

# Anthropogenic and environmental drivers of modern range loss in large mammals

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**The extinction of a species is inevitably preceded by the extirpation of a series of local populations. Ecological theory predicts that vulnerability to extirpation varies between populations and is ultimately linked to environmental heterogeneity. If populations of a species are present in multiple regions separated by abrupt changes in environmental conditions (e.g., biomes), spatial variation in vulnerability to extirpation may be closely linked to the distribution of these regions. In the absence of abrupt shifts in environmental conditions, populations at the edge of a species' range should have low growth rates and be more vulnerable to extirpation, whereas populations located in the core of the species' range should be exposed to more favorable environmental conditions, have higher growth rates, and be less vulnerable. Here, we ask whether the distribution of biomes or range position better reflects spatial variation in vulnerability for 43 mammal species distributed through four continents. We control for the distribution of human threats and quantify the importance of protected areas in population persistence. We conclude that the distribution of biomes is a better predictor of vulnerability than position in the geographic range. We also find that core populations are less vulnerable than edge populations (after controlling for threats levels and protected areas). Protected areas are important for the persistence of most species we studied. By providing a measure of vulnerability linked directly to the distribution of threats, our results offer insights for scaling up from species vulnerability to extinction risk.**

The geographic ranges of many species are composed of multiple interacting local populations (1). Range loss occurs as local populations are progressively extirpated (2). Focusing on range loss, and the extirpation of these local populations, provides insight into the process of extinction, and can help inform conservation action and management. For example, studies of range collapse can draw attention to declining species before they reach levels requiring intensive interventions (2, 3) and this focus can uncover the drivers of range loss, providing important insights for management (3, 4). Even if a species is still globally common, studying range loss can also identify where ecosystems are losing local populations of a given species (5).

Although it is clear that various forms of human modification of the environment are the major extrinsic drivers of extirpations (2, 6), there is ongoing debate about the role that other factors, including intraspecific variation in vulnerability play in determining patterns of range loss. A number of authors have theorized that the spatial distribution of suitable environmental conditions (including biotic interactions; e.g., ref. 7) leads to variation in the size and demography of local populations and that this variation influences these populations' ability to tolerate anthropogenic disturbance (threats; refs. 6 and 8). Consider two populations of the same species with similar birth rates but different adult mortality and imagine that some pollutant that lowers birth rates is introduced into both populations. For some level of pollutant, the population with lower adult mortality should persist, whereas the population with higher adult mortality is extirpated. In other words, one population is more vulnerable. If vulnerability differs greatly between local populations, this underlying natural het-

erogeneity could have consequences for range-wide priority setting, reintroductions, and other forms of conservation planning and management (9, 10). For example, accounting for variation between populations in their vulnerability may help us to better evaluate species level extinction risk. Furthermore, if intraspecific variation in vulnerability is related to climatic variables, understanding these relationships may allow us to predict where local populations are capable of persisting and/or colonizing under predicted scenarios of climate change and land use change.

The range structure and dynamics that result from the interaction of individuals of a species and the distributions of relevant environmental conditions within a species' range are complex and difficult to understand without some degree of simplification (11). One way that ecologists have made sense of this complexity is through the concept of a species ecological niche. A species ecological niche can be defined as the set of conditions under which a species has a growth rate greater or equal to zero (12). The growth rates of many species are influenced by interactions with humans (including interactions with environmental changes associated with humans such as land use change or hunting), and we argue that a species' response to interactions with humans should be thought of as a part of a species' niche. Although the growth rates of some species are increased by human actions, facilitating range expansion (e.g., ref. 13), we focus here on species that have been adversely affected and define the inability to tolerate interactions with humans as a species' vulnerability.

A species' niche also includes interactions between multiple environmental factors. For example, populations of a species might fail to grow under hot and dry conditions or cool and wet conditions, but have a positive growth rate at high temperatures under humid conditions. If we consider the ability to tolerate the consequences of human activities as an aspect of a species' niche, then we might expect similar interactions between the intensity of human activities and other aspects of the species' niche. For example, a species may be able to tolerate a given level of hunting in a wetter habitat, but have a negative growth rate for the same hunting intensity in an arid habitat. When a species persists throughout a large region and there is an abrupt shift in an important environmental condition within that region, we might expect populations on either side of the transition zone to vary substantially in their vulnerability. If dispersal links local populations across the transition zone, then natural selection favoring adaptations to the local environment in the more sparsely inhabited region may be inhibited, further magnifying the differences in demographic rates between the two populations (14).

