Title: Have human impacts exceeded climate in shaping mammalian distributions?

Running title: mammalian distributions

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Abstract

Human impacts are increasingly recognized as drivers of biogeographic patterns, yet it remains unclear whether they surpass climate in shaping species distributions. Here we aim to investigate the relative importance of anthropogenic vs. climatic factors in determining mammalian distributions. We modeled the relationship between the geographic distributions of 331 mammal species and 12 representative anthropogenic and climatic factors, and quantified variable importance with ecological niche models and explainable artificial intelligence in both environmental and geographic space. We also constructed the response curve of human impact index (HII) for each species, and investigated the association between the response curves and species' biological traits. We found that anthropogenic factors were ranked as top contributors for nearly half of the species examined, and the effect of human impact index has exceeded that of average and seasonal climatic conditions across spatial scales. While limiting effects of anthropogenic factors were consistent across the landscape, the climatic factors often show spatial clusters at different sub-sections of species' ranges. Species' response to human impacts displayed diverse patterns, and the positive responses were associated with traits of reduced conflicts with humans, faster reproduction, and greater mobility. The extent of human impacts has exceeded that of climate in shaping mammalian biogeography patterns. The heterogeneous responses of mammal species to human impacts highlight the need to broadly consider anthropogenic factors, in addition to climate, in studying biodiversity in the Anthropocene.

Introduction

Understanding the factors that shape species' geographic distributions is a central goal in ecology and biogeography (Lomolino *et al.* 2010; Relyea & Ricklefs 2013). Traditionally, large-scale distribution and biodiversity patterns have been attributed primarily to abiotic environmental gradients, especially climate, which forms the foundation of many biogeographic theories (Andrewartha & Birch 1954; MacArthur 1984). However, this climate-centric view increasingly fails to capture the full reality of biodiversity dynamics in the Anthropocene, where human influence is both widespread and intensifying (Feng *et al.* 2024; Frans & Liu 2024; Helmus *et al.* 2014).

Human impacts are increasingly acknowledged as important drivers of species distributions (Burton *et al.* 2024; Kays *et al.* 2024; Suraci *et al.* 2021). For instance, the global human footprint has been shown to profoundly influence both native (Kays *et al.* 2024; Suraci *et al.* 2021) and invasive (Andrewartha & Birch 1954; MacArthur 1984) terrestrial mammal distributions. Higher road density is linked to reduced dispersal and increased habitat fragmentation, which restricts species ranges (Bennett 2017; Forman *et al.* 2003). Agricultural expansion negatively affects many mammals via habitat loss, although opportunistic species may benefit from new food resources (Gallego-Zamorano *et al.* 2020). Also, nighttime light and higher human population densities can disrupt mammal activity patterns (Gaynor *et al.* 2018).

There is no doubt that anthropogenic factors profoundly alter biogeographic patterns, but do their effects surpass those of climate? This distinction is critical for theoretical and practical reasons, as natural environmental factors, especially climate, are considered the major driver in many biogeographic, ecological, and evolutionary theories (Andrewartha & Birch 1954; MacArthur 1984), and many biodiversity conservation strategies are centered on climate change and less on the direct impact of humans (Caro *et al.* 2022; Chapman *et al.* 2014). If anthropogenic factors are comparable to or exceed climate in influencing species distributions, then we will face a new norm of thinking that anthropogenic and climatic factors shall always be considered together in ecological and biogeographic research and biodiversity conservation (Feng *et al.* 2024).

While an increasing number of studies recognized the importance of anthropogenic factors, direct comparisons with climate remain rare. Gallardo et al. found human-related variables (e.g., distance to ports) to be the primary drivers for range expansion of ~17–25% of nonnative species (Gallardo *et al.* 2015; Gallardo & Aldridge 2013). In contrast, Kays et al. found human population density to be less important than climate in predicting native mammal abundance (Kays *et al.* 2024). Moreover, previous investigations often report only range-wide variable importance and overlook its spatial variation, even though spatially explicit information (e.g., variable importance for a given location) is critical for guiding conservation actions at local and regional scales (Franklin *et al.* 2014; Waldock *et al.* 2024). Hence, a comprehensive, quantitative assessment comparing anthropogenic and climatic drivers across different spatial scales is critical and currently lacking.

To fill this gap, we performed a systematic modeling experiment to investigate the effects of anthropogenic and climatic factors in determining the geographic distributions of 331 mammal species across North America. The study area is enriched with wide coverage of species distribution and environmental data, comprising gradients of anthropogenic and climatic conditions. We included six anthropogenic factors to represent different types of human effects (Feng *et al.* 2024), and included six climatic factors to represent mean and seasonal climatic conditions that are widely recognized for their effects in determining species' geographic distributions (Lomolino *et al.* 2010) (Table S2). We also leveraged the technique of explainable artificial intelligence (xAI) (Barredo Arrieta *et al.* 2020) to map the spatially explicit influence of both anthropogenic and climatic factors on species distributions. We further quantified the variation of species' responses to HII, a synthetic variable that stood out as the top contributing anthropogenic factor, and investigated their associations with a set of biological traits. We hypothesized that i) anthropogenic factors have exceeded the importance of climate in shaping contemporary mammalian distributions across spatial scales, and ii) the associations between species distribution and anthropogenic factors are related to species traits.

