



Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals

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Although habitat fragmentation is often assumed to be a primary driver of extinction, global patterns of fragmentation and its relationship to extinction risk have not been consistently quantified for any major animal taxon. We developed high-resolution habitat fragmentation models and used phylogenetic comparative methods to quantify the effects of habitat fragmentation on the world's terrestrial mammals, including 4,018 species across 26 taxonomic Orders. Results demonstrate that species with more fragmentation are at greater risk of extinction, even after accounting for the effects of key macroecological predictors, such as body size and geographic range size. Species with higher fragmentation had smaller ranges and a lower proportion of high-suitability habitat within their range, and most high-suitability habitat occurred outside of protected areas, further elevating extinction risk. Our models provide a quantitative evaluation of extinction risk assessments for species, allow for identification of emerging threats in species not classified as threatened, and provide maps of global hotspots of fragmentation for the world's terrestrial mammals. Quantification of habitat fragmentation will help guide threat assessment and strategic priorities for global mammal conservation.

conservation | extinction risk | habitat fragmentation | mammals

The diversity of life on earth is jeopardized by human activities (1) and the world's mammals are at great risk; 27% of mammalian species globally are threatened with extinction and the loss and degradation of habitat has been implicated as a primary threat (2). An important form of habitat degradation is fragmentation, the reduction of continuous habitat into smaller, spatially distinct patches immersed within a dissimilar matrix (3, 4). Fragmented habitat can result from abiotic and biotic factors that generate natural patchiness in landscapes, as well as anthropogenic disturbances that have rapidly accelerated and intensified habitat fragmentation globally (3). Fragmentation can create detrimental edge effects along the boundaries of habitat patches, precipitate population decline, restrict animal movement and gene flow, and sever landscape connectivity (5). Habitat fragmentation also interacts with and intensifies the effects of other agents of global environmental change, including facilitating species invasions and limiting the ability of organisms to shift distributions in response to climate change (6, 7). Despite this potential threat, the effects of habitat fragmentation on global biodiversity and its importance relative to other anthropogenic stressors has been the subject of considerable debate (4, 8). The degree of habitat fragmentation for the world's mammals, however, and its relation to extinction risk, have not been quantified globally. Furthermore, no study has specifically identified the location of global hotspots of fragmentation for terrestrial mammals, or indeed any major animal taxon. Consequently, although fragmentation is commonly assumed to be a driver of global extinction risk, it has not been consistently incorporated into extinction risk assessments (9).

Here, we quantify and map global patterns of habitat fragmentation for the world's terrestrial mammals. We used high-resolution

habitat-suitability models developed for mammals (10), including 4,018 species across 26 taxonomic Orders. For each species we quantified the degree of fragmentation of high-suitability habitat (i.e., preferred habitat where the species can persist) by calculating the average Euclidean distance into "core" habitat from the nearest patch edge (11, 12). We then conducted phylogenetic comparative analyses to examine the relationship between habitat fragmentation and various species characteristics, including International Union for Conservation of Nature (IUCN) Red List status, geographic range size (hereafter "range size"), body mass, and the proportion of high-suitability habitat within the range. We then mapped hotspots of fragmentation for terrestrial mammals globally.

Results and Discussion

Our analyses reveal that terrestrial mammal species with higher degrees of habitat fragmentation within their ranges are at greater risk of extinction (Fig. 1). Species classified as threatened in the IUCN Red List had higher levels of fragmentation compared with species classified as Least Concern and Near Threatened (phylogenetic generalized linear model $\beta \pm SE = -0.16 \pm 0.05$, $z = -2.94$, $P = 0.003$) (Table S1, Upper, model 1). Importantly, degree of fragmentation improved prediction of extinction risk even after accounting for the effects of key macroecological extinction risk predictors such as body size ($\beta \pm SE = 0.42 \pm 0.03$, $z = 12.22$, $P < 0.001$) and range size ($\beta \pm SE = -0.66 \pm 0.03$, $z = -19.23$, $P < 0.001$) (Table S1, Upper, model 1). Mammals with more fragmented

