

Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals

Kevin R. Crooks^{a,1}, Christopher L. Burdett^b, David M. Theobald^c, Sarah R. B. King^d, Moreno Di Marco^{e,f}, Carlo Rondinini^g, and Luigi Boitani^g

^aDepartment of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523; ^bDepartment of Biology, Colorado State University, Fort Collins, CO 80523; ^cConservation Science Partners, Fort Collins, CO 80524; ^dNatural Resource Ecology Laboratory, Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523; ^eARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, QLD 4072, Brisbane, Australia; ^fSchool of Earth and Environmental Sciences, The University of Queensland, QLD 4072, Brisbane, Australia; and ^gGlobal Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza Università di Roma, I-00185 Rome, Italy

Edited by James A. Estes, University of California, Santa Cruz, CA, and approved June 6, 2017 (received for review May 7, 2017)

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.

Author contributions: K.R.C., C.L.B., D.M.T., S.R.B.K., M.D.M., C.R., and L.B. designed research; K.R.C., C.L.B., D.M.T., S.R.B.K., M.D.M., C.R., and L.B. performed research; K.R.C., C.L.B., S.R.B.K., M.D.M., and C.R. analyzed data; and K.R.C., C.L.B., D.M.T., S.R.B.K., M.D.M., C.R., and L.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. Email: kevin.crooks@colostate.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1705769114/-DCSupplemental.

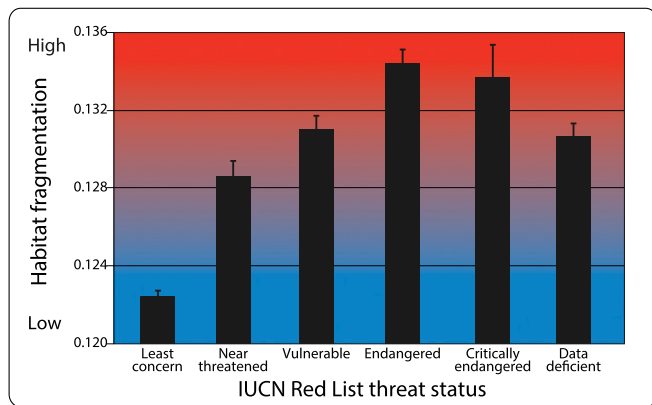


Fig. 1. Degree of habitat fragmentation predicts extinction risk for the world's terrestrial mammals. The fragmentation metric, measuring the amount of core (i.e., interior) habitat distributed within intact high-suitability patches, was ln-transformed and then inverse-coded so high values represent 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

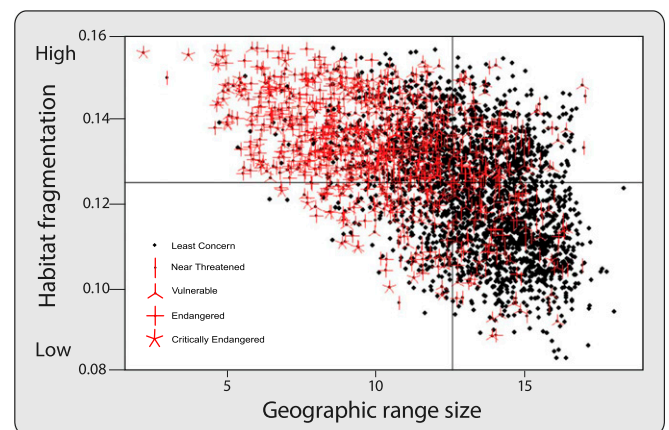


Fig. 2. Terrestrial mammals with higher degrees of habitat fragmentation and smaller geographic range sizes have a greater risk of extinction. Each black point represents an individual species, with the number of red line segments corresponding to extinction risk according to IUCN Red List threat status: 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 $\beta \pm \text{SE} = -1.00 \pm 0.13$, $z = -7.78$, $P < 0.001$). 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 $\beta \pm \text{SE} = -0.46 \pm 0.08$, $z = -5.86$, $P < 0.001$) and Data Deficient ($\beta \pm \text{SE} = -0.76 \pm 0.07$, $z = -10.67$, $P < 0.001$) 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,