Material and methods

Occurrence data

Our study focused on mammal species whose geographic ranges are mainly (> 70%) in North America, where large amounts of species observational records have been collected (Feng *et al.* 2022; Hughes *et al.* 2021). We used this criterion (see *Supplementary Methods*) to identify species that have abundant observation data across their ranges, thus to make more robust inferences on the relationship between species distribution and climatic or anthropogenic factors. We downloaded the presence records of these species from the Global Biodiversity Information Facility (GBIF) database (GBIF.org 2023). We filtered the presence records based on the basis of records and only kept records coded as preserved specimen, human observation, occurrence, material citation, machine observation, and material sample (see the treatment and sensitivity analysis of sampling bias below). We retained the presence records that were collected between 1990 and 2020 to represent the more recent distribution of the focal species; this temporal extent was also aligned with that of the environmental variables to be used in the ecological niche model (Feng *et al.* 2019b). We excluded the presences that were outside of slightly enlarged IUCN range maps (buffered by 1/10 of the radius of a range map assuming its circular shape) to avoid potential vagrant records. The buffered IUCN range was subsequently used as the modeling domain for each species. We applied spatial thinning to the occurrence data and only kept one occurrence in each 10 km grid to minimize the impact of sampling bias (Boria *et al.* 2014). We further excluded species with less than 10 spatially unique presence records to ensure a baseline of model performance (Papeş & Gaubert 2007). We also excluded species that have relatively low model evaluation metrics. Following the criteria discussed above, we retained a list of 331 species (Table S1, Fig. S1) for investigating the influence of climatic and anthropogenic factors on their distributions.

Bioclimatic and anthropogenic factors

For the ecological models, we selected six out of 19 bioclimatic variables that are commonly used in ecological niche modeling literature, and selected 6 out of 25 representative anthropogenic factors that may potentially affect species' geographic distributions compiled in (Feng *et al.* 2024). The six bioclimatic factors were annual mean temperature (Annual mean T), annual precipitation (Annual P), mean temperature of warmest/coldest quarter (Maximum/Minimum T), and precipitation of wettest/driest quarter (Wettest/Driest P) (Table S2). These variables represent the mean and seasonal climatic conditions that are widely recognized for their effects in determining species' geographic distributions (Lomolino *et al.*

2010). We calculated these bioclimatic variables based on monthly climatic data between 1990-2020 at 1 km resolution from AdaptWest database (AdaptWest Project 2022).

The six representative anthropogenic factors were human impact index (HII), highway density, cropland percentage (Cropland), pasture percentage (Pasture), nighttime lights, and human population (Table S2). We also avoided high correlation [correlation coefficient $|r| < 0.7$, Fig. S2; (Dormann *et al.* 2013; Feng *et al.* 2019a)] among them and better matching their temporal extents (2010-2018) to those of species' occurrence and climatic data. These variables have been found to influence mammalian distributions from regional to global scales (Burton *et al.* 2024; Cheeseman *et al.* 2024; Guarnieri *et al.* 2024; Tucker *et al.* 2021). Please see more detailed justifications of each variable in *Supplementary Methods*. The selected variables encompassed a wide spectrum of human impacts, allowing a more comprehensive comparison of human impacts against those of climate in shaping present mammalian distributions across North America. All environmental layers were aligned with North America at 1 km spatial resolution.

Modeling

We performed ecological niche models using the Maxent algorithm (version 3.4.3). Maxent effectively handles presence-background data and has demonstrated consistently high accuracy in modeling a variety of species distributions (Elith *et al.* 2006; Phillips & Dudík 2008). We included linear and quadratic features to avoid overly complex response functions to ensure ecologically relevant interpretation of the relationship between species' geographic distribution and environmental predictors (Merow *et al.* 2013). The default regularization parameters of Maxent were used. To account for sampling bias that may occur in the occurrence data (e.g., research-grade data from iNaturalist that are part of the GBIF download), we generated target group background data with the same underlying bias as the occurrence data for each species (Phillips *et al.* 2009). The selection of 10,000 target group background points was weighted by the sampling bias surface of occurrences obtained through kernel density estimation (Fitzpatrick *et al.* 2013). The sampling bias surface was restricted within the modeling domain (i.e., buffered IUCN range) for each species. To assess model performance, we randomly partitioned occurrence data of each species into training (95%) and test (5%) datasets, and evaluated model performance using the area under the receiver operating characteristic curve (AUC) and continuous Boyce index (CBI). The evaluation was repeated 20 times (see more details in *Supplementary Methods*).

Besides using target group background data, we performed an additional sensitivity analysis to evaluate the impact of potential sampling bias in the model outcomes; we repeated the modeling experiment by excluding all human observations (mostly data from iNaturalist) and obtained largely consistent results (Figs. S3 & S10).

We used permutation importance of each variable to represent its contribution to the ecological niche model. The permutation importance of a variable is the amount of decrease in training AUC when the values of a focal variable were permuted. Larger values of permutation importance indicate greater variable importance in modeling the relationship between species' distribution and environmental conditions. The permutation importance is typically normalized to percentages, running from 0 to 100% (Phillips 2005). Here we used permutation importance to compare the relative contribution of anthropogenic factors versus bioclimatic factors. The influence of collinearity on the permutation importance was expected to be minimal, as the predictors included were not highly correlated (Strobl *et al.* 2007) (Fig. S2). In addition, we also calculated the rank of variable contribution, ranging from 1, meaning most important, to 12, meaning least important.

We performed two additional experiments to evaluate the robustness of the modeling results toward the choice of modeling algorithm (using boosted regression tree, or BRT) and variable collinearity (principal component analysis of climatic variables). Please see more details in *Supplementary Methods*.