Significance

Despite the critical threat of habitat fragmentation, global patterns of fragmentation and its relationship to extinction risk have not been quantified for any major taxon. We developed high-resolution models that provide a global assessment of the degree of habitat fragmentation impacting the world's terrestrial mammals. Results demonstrate that mammals with more fragmentation are at greater risk of extinction, even after accounting for the effects of key macroecological predictors, such as body size and geographic range size. Species with higher fragmentation had smaller ranges and a lower proportion of high-suitability habitat within their range, and most high-suitability habitat occurred outside of protected areas, further elevating extinction risk. Quantification of habitat fragmentation will help guide strategic priorities for global mammal conservation.

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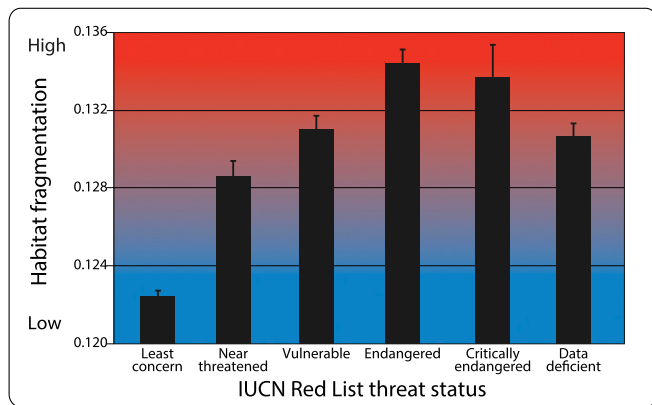


Fig. 1. Degree of habitat fragmentation predicts extinction risk for the world's terrestrial mammals. The fragmentation metric, measuring the amount of core (i.e., interior) habitat distributed within intact high-suitability patches, was ln-transformed and then inverse-coded so high values represent high degrees of fragmentation. Bars represent means and SE ($n = 4,018$ species). Extinction risk assessed by IUCN Red List threat status. Vulnerable, Endangered, and Critically Endangered species had higher levels of habitat fragmentation compared with Least Concern and Near Threatened species. Similarly, Near Threatened and Data Deficient species had higher levels of fragmentation than Least Concern species (see main text).

habitat, smaller ranges, and larger body sizes face the highest risk of extinction. The model including fragmentation along with body size and range size had the strongest empirical support from the data, with a model probability of 88% (Table S1, Upper, model 1). This top model was 7.4 times more likely than the next ranked model (Table S1, Upper, model 2), which excluded fragmentation [model probability = 12%; Δ AIC (Akaike's Information Criterion) = 4]. Furthermore, when assuming Near Threatened species face some extinction risk, a conservative and precautionary approach (13), the second-ranked model without fragmentation had very little empirical support (Table S1, Lower, model 2) (model probability < 0.001; Δ AIC = 15) and was 1,808 times less likely compared with the top model including fragmentation (Table S1, Lower, model 1) (model probability = 1.00).

Range size was the most important predictor of extinction risk, occurring in all top models (Table S1), consistent with prior findings identifying range size as a key extinction risk correlate (12, 14–16). Data from range size alone, however, can provide misleading information on conservation status, potentially misclassifying naturally narrow-ranging species as threatened and wide-ranging species as nonthreatened (17) and incorrectly assuming species to be homogeneously distributed throughout their range (10, 18). Our analyses indicated that fragmentation, consistently in the most supported models, had explanatory power beyond that provided by range size alone. Indeed, our models implicate habitat fragmentation as a potential mechanism underlying the well-known relationship between range size and extinction risk, empirically demonstrating that greater fragmentation in small-ranged species ($r = 0.43$, phylogenetic generalized least-squares $\beta \pm SE = 0.17 \pm 0.01$, $t_{4,018} = 34.44$, $P < 0.001$) (Table S2, model 1) contributes to elevated extinction risk (Fig. 2 and Fig. S1). Large-ranged species tend to be habitat generalists (19), whereas range-restricted species often have more narrow environmental niches and specialized habitat preferences, characteristics that increase extinction risk (20–22). Specifically, range-restricted specialists are particularly vulnerable to habitat fragmentation given discontinuous distributions, reduced local abundance, and sensitivities to anthropogenic disturbances (23, 24). Habitat fragmentation was not associated with body mass ($r = -0.02$, phylogenetic generalized least-squares $\beta \pm SE = -0.01 \pm 0.03$, $t_{4,018} = -0.40$, $P = 0.687$) (Table S2, model 4).