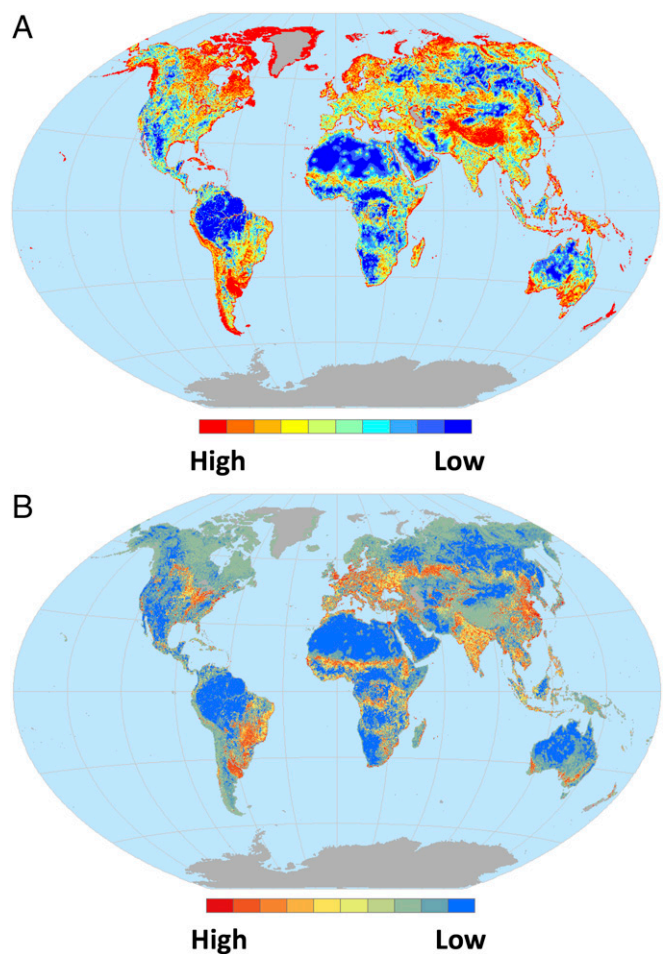


Fig. 3. Degree of habitat fragmentation for the world's terrestrial mammals. (A) Degree of habitat fragmentation as indexed by the fragmentation metric, measuring the amount of core (i.e., interior) habitat, and (B) degree of anthropogenic habitat fragmentation, calculated by weighting data in A by a 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

potential latent influence of scale-dependent effects on species-specific responses to fragmentation, and inclusion of dispersal estimates would potentially lead to circularity and redundancy with our body size covariate. Rather than speculate about the effects of spatial scale on dispersal distance or other species-specific responses to fragmentation, our primary assumption is that further distance into the interior of a habitat patch is beneficial, given that it signifies larger patches and fewer edge and fragmentation effects [see also Haddad et al. (8) for a similar assumption to assess global forest fragmentation].

Phylogenetic Comparative Methods. We used phylogenetic comparative methods to examine the relationship between the fragmentation metric and various species characteristics, including IUCN Red List status, range size, body mass, and the proportion of high-suitability habitat within the geographic range. We first used Pagel's λ (53) to determine the strength of the phylogenetic signal in these variables. We found that the phylogenetic signal in the fragmentation metric was moderate ($\lambda = 0.60$) and similar to the values we obtained for range size ($\lambda = 0.56$), the proportion of high-suitability habitat within the range ($\lambda = 0.45$), and IUCN Red List status ($\lambda = 0.67$). Pagel's λ value, however, was much higher for body size ($\lambda = 0.99$), a variable for which a strong phylogenetic signal was expected given that it is an evolved trait intrinsic to organisms. We therefore corrected for phylogenetic signal in our analyses. Because of nonnormal distributions, we ln-transformed the fragmentation metric, range size, and body mass, and arcsine square-root-transformed the proportion of high-suitability habitat in all statistical analyses.

Mammal Phylogeny and Life-History. We used the extant mammalian supertree phylogeny developed by Bininda-Emonds et al. (54, 55) that used the best estimates of divergence times ($n = 4,510$). To link this phylogeny to the taxonomy used by Rondinini et al. (10), we edited the two datasets to reconcile synonym species using Wilson and Reeder (45), and deleted species that were not common to both datasets. We did not incorporate new species into either dataset, and pruned all nonterrestrial mammals (cetaceans, seals, and sirenians) and *Homo sapiens* from the phylogeny, leaving a total of 4,018 species from 26 taxonomic orders. All phylogenetic analyses were conducted in the R statistical package (v3.1.3, R Development Core Team, 2015) using the ape (56), Geiger (57), and phylolm (58) packages.