Response to human impacts in environmental and geographic space

In our preliminary analysis, HII stood out to be highly important for most mammal species. Therefore, we further investigated the response curve of HII for each species. The response curve represents the predicted relative probability of presence of a species given a gradient of an environmental variable, which is HII in this case. To compare the response curve of all species, the response curve was projected to the range of HII values available in North America. Each response curve was evenly separated into ~500 segments. The slope of each segment and increment/decrement along the y-axis were both recorded and summed over all segments. We used the summed slope along the response curve to determine the overall trend of species response to human impacts. A higher summer slope represents an overall higher probability of presence under higher HII. Based on the summed slopes, we classified the species into four groups (Q1, Q2, Q3, Q4) based on the 25th, 50th, and 75th quartiles of all the values. A monotonically decreasing/increasing response curve will likely fall in Q1/Q4. Flat or parabola-shaped curves will likely fall in Q2 and Q3.

We also generated SHapley Additive exPlanations (SHAP) (Lundberg & Lee 2017; Shapley 1953) maps to show species' response to environmental factors across the geographic space. SHAP is one of the explainable artificial intelligence (xAI) tools that provides an interpretation of the covariate effect on the predicted outcome at the observation level (here, a grid cell). A SHAP value indicates the difference between what a variable contributes to a prediction in each location, and what the variable is expected to contribute given the mean model prediction. Compared with permutation importance, a SHAP value represents a predictor's contribution to the prediction for that specific grid cell, i.e., the location-specific effect of each predictor (Waldock *et al.* 2024). A SHAP value of 0 suggests no contribution, while a deviation from 0 indicates a larger positive or negative contribution. We calculated SHAP values for each of the 12 variables used in the main modeling experiment across the modeling domain of a focal species using the R package 'itsdm' with 100 times of simulations (Song & Estes 2023). To understand the most important factor for species presence at each location, we identified the variable with the highest absolute SHAP values (among 12 variables) for each pixel in the modeling domain given a focal species. In other words, this step identified pixel-specific dominating variables for a focal species. The SHAP results for 8 exemplary species (two species for each of the four-quartile groups) were shown in Fig. 4.

Traits data

To further investigate whether species' response to HII was affected by their biological traits, we compiled a set of mammal traits from the COMBINE database (Soria *et al.* 2021). Overall, we selected the trait data that are known to be strong predictors of mammals' response to human impacts and that are available for the 331 species (Table S3). We avoided trait variables that were highly correlated. The 15 selected traits include: 1) body mass, 2) female sexual maturity, 3) gestation length, 4) litter size, 5) number of litters, 6) weaning age, 7) generation length, 8) hibernation or torpor, 9) diet breadth, 10) habitat breadth, 11) trophic level, 12) foraging strata, 13) fossoriality, 14) activity cycle, and 15) volant capacity. Please see more detailed justifications of the selected traits in *Supplementary Methods*.

Statistical analyses

We conducted linear regressions using ordinary least squares (OLS) to investigate the relationship between species' responses to HII and species traits. We used the cumulative sum of the relative probability of presence along the response curve of HII as the response variable and 15 biological traits (6 categorical and 9 numerical) as candidate predictors (Table S3). The adult body mass was log transformed to minimize the difference between extreme large and small values. All the numerical variables were scaled to have a mean of zero and standard deviation of one for easier comparison among their corresponding regression coefficients derived from the OLS models. With all species (331), we performed a stepwise model selection based on the Akaike information criterion (AIC) to obtain the models with the lowest AIC. In addition, we built stepwise models using OLS for each mammal order to investigate potential differences among their responses to HII; in this case, a predictor would be excluded from a model if all species in that order have the same values for the variable (i.e., no variation present among species).

Results

Anthropogenic vs. climatic factors

The test AUC values of the ecological niche models were 0.76 ± 0.07, and test CBI values were 0.76 ± 0.18, suggesting good model performance. Overall, HII and seasonal climate (mean temperature of the coldest and warmest quarter, or Minimum/Maximum T) stood out to be the top three contributing predictors among all predictors; the mean permutation importance was 27.9 (sd = 23.3), 12.6 (sd = 14.0), and 11.3 (sd = 12.6) for HII, Minimum T, and Maximum T, respectively (Fig. 1). Similar patterns were also found in the modeling results by using non-human observations, BRT, or PCA (Figs. S10-S12). The permutation importance of HII was significantly greater than that of Minimum/Maximum T across all species (Fig. 1A, Wilcoxon signed-rank test, $p < 0.001$). This significant difference in variable importance between HII and Minimum/Maximum T was consistent among Artiodactyla, Carnivora, Chiroptera, and Rodentia orders (Fig. S6A). Likewise, the rank of variable importance between HII and Minimum/Maximum T was significantly different across all species (Fig. 1B, Wilcoxon signed-rank test, $p < 0.001$) and Carnivora, Chiroptera, and Rodentia orders (Fig. S6B).

Anthropogenic factors were ranked as the top contributor for 47.4% ($n = 157$) of the cases considered (Fig. 2). The percentage varied between 42.4% and 58.9% (Figs. S3-S5) in the sensitivity analyses when human observations were excluded, using a different algorithm, or when raw climatic factors were replaced with principal components. In particular, HII stood out as the top contributor for 36.5% of the species considered (Fig. 2A). This pattern was more pronounced for Artiodactyla (66.7%; *n* = 6), Chiroptera (58.5%; *n* = 19), Carnivora (57.9%; *n* = 10), and Didelphimorphia (50.0%; *n* = 1), than for Rodentia (46.9%; *n* = 73), Lagomorpha (44.4%; *n* = 8), and Soricomorpha (27.3%; *n* = 9).