Predictably, species with more fragmented habitat had a lower proportion of high-suitability habitat within their range ($r = 0.77$, phylogenetic generalized least-squares $\beta \pm SE = 2.10 \pm 0.03$, $t_{4,018} = 77.07$, $P < 0.001$) and a lower proportion of high-suitability habitat within protected areas ($r = 0.16$, $\beta \pm SE = 1.46 \pm 0.20$, $t_{4,018} = 7.48$, $P < 0.001$), further elevating extinction risk. As sole predictors of extinction risk, the model with fragmentation ($\beta \pm SE = -0.89 \pm 0.06$, $z = -15.0$, $P < 0.001$; model probability = 1.00) had considerably more explanatory power (Δ AIC = 387) compared with the model with proportion of high-quality habitat ($\beta \pm SE = -0.69 \pm 0.12$, $z = -5.57$, $P < 0.001$; model probability < 0.001). These findings emphasize the utility of measuring not only the proportion of suitable habitat remaining within the range (reflecting habitat loss per se), but also evaluating how such remaining habitat is distributed within large, intact patches of core habitat, as assessed by our fragmentation metric.

Notably, the relationship between fragmentation and extinction risk remained evident ($\beta \pm SE = -0.59 \pm 0.08$, $z = -7.04$, $P < 0.001$) even after excluding threatened species that met IUCN Red List criterion B, used to list species that have restricted geographic ranges (13). Species listed under criterion B have severely fragmented ranges or exist in few locations (subcriteria B1a/B2a), or are undergoing continuing decline (B1b/B2b) or extreme fluctuations in population size or distribution (B1c/B2c) (13). Exclusion of criterion B species avoids potential circularity between our extinction risk modeling and the IUCN criteria adopted to classify extinction risk, thus providing stronger inference regarding the relationship between fragmentation and extinction risk (25–27). Even when excluding criterion B species, the most-supported models still included fragmentation and had the greatest weight of evidence from the data (Table S3, Upper and Lower, model 1), with the remaining models having little to no support.

Our quantitative measures of fragmentation also allowed evaluation of extinction risk assessments by IUCN experts to evaluate if a taxon belongs in a threatened category, in particular those assessed using subcriteria (B1a/B2a) relating to habitat fragmentation. As expected, threatened species classified under subcriteria B1a/B2a had significantly more fragmentation than threatened species that did not meet the B1a/B2a subcriteria (phylogenetic

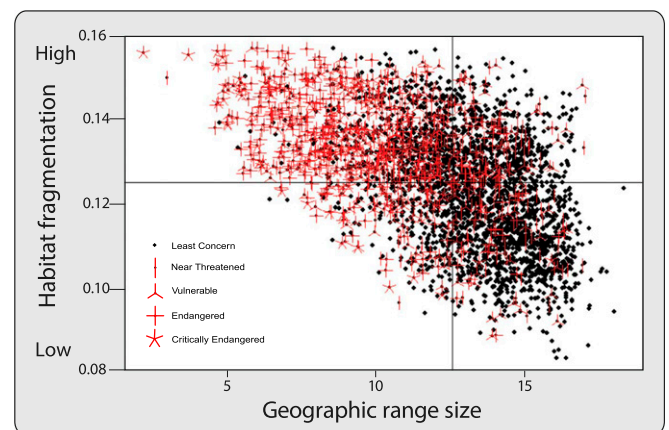


Fig. 2. Terrestrial mammals with higher degrees of habitat fragmentation and smaller geographic range sizes have a greater risk of extinction. Each black point represents an individual species, with the number of red line segments corresponding to extinction risk according to IUCN Red List threat status: Least Concern, Near Threatened, Vulnerable, Endangered, and Critically Endangered (see legend within figure). Visually, across the scatter plot of all points, more red represents higher extinction risk. Fragmentation and geographic range size (km^2) ln-transformed, and the fragmentation metric then inverse-coded so high values represent high degrees of fragmentation. Vertical and horizontal lines represent means (see also Fig. S1).