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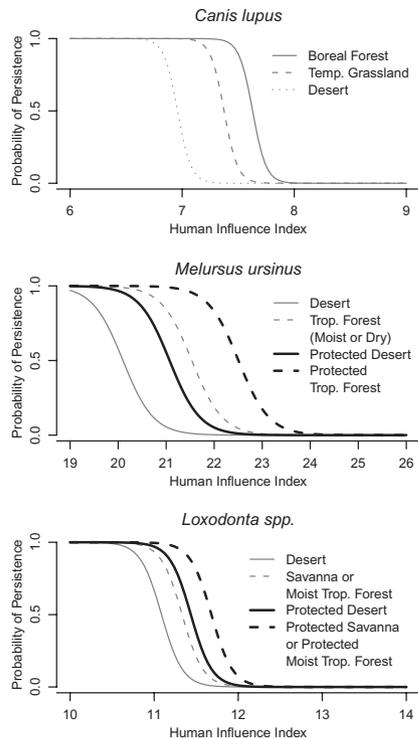


## Results

The distribution of biomes was a better proxy for vulnerability than the distance to the centroid of range. The distribution of 37 of the 43 species included in the analyses spanned more than one biome. For 26 of these 37 species, the biome model was a better fit to the data than the distance to centroid model based on deviance information criterion values (Fig. S1 and Tables S1 and S2). Species varied greatly in their mean vulnerability to human impacts and in the relative differences in vulnerability between biomes (Fig. 2); however, there were some consistent patterns across species. For example, temperate species (mostly North American) appeared to be less vulnerable in coniferous forest and more vulnerable in grasslands, with deciduous forests falling somewhere in the middle (Table S2). Tropical species (mostly African), on the other hand, were less vulnerable in savannah/grassland biomes, and more vulnerable in more arid desert regions and in wetter forests.

Contrary to the conclusions of previous studies, we found consistent and broad support for the prediction that edge populations are more vulnerable than core populations (Table S1). Based on 95% credible intervals, 27 of 43 species supported this hypothesis, and no species contradicted it. Using less conservative 50% credible intervals, 37 species supported this hypothesis and only 2 contradicted it. Support for the distance-to-centroid predictor was relatively constant across taxonomic orders and continents.

The hypotheses that greater human impacts decrease population persistence and that protected areas increase persistence were also supported. Both the protected areas variable (14 of 37 species) and the human influence index (18 of 37 species) were significant and had expected signs across a similar percentage of species in the biome model as in the distance-to-centroid model (Table S1 and S2). Our proxy for threats was significant in 60% of



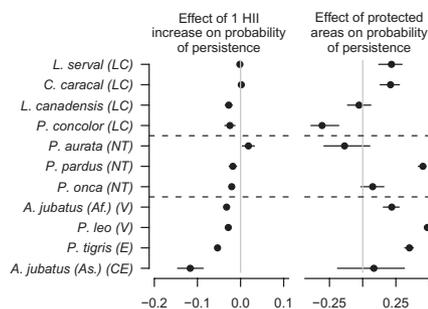
**Fig. 2.** The relationship between the human influence index and the predicted probability of persistence varies as a function of biome and protection status. Curves are for the same three species in Fig. 1 and represent the most common biomes in the species' historic ranges. Protected areas were not included for *Canis lupus* because they relationship with persistence was not significant in our models (Table S2).

species classified as threatened by the International Union for Conservation of Nature (IUCN; 9 of 15) as opposed to 38% of species that were not classified as threatened (10 of 28). Similarly, the presence of protected areas significantly increased persistence for 67% of threatened species (10 of 15) versus 46% of non-threatened species (13 of 28). For 68% of species (25 of 37), the impact of protected areas was greater than the difference in vulnerability between biomes (Table S2 and Fig. 2). As we consider progressively more threatened species in the most well represented family in our dataset, the family Felidae, the impact of protected areas becomes more positive and the effect of the human influence index on persistence generally decreases (Fig. 3).