Following HII and seasonal climate, the highly influencing variables were percentages of Cropland and Pasture among anthropogenic factors and annual mean temperature (Annual mean T) and annual precipitation (Annual P) among climatic factors. In such cases, Cropland was ranked as the top contributing variable for 18 species, and Pasture for 12 species; these species were mainly in Rodentia, Chiroptera, and Carnivora orders. Annual mean T and Annual P were ranked as top contributing variables for 62 species.

The significant difference was also found between the permutation importance, as well as the rank of importance, of HII and Annual mean T and between HII and Annual P (Fig. 1A, Wilcoxon signed-rank test, $p < 0.001$), and this pattern was consistent among Artiodactyla, Carnivora, Chiroptera, and Rodentia orders (Figs. S8-S9).

Effects of anthropogenic factors

We classified the species into four groups (Q1, Q2, Q3, and Q4) based on their response curves along HII (Fig. 3). The greatest percentage of Q4 (51.2%) was found for Chiroptera order, suggesting a stronger positive association between their geographic distributions and HII. The greatest portion of Q1 was found for Soricomorpha (36.4%) and the largest number of Q1 was from Rodentia (*n* = 59), indicating more negative associations between their distribution and HII.

Despite the species showing dramatic responses to HII in Q4 and Q1, we also identified a large number of species that showed a unimodal response curve (mainly in Q2 to Q3), and a smaller number of species (mainly in Q2) showing nearly flat response curves (Fig. 4).

The dominating role of HII was also evident from the SHAP maps. HII accounted for the largest number of pixels across the modeling domains of the focal species regardless of the quartile groups they were from (Fig. 4). Compared with the widespread dominating effect of HII, the other variables showed spatial clusters at regional scales. The pixels where cropland was the dominating factor [for bobcat (*Lynx rufus)*, little brown bat (*Myotis lucifugus*), and gray fox (*Urocyon cinereoargenteus*)] were concentrated in the upper Midwest and Great Plains of the United States. In contrast, the areas dominated by temperature occurred in the northern and southern edges of species' ranges (Fig. 4). Despite the pronounced patterns, we also found that limiting factors varied spatially across a species' range, with geographic distributions often constrained by a combination of anthropogenic and climatic factors rather than by a single factor. (Fig. 4).

Biological traits and species response to HII

We found three biological traits significantly related to species' response (summed slope of response curve) to HII when considering all species together (Fig. 5). Among the three traits, the two numerical traits were adult mass and gestation length, and the ordinal trait was volant capacity. Adult mass had significant positive effects when considering most mammal orders, except for the significant negative effect for Carnivora.

Among the six traits of growth and reproduction strategies, gestation length had significant negative effects for Rodentia and when considering all species together. For order Rodentia, gestation length had a significant negative effect, and weaning age together with litters per year had significant positive effects. For Chiroptera, weaning age also showed a significant positive effect.

The effects of habitat breadth were positive and significant only for order Soricomorpha. Diet breadth had a significant negative effect for the order Rodentia. When looking at trophic levels, omnivory had a significant positive effect compared with herbivory for the order Lagomorpha, while the effect of carnivory was significantly positive for Soricomorpha.

When assessing species' activities vertically, volant terrestrial mammals showed positive association with HII compared with non-volant species. For the volant mammals (e.g., Chiroptera), ground and arboreal foraging showed significantly negative effects compared to aerial foraging. Above-ground dwelling had a significant negative effect for Soricomorpha, compared with ground dwelling. When assessing species' activities temporally, mixed activity patterns (nocturnal/crepuscular/diurnal) showed positive effects, compared with nocturnal-only for Carnivora.

Discussion

Anthropogenic vs. climatic factors

We performed a systematic modeling experiment to investigate the effects of anthropogenic and climatic factors in determining the geographic distributions of 331 mammal species across North

America. We found that anthropogenic factors exceeded climatic factors in shaping the contemporary distributions for these mammal species. The mean effect of anthropogenic factors, especially HII, has exceeded that of both average and seasonal climatic conditions (Fig. 1). Anthropogenic factors were ranked as top contributors for the geographic distribution of nearly half of the North American mammals. These patterns are robust to the choice of occurrence data, modeling algorithm, and predictor collinearity. The dominating role of HII was also evident from pixel-wise analysis of limiting factors based on SHAP values.

The importance of human impacts has been recognized in influencing the historical and contemporary distributions of mammals (Pacifici *et al.* 2020; Pineda-Munoz *et al.* 2021). Our findings suggest the human impacts have exceeded that of climate. Our conclusion was different from (Kays *et al.* 2024); despite the differences in the methodology, the different conclusions could lie in the use of human predictors. We have considered more human predictors in our study, including a synthetic index that incorporates multiple dimensions of human impacts. Also, the camera trap data used in (Kays *et al.* 2024) might be slightly biased toward more natural areas, as the goal of camera traps is usually to observe wildlife in natural settings (Suraci *et al.* 2021).

HII was found to be the most determinant factor among the anthropogenic factors assessed. HII is a synthetic index that represents multiple dimensions of human impacts. Areas with high HII could either represent a high value of individual human effects or a high combined sum, though potentially masking the importance of these individual predictors. Nevertheless, given the synthetic nature of HII and its importance found here, HII can potentially be used broadly in studying global change biology under human impacts, especially when the underlying human-related drivers on biological responses are unknown.