generalized linear model $\beta \pm SE = -1.00 \pm 0.13$, $z = -7.78$, $P < 0.001$). IUCN Red List assessments are based on expert opinion, which can rely on qualitative knowledge, especially for poorly known species. Consequently, assessments of habitat fragmentation for different species can suffer from limited consistency (9). Furthermore, subcriteria B1a/B2a do not distinguish between the two conditions of fragmentation and restricted number of locations. By quantifying fragmentation specifically, our models thus can improve threat assessment. For example, because of a lack of information regarding fragmentation, a recent attempt to use satellite imagery to consistently assess extinction risk of >11,000 forest-dependent species necessarily assumed that all species with small ranges and declining habitat were also subject to significant levels of fragmentation (9). Our fragmentation models can fill this important methodological gap, allowing more accurate satellite-derived classification of fragmentation and hence extinction risk using Red List criterion B.

Our models also reveal evidence for increased fragmentation in species not classified as threatened by the IUCN (Fig. 1). Specifically, species classified as Near Threatened (phylogenetic generalized linear model $\beta \pm SE = -0.46 \pm 0.08$, $z = -5.86$, $P < 0.001$) and Data Deficient ($\beta \pm SE = -0.76 \pm 0.07$, $z = -10.67$, $P < 0.001$) had more fragmented habitat than Least Concern species (Fig. 1). Although Data Deficient species have inadequate information to formally assess extinction risk (13), they tend to have smaller body and range sizes (17, 28), are nocturnal and thus difficult to study (28), and many are likely to be threatened (17). It is possible that the range size of many of these poorly known species is underestimated, and the degree of ecological specialization overestimated, because of limited available information (17), potentially inflating our measure of habitat fragmentation. More information regarding the distribution, life history, and ecology of Data Deficient species, including their habitat affinities and responses to human disturbances, will help refine our models. Nonetheless, available evidence suggests that both Near Threatened and Data Deficient species have increased fragmentation within their known ranges, indicating that the threat of fragmentation exists at the earliest and least-understood stages of endangerment. Our models quantifying fragmentation allow us to better identify such emerging threats.

Summing the fragmentation metric across all species reveals global patterns of core habitat and fragmentation for the world's terrestrial mammals (Fig. 3A). Primary areas of intact high-quality core habitat include northern Africa and much of the Amazon Basin in South America, and portions of western and central North America, sub-Saharan Africa, Australia, and northern, southwestern, and southeastern Asia. Of these areas, the Amazon Basin supports the greatest richness of terrestrial mammals, followed by sub-Saharan Africa and portions of western and central North America and southeastern Asia (Fig. S24). Standardizing the fragmentation models by species richness more strongly highlights species-poor locales (most notably desert regions of northern Africa and southwestern Asia) with extensive core habitat for the relatively few species that occur there (Fig. S2B). Terrestrial mammalian diversity, however, is sufficiently low in these regions that they are de-emphasized as core habitat in our global fragmentation models (Fig. 3).

Conversely, fragmentation hotspots are regions with relatively low interior distances within high-suitability habitat, summed across all species present in an area (Fig. 3A). Such regions include much of South America outside the Amazon Basin, as well as portions of south-central Asia, eastern North America, and Europe. Interestingly, our models identify notable fragmentation for high-latitude (e.g., arctic) and high-elevation (e.g., Himalayan) species (Fig. 3A). For the arctic, the models are primarily identifying natural fragmentation of suitable habitat because of ice, water bodies, coastlines, and islands at the edge of species ranges. Similarly, for high-elevations, the models are identifying patterns of natural fragmentation above the altitudinal limits of species. Weighting the global fragmentation map with a recently developed high-resolution,