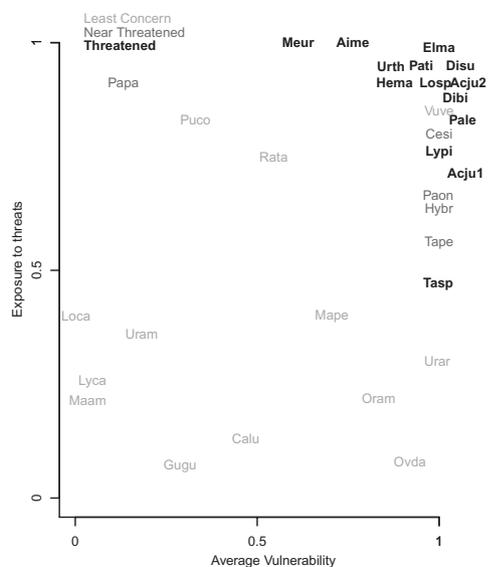
The focus of our study was intraspecific variation in vulnerability, but our results also offer insights about interspecific variation in extinction risk. Specifically, we can use our models to distinguish the roles that mean vulnerability (i.e., the predicted vulnerability of an average population outside a protected area subjected to a low intensity of human activities) and aggregate exposure to threats (i.e., proportion of range exposed to a low intensity of threats) play in determining the conservation status of a species (Fig. 4). This type of analyses allows us not only to explain current conservation status but also to predict which species are most likely to become more threatened as the extent of human influence (i.e., exposure to threats) increases within their range. For instance, *Panthera onca* (*Po*), *Hyaena brunnea* (*Hb*), and *Ursus arctos* (*Uar*) are currently listed as being of least concern or near threatened; however, they appear predisposed to significant range collapse if a greater portion of their ranges became exposed to higher levels of human modification.

## Discussion

We found broad support for the hypothesis that intraspecific variation in vulnerability has helped shape patterns of range loss during modern times. For those species for which we compared the biome and distance to centroid models, the biome model was favored in 27 of 37 species. The results from the biome model suggest some trends in the factors that determine vulnerability across large mammals. Among temperate species, vulnerability was highest in grasslands and lower in both deciduous and coniferous forests. Among tropical species, vulnerability was higher in deserts and moist forests. However, further study is required to determine whether these patterns apply to other continents (they are based mostly on North American and African species)



**Fig. 3.** Among the 11 cat species in our study the estimated effect sizes of increasing human impacts (predicted to be negative) and protected areas (predicted to be positive) were greater in species of greatest conservation concern. Codes in parentheses are abbreviations for their status (least concern, LC; near threatened, NT; vulnerable, V; endangered, E; critically endangered, CR), with the horizontal dashed lines showing the divisions between threatened, near threatened, and least concern species. Bars around estimates represent 2 SDs. Values were calculated as the change in the predicted probability of persistence based on the addition of either parks or a one unit increase in the human influence index to a range cell with a predicted probability of persistence of 50%.



**Fig. 4.** Conservation status of species is related to both their exposure to threats and their vulnerability (where vulnerability is defined as a species ability to tolerate human modification of their environment). For each species in this analysis, we defined a species' average vulnerability as the predicted probability of persistence based on the parameter estimates of each species in the distance to centroid model (Table S1) and following values for the covariates: human influence index equal to 5 (the human influence index ranges from 0 to 50, with most values between 4 and 20; a value of 5 corresponds to an untransformed area within 2–15 km of a road with a population density of 1 human per km<sup>2</sup>); distance to the centroid equal to half of the maximum distance; spatial random effects equal to 0 and outside of a protected area. Exposure to threats was defined as the percentage of the grid cells in the historic range where the median human influence is  $\leq 5$ . Letters indicate codes for species derived from the first two letters of their genus and species and their shade of gray indicates whether the species are least concern, near threatened or threatened according to the IUCN red list (69). Five of the species (Disu, Dibi, Acju2, Acju1, Pale) with vulnerability just barely below 1 were shifted over one for the purposes of clarity; however, all values were  $< 1$ .

and to a larger suite of species. We suspect that vulnerability in many species will be associated with habitat productivity within their ranges. Gaining a better understanding of these relationships and their generality across species is important for understanding past range loss and for predicting how ongoing climate change and concomitant shifts in the distribution and productivity of biomes may alter the future distribution of intraspecific variation in vulnerability.