The dominant effects of anthropogenic factors support the claim that they should be treated as additional dimensions of the ecological niche "hypervolume" (Feng *et al.* 2024). Besides the ones analyzed here, many other anthropogenic variables are available at broad spatial and temporal extents (Feng *et al.* 2024; Frans & Liu 2024), which makes them easily usable in biogeographic and ecological studies, biodiversity conservation, and beyond. The challenge is these factors blur the classic abiotic–biotic distinction: human-generated conditions (e.g., heat islands, pollution, noise, and light) resemble abiotic factors, while human-provided resources (e.g., food, water) function as biotic subsidies. Thus, additional theoretical guidelines are needed.

The multifaceted responses to human impacts

Species' response curves to HII displayed diverse patterns with monotonic increases or decreases, parabolic shapes, or flat trends (Figs. 3-4). Our findings of the positive and negative associations between species distribution and human impacts are comparable to the scenarios of range expansions and contractions in terrestrial mammals since the 1970s (Pacifici *et al.* 2020). Given the projected increase of human impacts (Steffen *et al.* 2015), we may expect that there will not be uniform impacts on species distributions, but rather homogenization of fauna and decreased beta diversity in the future. The homogenization of biodiversity was known to be caused by the spread of non-native species (Aulus-Giacosa *et al.* 2024; Capinha *et al.* 2015); our study suggested that the homogenization of biodiversity could happen within the native fauna, by increasing the geographic distribution of species that are positively associated with human impacts and decreasing the ones that are not.

We also found more monotonic increases to human impacts than monotonic decreases (Fig. 4). One possible explanation is that the species assessed here were the "survivors" of historical impacts (Pineda-Munoz *et al.* 2021) (e.g., the megafauna extinction (Sandom *et al.* 2014)); thus, the species distribution data (between 1990 and 2020) and patterns could be the results of human impacts (Pineda-Munoz *et al.* 2021). Similarly, Finn et al. found the highest number of mammal species with increasing populations in North America and relatively fewer species with decreasing populations, despite more "losers" than "winners" at global scale (Finn *et al.* 2023).

Compared with monotonic increases or decreases, we found a high proportion of parabolic-shaped response curves to HII, suggesting many species could coexist with human pressure to a certain extent (Larson *et al.* 2020). However, the built environment in urban centers (e.g., parking lots) could be non-habitable for many species, and wild animals can suffer great human disturbance and mortality risk, e.g., because of noise and traffic (Soga & Gaston 2020; Suraci *et al.* 2021).

Biological traits and species' response to human impacts

We found that species more positively associated with human impacts shared traits of larger body mass (except for Carnivora), shorter gestation length, and flying capacity. These traits could potentially reduce the conflicts with humans, reflect faster reproduction, and enhance mobility to explore new habitats and avoid disturbances.

Body mass is a broadly recognized biological trait that is related to many other biological traits and macroecology patterns (Smith & Lyons 2011). Similarly, we found body mass to be a significant predictor for the response of species' geographic distribution to human impact. Interestingly, a smaller adult mass was selected for Carnivora, but a larger size for other mammal orders. Rodents grow larger as human population density increases, likely because of the increase in quality and abundance of rodent food sources (Pergams & Lawler 2009). Bats were found to have increased morphological traits, such as forearm length, a standard general index of body size in bats (Kunz 1974), as responses to Anthropogenic environmental change (Yue *et al.* 2019). In contrast, Carnivora are commonly predators that compete for food and space with humans (Treves & Karanth 2003). Such conflicts lead to higher extinction risk for large-bodied predators. Medium-sized carnivores, such as raccoons and skunks, adapt well to anthropogenically modified landscapes by exploiting food sources and shelters in urban environments, achieving high population densities (Bateman & Fleming 2012).

Omnivory provides flexibility for species' food resources, and here omnivory was found to be positively associated with the presence of North American lagomorphs under human impacts. Indeed, with the expansion of human population and settlement, humans have distributed anthropogenic foods (e.g., trash, livestock, and crop) worldwide (Oro *et al.* 2013), which have been broadly used by omnivorous mammals (Fedriani *et al.* 2001). Similar patterns have been found in China, where the proportion of omnivores increased with human presence and modification of the landscape (Li *et al.* 2022). Besides mammals, the proliferation of omnivorous species in human-modified landscapes was also found in birds (Cristaldi *et al.* 2017) and fish

(Neves *et al.* 2024). Despite the positive effect of omnivory, the use of anthropogenic foods can also be associated with high mortality rates in urban areas because of human-wildlife conflict or roadkill; thus, anthropogenic foods could become ecological traps (Grilo *et al.* 2020; Lamb *et al.* 2017). Interestingly, diet breadth was negatively associated with Rodentia. It is possible that, in urban areas, rodents such as rats have access to abundant resources, leading to a more homogeneous and specialized diet focused on high-quality, protein-rich animal sources (Guiry & Buckley 2018).

Shorter gestation length was found to be favored under human impacts. As opposed to slow development and fewer offspring, the strategy of faster reproduction has been selected for under human disturbance landscapes. This strategy is commonly associated with successful invaders that leverage opportunities to obtain propagule pressure to get established (Bielby *et al.* 2007; Sakai *et al.* 2001). Faster reproduction may help mammals to offset human-induced disturbances and mortalities (Santini *et al.* 2019; Suraci *et al.* 2021).