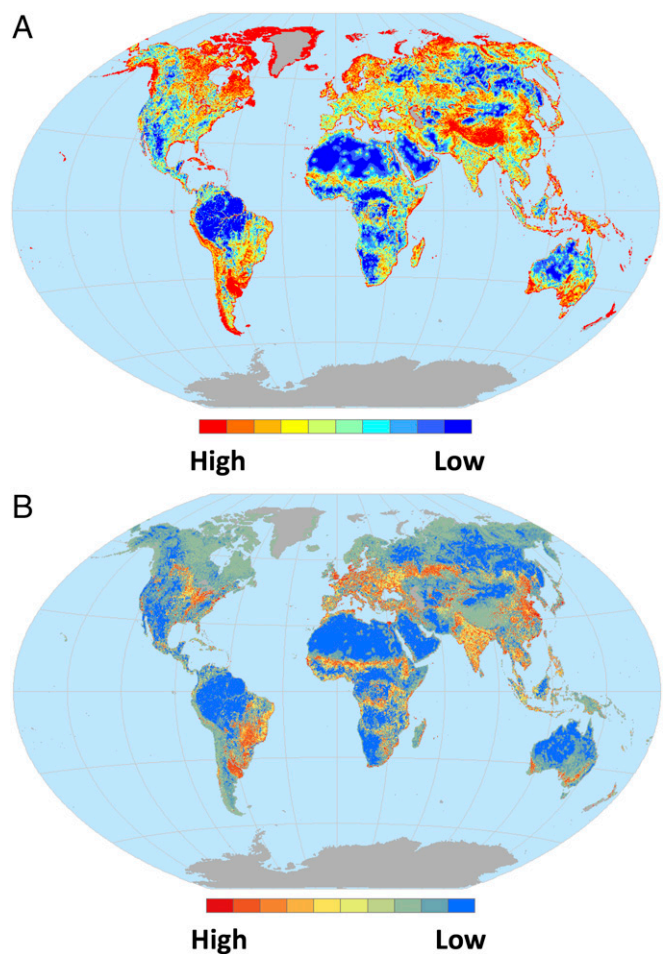


Fig. 3. Degree of habitat fragmentation for the world's terrestrial mammals. (A) Degree of habitat fragmentation as indexed by the fragmentation metric, measuring the amount of core (i.e., interior) habitat, and (B) degree of anthropogenic habitat fragmentation, calculated by weighting data in A by a recently developed global HM model (Fig. S3). The resulting map identifies regions that have been fragmented by human development specifically, and de-emphasizes regions that are naturally fragmented such as high-elevation areas and landscapes with water bodies interspersed. The color gradient in the legends are the original (A) and weighted (B) fragmentation values binned into deciles. Blue denotes regions with low fragmentation, where mammal species occur in large patches of intact high-suitability core habitat. Red denotes regions with high fragmentation, where mammal species have little core habitat. Fragmentation metrics are spatially quantified by summing the metric at each 300×300 -m cell for all terrestrial mammal species worldwide.

global human modification layer (29) highlights regions that have been fragmented by human development specifically and de-emphasizes regions with natural fragmentation, such as high-latitude and high-elevation areas (Fig. 3B and Fig. S3). We emphasize, however, that arctic and montane species, including high-altitude endemics, are particularly vulnerable to climate change (30, 31) and thus still impacted by natural fragmentation that might prevent distributional shifts in response to altered climate regimes.

On average, across the 4,018 species of terrestrial mammals included in our analyses, only 48.6% (range: <0.001–100%; SE = 0.004) of the current geographic range of a species was comprised of high-suitability habitat (10). Moreover, only 3.6% (range: 0–100%; SE = 0.001) of the average range was comprised of high-suitability habitat located within known protected areas, well below the approximately 15% of terrestrial areas that are currently protected globally (32), further emphasizing the inadequacy of the global network of protected areas (33). Of additional concern is that

habitat degradation is especially prevalent in many of the global hotspots of mammal habitat identified in our models, particularly tropical regions in the Americas, Africa, and Asia that experience high deforestation (2). For example, much of the tropical forest in the Amazon Basin, a critical global hotspot of core mammalian habitat, had experienced rapid deforestation from human development (34, 35), although it appears that such habitat destruction has slowed recently as a result of policy-driven government action (36).