In contrast to results from previous studies, we found strong support for greater vulnerability of edge populations relative to those located near the core of the range. Our analysis differed in three important ways from past studies that have found that edge populations are more likely to persist than core populations (6, 25). Unlike past studies, we controlled for threat levels, protected areas, and spatial autocorrelation, which should lead to more robust inference. On the other hand, we restricted our analysis to large mammals that tend to have large geographic ranges, whereas previous studies examined a more diverse sample of species. The choice to focus on large mammals was motivated by the belief that the human influence index would be a reasonable proxy for threats in these species, an assumption that is generally supported by our results. Our methods could be extended to other taxonomic groups as long as the appropriate threats can be identified and mapped. Lastly, we defined position in range based on the distance from centroid, whereas past studies divided a species range into two categories (core and edge) based on distance from the edge. We preferred our

measure because it is continuous; however, these two measures were highly correlated for all species we examined.

The degree to which persistence in grid cells responds to the environment (including changes in the intensity of anthropogenic threats) is a function of a species' niche, but is also contingent on patterns of dispersal and the resulting spatial population structure (32). We have represented vulnerability in the distance to centroid model as declining linearly, under the assumptions that growth rate is linked to environmental conditions and environmental conditions vary gradually. In the biome model, we assumed environmental conditions step up abruptly between biomes and result in an immediate change in growth rate. Clearly, neither of these caricatures is true, because heterogeneity in environmental conditions is more subtle and dispersal from neighboring areas also influences species demographic rates (31, 32). If the persistence of populations in the periphery of a species range is linked to metapopulation dynamics, the degree of range loss may vary depending on initial colonization and extinction rates and on the influence of anthropogenic on extinction rates, colonization rates, and habitat availability (11). Furthermore, if competition or predator–prey dynamics plays an important role in determining a species' historic range limit, changes in the regional demographic rates of strongly interacting species may lead to unexpected responses to local environmental change (including increasing anthropogenic influences; refs. 7 and 33). Although the complexities of spatial population structure and ecological interactions can hinder our ability to detect the impacts of environmental heterogeneity, threats, and protected areas on patterns of range loss, it should not introduce a systematic bias in our results.

Explicitly linking range loss and population loss is difficult. Defining a local population and determining its spatial extent is often arbitrary, even though populations play a central role in ecological theory (34–36). The difficulties in linking ranges and populations and defining the area of a population arise from the fact that populations are a theoretical construct, whereas ranges (and area) are empirical constructs (37). The link between range loss and population loss is only an approximation. In this study, we chose our grid cell size after considering average home range sizes and persistence in protected areas for large mammals (38, 39). We also wanted to avoid confusing individual mortality or migration away from areas of human conflict with population loss, so we further assumed that it was preferable to err on the side of overestimating the spatial extent of local populations. So although persistence in our grid cells is only approximately related to population loss, it is a defensible approximation.

Including protected areas and the human influence index in our models allowed us to control for coarse spatial variation in the distribution of threats. Both the human influence index and the presence of protected areas explained patterns of range collapse in species from four taxonomic orders across four continents. Both variables were more likely to be included in the models of species that are considered to be most threatened by the IUCN (Fig. 3). For many species, the effect of protection status was of a similar or greater magnitude than the differences between biomes in vulnerability (Fig. 2 and Table S2). It is reassuring that protected areas and the human influence index were significant in so many species given the complications introduced by spatial population structure (see above), range map limitations (40), and the coarseness of both proxies. Despite these robust patterns, two important caveats to our conclusions bear discussion. First, historical threats have played a role in determining current ranges. For example, *Puma concolor* was extirpated from many parts of eastern North America before the creation of protected areas in this region, and this may explain why this species has a negative coefficient for protected areas. Second, the human influence index combines the impacts of multiple factors (e.g., land use change, human population density, roads) that negatively impact large mammals. This index,

however, cannot control for variability between species in their relative vulnerability to different threats (e.g., one species might be more vulnerable to hunting than land use change, whereas another is more vulnerable to land use), nor can it account for nonlocal threats such as climate change.

We have attempted to link our study of range collapse and intraspecific variation in vulnerability to the well developed literature addressing interspecific variation in extinction risk. Our results suggest that an estimate of species-level average vulnerability, coupled with information on the extent of human impacts, can provide a reasonable prediction of a species extinction risk. Extended to a larger suite of species, this approach could complement current studies linking species traits (e.g., body size and space requirements) to their IUCN conservation status (e.g., refs. 41–44). In particular, such an analysis could help shed light on the degree to which variation between species in extinction risk is related to the distribution of threats versus differences in life history strategies, traits, or taxonomic affiliation (45). Furthermore, studying how these same traits diverge within species and how these patterns are related to intraspecific variation in vulnerability may offer unique insights into understanding how traits are causally linked to extinction risk. For example, intraspecific variation in home range size in some carnivore species is substantial (e.g., 80–1,800 km<sup>2</sup> in *Canis lupus*) and can be comparable to variation between species (46, 47). Studying intraspecific variation in vulnerability could also determine whether the required size of a protected area for species persistence varies at different locations within a species range, just as it varies between different species.

