Sherry 1995; Rendon et al. 2008). Our results indicate that for waterbirds, anthropogenic landscape use helps in the maintenance of common species. In contrast to our results, common farmland birds have declined in Europe over the past 30 years, which is mainly due to changes in farmland, the dominant habitat type, associated with agricultural intensification (Inger et al. 2015). Therefore, improving the quality of anthropogenic landscapes is important for population maintenance in human-influenced landscapes.

Our results indicated that waterbird populations in the Asia-Pacific region were more likely to be in decline than those in Europe-Africa or the Americas, which is consistent with other comparative analyses (Wetlands International 2015). In contrast to our prediction, anthropogenic landscape use did not mitigate population decline of waterbirds in the Asia-Pacific region. This may be because there are more serious pressures on waterbirds in anthropogenic landscapes in the Asia-Pacific region than in other regions. For example, in the Yangtze basin, which is the largest nonbreeding area for migratory waterbirds in the Asia-Pacific region, geese experience intense human disturbance and illegal hunting in farmland, resulting in declining populations. In Europe and North America, in contrast, geese benefit from extensive use of farmland as a supplementary foraging habitat in winter, resulting in flourishing populations (Yu et al. 2017). In North America, the population declines of many waterbirds have been reversed by habitat protection, restoration, and adaptive management (Rosenberg et al. 2019). This suggests that the ability of anthropogenic landscapes to mitigate population decline differs among regions that differ in how management affects habitat quality. Well-managed anthropogenic landscapes can play important roles in wildlife conservation, whereas poorly managed anthropogenic landscapes may contribute little to or may even harm wildlife conservation.

Extinction risk tends to be greater for large birds than for small birds (Ripple et al. 2017). However, we found a significant relationship between body size and population trends for all the species. Interestingly, for the species of conservation concern, large species had a lower probability of population decline than small species. Although many populations of large waterbirds have declined and some are listed as threatened, they are more likely to get attention and become targets of

conservation than small birds (Barnes et al. 2016; Amano et al. 2018). Benefiting from effective conservation measures, some populations of large species are no longer declining and some are even increasing, such as the crested ibis (*Nipponia nippon*) and the Siberian crane (*Leucogeranus leucogeranus*) in East Asia (Wang et al. 2018). Our results suggest that conservation of small species (e.g., shorebirds), which face more serious threats from habitat loss than large species (Owens & Bennett 2000), requires additional attention.

Due to habitat loss at stopover sites, many populations of long-distance migratory have declined over the past several decades (Vickery et al. 2014). However, we did not find a significant relationship between migration distance and population trends in waterbirds. Long-distance migratory waterbirds mainly breed in high northern latitudes, where there is less human activity than in lower latitudes. The tropical and temperate regions, with intensive human disturbance and habitat loss (Gaston et al. 2003), are the major distribution regions for both nonmigratory species and migratory species (nonbreeding and stopover sites) (Gaston et al. 2003; Somveille et al. 2013). Our results suggest that waterbirds, regardless of their migratory traits, experience similar pressures on a global scale.

Our study had two major limitations. First, the inferences are based on correlation and should, therefore, be viewed with caution. Second, we did not consider all possible factors linked to waterbird population trends. Previous studies show that species with long life spans and late sexual maturity, at high trophic levels, and with small range size and that are habitat specialists tend to exhibit population decline (Purvis et al. 2000; Reynolds et al. 2003; Lee & Jetz 2011; Soykan et al. 2016). We, nevertheless, suggest that we usefully assessed the strengths and limitations of anthropogenic landscapes in conservation and provide reference for species conservation and habitat management. Our results highlight that the relationship between anthropogenic landscape use and population trend differs between common and less common waterbirds. More specifically, anthropogenic landscapes appear to help common species but not less common species, especially threatened species, cope with large-scale loss of natural habitats.

Our results suggest a dual strategy of conserving intact natural areas while managing anthropogenic landscapes to improve habitat quality for waterbirds. The latter is especially useful in highly human-transformed landscapes, where few natural wetlands remain (Jackson et al. 2020). Given the ongoing loss of natural habitat and the increase of anthropogenic landscapes due to the unprecedented rate at which human activities are altering ecosystems, anthropogenic landscapes represent a targeted opportunity for improving the conservation of some species (Oertli 2018; Sievers et al. 2018). With well-protected natural habitat and well-managed anthropogenic landscapes, an integrated conservation system may be the key to reversing the global decline of biodiversity.

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## SUPPORTING INFORMATION

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

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