Our models can inform the management and conservation of mammals globally. First, unlike most comparative extinction-risk analyses, we focus on an urgent yet manageable anthropogenic threat (i.e., habitat fragmentation) rather than solely on intrinsic biological traits (e.g., body mass), which addresses ongoing concerns about the utility of comparative analyses for applied conservation (15, 37). Second, our habitat models narrow the focus of mammal distribution to include only regions of high-suitability habitat; this is critical, because species are not homogeneously distributed throughout their ranges (18) and less than half of the range of terrestrial mammals is on average comprised of high-suitability habitat (10). Third, our fragmentation models not only evaluate global patterns of species richness based on suitable habitat (10), they also quantify the degree to which suitable habitat exists within core habitat patches. This is essential, given that hotspots of species richness and extinction threat may not overlap (38, 39), and our analyses demonstrate that the degree of fragmentation of patches influences extinction risk. Finally, the 300-m resolution of the global-habitat models facilitates more detailed analyses of fragmentation patterns at the local scale, which approaches the scale of conservation action (40). For example, our models can be used to identify the degree to which reserve networks designed for umbrella species, such as jaguars, maintain high-quality core habitat for sympatric mammals (41). Such real-world application of our fragmentation models demonstrates their utility for conservation practitioners, particularly in comparison with simple boundaries of the geographic range, which provide no information about the expected occurrence of species within their broad distributional extents.

Additional efforts to apply these models to local scales, and validating them with empirical data on fine-scale distribution and habitat use, such as that derived from GPS telemetry or remote camera surveys, will help to more thoroughly assess their utility for real-world conservation application. In addition, exploration of alternative fragmentation and connectivity metrics, including metrics that assess patch isolation and configuration (5, 12), would also yield further insight into how habitat fragmentation and landscape connectivity are related to extinction risk. More complex patch and landscape metrics might be particularly valuable at finer scales or for smaller subsets of species. Development of a comprehensive database estimating dispersal distances for mammal species, and incorporation of such data to assess how variability in species-specific dispersal ability influences scaling of patch sizes and responses to fragmentation effects, would represent another important advancement. Finally, given that anthropogenic fragmentation increases contact and potential conflict between humans and wildlife, human tolerance of and behavior toward wildlife are fundamental determinants of their ability to persist within fragmented landscapes; consequently, social science research will be critical to mitigate fragmentation effects in human-dominated systems (42–44).

Ultimately, habitat fragmentation has severe effects on the composition, structure, and function of ecosystems (3, 5, 8), and our results demonstrate that fragmentation degrades suitable habitat and increases the extinction risk of mammals globally. Such impacts warrant intensified efforts to protect remnant habitat and restore broad-scale landscape connectivity to ameliorate the effects of fragmentation (5, 12). Quantification of fragmentation will help prioritize such global conservation efforts and develop more effective strategies for conserving the world's mammals.

Methods

Habitat-Suitability Models. As the basis of our fragmentation models, we used habitat-suitability models developed by Rondinini et al. (10) for the world's extant terrestrial mammals ($n = 5,027$ species). The completion of the Global Mammal Assessment by the IUCN Species Survival Commission (IUCN/SSC) (2) provided an unprecedented opportunity to develop global-habitat models for all terrestrial mammals. The Global Mammal Assessment dataset, based on the taxonomy published by Wilson and Reeder (45), received the input of thousands of mammal experts belonging to more than 30 Specialist Groups of the IUCN/SSC. The dataset, which contains the known geographic range (i.e., extent of occurrence as defined by IUCN), species-specific qualitative textual descriptions of habitat preferences, and conservation status of each mammal species, is available through the IUCN Red List of Threatened Species (1).