Volant capacity is also favored under human impacts. This is likely because non-volant mammals usually face increased mortality risks because of vehicle collisions, predation by domestic animals, or limited dispersal across anthropogenic matrices (de Andrade 2022; Corrêa *et al.* 2018). Volant capacity can enhance the mobility and dispersal of mammals, especially bats (Yalden & Morris 1975), and thus put volant mammals in an advantageous position under urban settings (Parkins & Clark 2015) or make them less or unaffected by urbanization (Richardson *et al.* 2021).

Humans have also profoundly changed the temporal activity of wild animals. Mammals are known to become more nocturnal in order to avoid humans (Gaynor *et al.* 2018). We found that carnivorous mammals with a wider temporal niche (mixed activity patterns) are more associated with higher human impacts. If species have a narrower temporal niche, it might result in increased intensity of competition and predation due to a larger overlap of temporal niches (Van Scoyoc *et al.* 2023). This may explain the negative effect between activity of nocturnal-only and species' response to human impacts found here.

The mixed responses to human impacts and their association with biological traits highlight new challenges of biodiversity conservation in the human-dominated era. Species may benefit from one factor (e.g., food subsidies) but be harmed by another (e.g., traffic). Understanding species' tolerance to multiple anthropogenic factors will help guide mitigation, regulation, and conservation priorities (Burton *et al.* 2024; Howard *et al.* 2020; Venter *et al.* 2016). Current conservation strategies focus heavily on climate change, but our findings highlight the need to also incorporate anthropogenic drivers such as urbanization, population growth, and pollution, which are increasingly available in future projections (Gao & O'Neill 2020; Li *et al.* 2021).

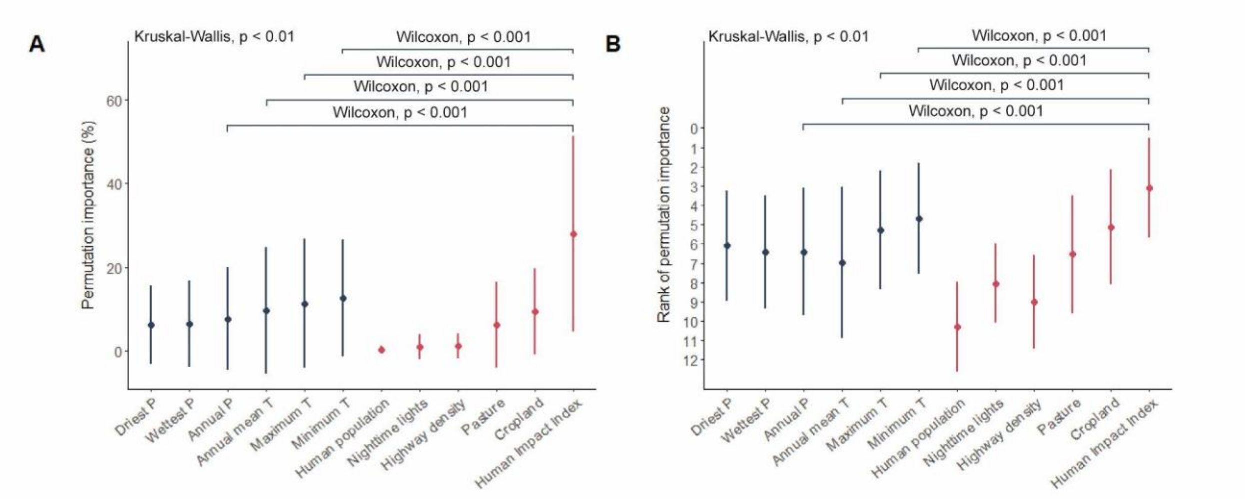

Fig. 1. Variable importance for each predictor. Panel A shows the variable importance, and panel B shows the rank of variable importance for each predictor variable. Climatic variables are colored as blue, and anthropogenic factors are colored as red. The error bars represent the one SD around the means. The differences in variable importance and rank of variables were found using the Kruskal-Wallis test. The pairwise differences were performed between human impact index and the top four climatic variables, using the Wilcoxon signed-rank test (Wilcoxon) with a Hommel (Hommel 1988) correction for multiple hypothesis testing. The p-values < 0.01 and < 0.001 indicated significant differences.

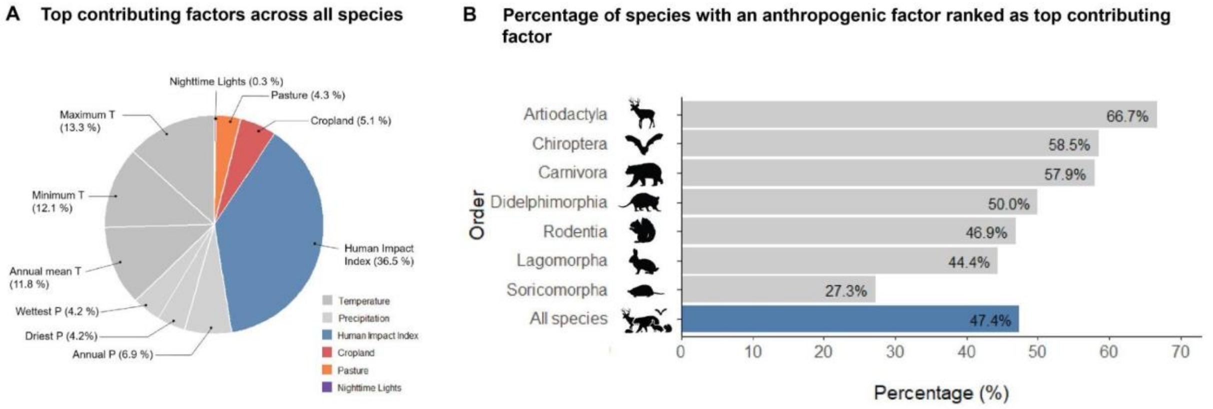

Fig. 2. Overview of top contributing factors. Panel A shows the percentage of top contributing factors across all North American mammals (*n* = 331). Panel B shows the percentage of species within each mammal order that has an anthropogenic factor ranked as the top contributing factor. The mammal icons were from phylopic.org (Public Domain).