We conclude that intraspecific variation in vulnerability plays an important role in explaining patterns of range loss in large mammals. The degree of persistence at a given intensity of human modification varies between biomes and is greater in the core of a species range. Because multiple factors influence patterns of range loss, the importance of intraspecific variation in vulnerability must be understood in the context of the distribution of anthropogenic drivers of extirpation and intrinsic predictors of between species variation in extinction risk. Given the important biological differences between populations of large mammals in different biomes, the often unique roles these species play in ecosystems, the large uncertainties introduced by unstable governments and environmental variability, and the potential role of rapid evolution to ongoing environmental change, we suggest that effective and sustainable conservation strategies requires spreading efforts across the entirety of a species' range with the recognition that requirements for persistence may vary between different sites.

## Methods

The 43 mammal species included in this study were chosen based on two criteria: (i) availability of reasonably accurate historic and current maps (28, 48–61); (ii) range loss >20% of historical extent, but with current range not smaller than 25,000 km<sup>2</sup>. In other words, we chose mammals that have experienced range loss but still have substantive range remaining. Although we carefully examined historic and current maps, range maps often contain

errors (40), which may introduce noise, but should not have systematically biased our analyses. For most species, the historic range was one continuous polygon; however, for those species that had discontinuous historic ranges (multiple discrete polygons), we only included those natural populations (discrete polygons) in which there had been some but not total range loss. Removal of these polygons (typically small islands) was necessary for the spatial models to converge. Parameter estimates from nonspatial models with and without these islands were similar, so we are confident that the removal of these islands did not bias our results.

For each species, we divided the historic ranges into grids with 50 × 50-km cells and determined whether any part of the current range overlapped with each cell. Human activities were included in the models in two ways. The human influence index, which is based on human population densities and land-use change (62), was included as a metric of threats. We chose the human influence index over the human footprint because the former has a consistent interpretation across all biomes, whereas the latter was modified based on the minimum and maximum human influences within each biogeographical region and thus must be interpreted within the context of each biome. The distribution of protected areas, obtained from the world database of protected areas (63), was also included in the models because these management structures can be instrumental in population persistence (64). Although not a comprehensive metric of wildlife management structures, geographically explicit data for protected areas are readily available. At finer spatial resolutions it was clear that the current range data and the World Commission on Protected Areas data were misaligned, however this misalignment was greatly lessened once we resampled at the 50 × 50-km resolution. To determine whether vulnerability varied between biomes, we included biome as a random effect in our models. For the biome model we focused only on the 37 species with at least 15 cells (37,500 km<sup>2</sup>) of current range and 15 or more cells of lost range in two or more biomes. Biome type for each cell was derived from the Terrestrial Ecosystems of the World Database (15). To determine the effects of position in the range on extinction in all 43 species, we first determined the centroid of each polygon in the historic geographic range and then calculated the distance from the center of each grid cell to the centroid of the polygon that contained it. The response variable was the current occupancy state of each cell (i.e., whether a cell did or did not overlap with a portion of the current range), given the cells in the historic range of a species. We modeled error using a Gaussian conditional autoregressive hierarchical Bayesian model with binary errors (65, 66). Parameters were estimated using WinBugs 1.4.3 with weak or noninformative priors. We compared the distance to centroid and biome models using deviance information criterion (67, 68).

To account for spatial autocorrelation, the original 50 × 50-km cells were grouped into larger 100 × 100-km blocks, and random effects for each block were conditioned on the model predictions for neighboring blocks. One consequence of this hierarchical design is that blocks centered on the border of the current range, where some, but not all, cells were occupied, were distinguishable from blocks where all cells shared the same value (i.e., whether the whole block was part of the current range or absent from the current range). The effect of this structure is to focus more attention on patterns of range loss along edges of the current range. We chose the spatial scales of the cells and blocks based on accepted accuracies of our coarsest range maps, examination of residuals, and past analyses that determined how much area was needed for different species of carnivores to have a >50% probability of persistence (38, 39).

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