From this database, the habitat-suitability models were developed at a 300-m resolution and limited to occur within the geographic range of the species (10). Three environmental variables formed the basis of the habitat models: elevation, type of land cover, and hydrological features. Elevational range where a species is found, when known and recorded in the IUCN Red List, was incorporated into the habitat models. Expert information on other habitat affinities, including preferred types of land cover, tolerance to human impact, and relationship to water bodies, were extracted from textual description within the IUCN database and input as quantitative data into the habitat models. Habitat models ranked areas with a three-level gradient of habitat suitability: (i) high, corresponding to primary habitat (i.e., preferred habitat where the species can persist); (ii) medium, corresponding to habitat where a species can occur, but not persist without nearby primary (i.e., high-suitability) habitat; and (iii) unsuitable, where a species is expected to seldom or never be found (10). A subset of models and their associated habitat-suitability ranks were validated against available points of known species occurrences. Habitat was further classified as to if it occurred within protected areas, using IUCN categories I–IV from the World Database of Protected Areas (46, 47). Full details regarding the development of these habitat models are available elsewhere (10), and data are available upon request from the model developers (<https://globalmammal.org/activities/research/distribution-modelling/>).

Fragmentation Models. We measured fragmentation of high-suitability habitat, because such habitat is defined as essential for species persistence. When delineating high-suitability patches in the geographic range, we eliminated small patches (<four adjacent cells at 300-m resolution) potentially created by artifacts contained in underlying land-use and cover maps. This approach reduced the influence of spurious, isolated patches and improved computational efficiency of our fragmentation analyses. We then defined high-suitability habitat patches to be formed as clusters of suitable cells that were adjacent in any of the eight-neighborhood cells.

For each species we quantified the degree of fragmentation of high-suitability habitat by calculating the average Euclidean distance of all cells within high-suitability habitat from the nearest edge [that is, "GISfrag" (11, 12)]; edges demarcated the boundary between high-suitability and medium-suitability or unsuitable habitat, distributed either in the matrix external to habitat patches or as internal perforations within a patch. Low values of the average Euclidean distance into habitat for each species represent more highly fragmented habitat, whereas high values represent more core habitat and less-fragmented habitat. We considered a variety of other landscape metrics (including FRAGSTATS) and selected the GISfrag metric because it does not require an arbitrary distance threshold of what constitutes an "edge," accounts for different shapes of patches and landscapes patterns and arrangements, is a robust measure that accounts for the distribution of patch area (48), is comparable across landscapes of different extents, and provides stable, readily interpretable information (12). Furthermore, Euclidean distance-to-edge was found to be singularly valuable in quantifying global forest fragmentation (8). We did not calculate distance between patches through the intervening landscape "matrix," so our metric does not report on patch isolation or landscape configuration. For graphical display (Figs. 1 and 2 and Fig. S1), we inverse-coded the GISfrag metric to facilitate a more intuitive interpretation, where high GISfrag values represented high degrees of fragmentation.

Our analysis of fragmented habitat is also robust to any specific scaling assumption. Although information on dispersal ability can help inform the scale of fragmentation effects (49, 50), a comprehensive database of dispersal distance for all mammal species does not exist. Prior studies have attempted to approximate dispersal using allometric relationships based on body mass alone (51, 52). However, dispersal distances are highly heterogeneous even within the same species and are influenced by a variety of life-history traits and ecological factors, such as diet, sociality, and home-range area; thus, body size can be an inaccurate predictor of dispersal (50). Additionally, our inclusion of body mass as a predictor of extinction risk (see next section) further accounts for the

fragmentation specifically by weighting the global fragmentation map with a recently constructed human modification (HM) model, which combines the effects of multiple stressors (e.g., urban and agricultural land cover, energy production, nighttime lights, and roads) into an overall score of HM globally [approach and technical details in Theobald (29) and *Supporting Information*]. When weighting our original fragmentation map with the HM model, the resulting map identifies regions that have been fragmented by human development specifically, and de-emphasizes regions that are naturally

fragmented such as high-elevation areas and landscapes with water bodies interspersed (e.g., relictual glaciated areas).

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