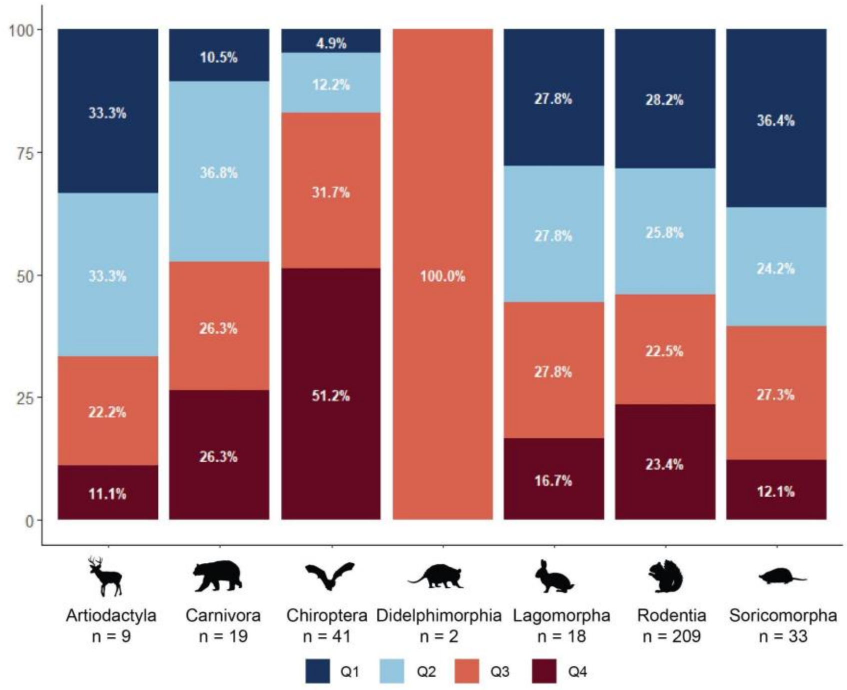

Fig. 3. Percentages of species that are categorized in four quartile groups (Q1-Q4) in each mammal order. The categorization of Q1-Q4 is based on the summed slope of the species response curve to human impact index (see Methods; Fig. 4). The mammal icons were obtained from phylopic.org (Public Domain).

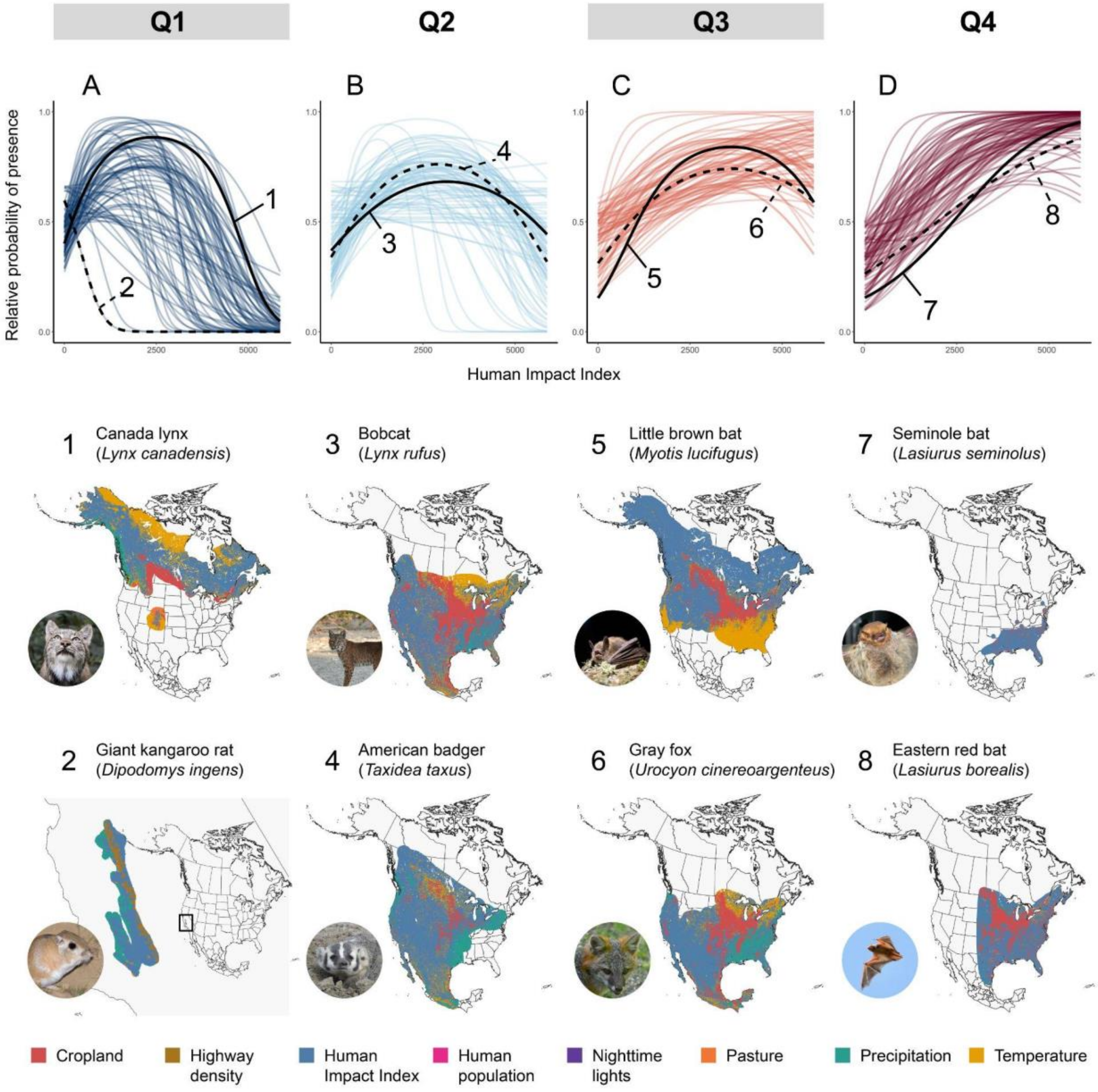

Fig. 4. Response curves of human impact index (HII) for each mammal species and maps of top limiting factors for eight species. Response curves of 331 species are categorized into four groups based on the quartiles of summed slopes: Q1 ≤ first quartile, first quartile < Q2 ≤ second quartile, second quartile < Q3 ≤ third quartile, and Q4 > third quartile. The x-axis of a response curve represents the magnitude of HII. For instance, a value of < 100 would represent the areas with little or no human impact (e.g., natural forests and wetlands), a value around 2500 would

indicate a medium level of human impact (e.g., suburbs of St. Louis, Vancouver, or Guadalajara), and values up to 5,000 would represent areas with high human impacts (e.g., metropolitan districts in New York City, Toronto, and Mexico City) (see Fig. S1). Two example species from each group, labelled as 1-8, are highlighted with solid or dashed lines: giant kangaroo rat (*Dipodomys ingens, Di)* and Canada lynx (*Lynx canadensis*, Lc) for Q1, Bobcat (*Lynx rufus*, Lr) and American badger (*Taxidea taxus*, Tt) for Q2, little brown bat (*Myotis lucifugus*, Ml) and gray fox (*Urocyon cinereoargenteus*, Uc) for Q3, and seminole bat (*Lasiurus seminolus*, Ls) and eastern red bat (*Lasiurus borealis*, Lb) for Q4. A map for each species is provided to show the top limiting factor for all locations (pixels) across its range. Photography source: iNaturalist. Credits to: U.S. Department of Agriculture (Ls), Aaron Marshall (Lb), Jason Headley (Ml), Craig K. Hunt (Uc), Brian Daniels (Lr), Ellyne Geurts (Tt), Stephen DeHart (Lc).

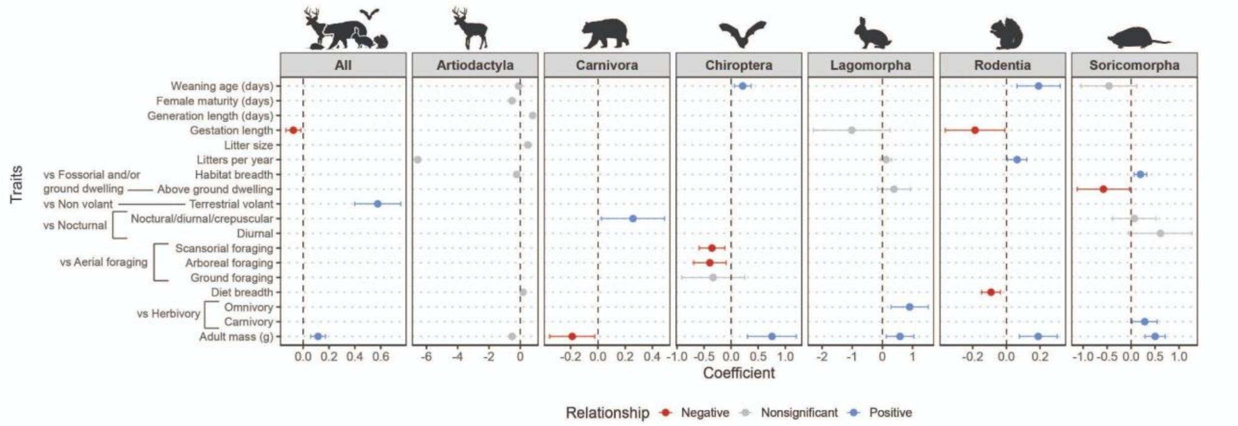

Fig. 5. Relationships between the responses to human impact index (HII) and mammal traits. The panels show the estimated coefficients of the linear regression for the stepwise-selected models based on AIC. The response variable is each species' cumulative responses to HII and the predictor variables are the biological traits of modeled species (see Methods). The models are performed for all species and different mammal orders. The control group of a factorial trait is labeled along the y-axis. The coefficients of the predictors are labeled as blue (significant positive), red (significant negative), and gray (nonsignificant). The mammal icons were from phylopic.org (Public Domain).

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