Data on body mass were extracted from the PanTHERIA database (59). Where no body mass was listed, we first checked if it was present in the MOM database (60). If it was not, we followed the same methods as in Crooks et al. (12) and used the midpoint of the body mass range presented in Nowak (61) for that species. If not listed in Nowak (61), we used data from the closest member of the same species group, sister species of the same genus, or closest relative as indicated by Wilson and Reeder (45). If no other data were available, an average of all species in the genus was used. In other cases where PanTHERIA data were missing, information was copied and pasted from a synonym or sister species.

Fragmentation as a Predictor of Extinction Risk. We used a phylogenetic generalized linear model (58) to evaluate the relative capacity of our fragmentation metric and two widely used macroecological variables, body mass and range size, to explain extinction risk, as indexed by IUCN status categories (13). Data Deficient species ($n = 388$) were initially excluded from these analyses given they have inadequate information to assess extinction risk (13), so we evaluated five status categories, including Least Concern ($n = 2,633$ for phylogenetic analyses), Near Threatened ($n = 266$), Vulnerable ($n = 345$), Endangered ($n = 315$), and Critically Endangered ($n = 71$). A species is classified by the IUCN as Least Concern when it is widespread and abundant and does not qualify for listing in other categories, and as Near Threatened when it does not qualify for a threatened category now but is close to qualifying for a threatened category in the near future (13). A species is classified as Vulnerable, Endangered, or Critically Endangered when the best available evidence indicates it faces a high, very high, or extremely high risk of extinction in the wild, respectively. Given these criteria, we reclassified the IUCN categories into a binary threat using two classification schemes. In the first analysis, we assumed species classified by the IUCN as Least Concern and Near Threatened faced no immediate extinction risk, whereas species classified as "threatened" (i.e., Vulnerable, Endangered, and Critically Endangered) faced some degree of extinction risk. This is a standard binary classification scheme in prior extinction-risk studies (16). We then conducted a second analysis, again categorizing Least Concern species as having no immediate extinction risk, but assuming Near Threatened species face some extinction risk, given that the IUCN identifies such species as close to being threatened; we thus view this comparison as a conservative and precautionary approach regarding extinction risk of Near Threatened species (13). We used AIC (62, 63) to compare models with all combinations of fragmentation, body mass, and range size as predictors of extinction risk; AIC analyses included calculations of model probabilities (the likelihood of the model given the data and model set) and evidence ratios (the weight of evidence of each model

relative to the best model). Finally, to further explore patterns of fragmentation in species classified as nonthreatened by the IUCN, we also used phylogenetic generalized linear models to compare species listed as Least Concern to those listed as Near Threatened or Data Deficient.

The IUCN Red List process is expert-driven, and the IUCN uses five criteria to assign species to categories of extinction risk (13). One of those criteria is criterion B, used to list species that have restricted geographic ranges, with subcriteria for species that are severely fragmented 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). To evaluate the reliability of criteria used by the IUCN to assess if a taxon belongs in the threatened category, in particular those subcriteria (B1a/B2a) relating to habitat fragmentation, we used a phylogenetic generalized linear model to compare fragmentation levels for threatened species classified under subcriteria B1a/B2a to fragmentation levels for threatened species that did not meet the B1a/B2a subcriteria. As expected, threatened species classified under subcriteria B1a/B2a had significantly higher degrees of fragmentation (*Results and Discussion*).

These results, however, might imply that our use of habitat fragmentation as a predictor of extinction risk may lead to potential circularity with the IUCN Red List criteria. To explore this issue, we followed prior approaches (25–27) and conducted additional analyses after first excluding threatened species listed under relevant listing criteria. Red List assessment guidelines stipulate that assessors should evaluate each species against all listing criteria, and all relevant criteria should be applied (13). Furthermore, the Red List guidelines encourage assessors to adopt a precautionary attitude to uncertainty when applying the criteria, so if range restriction or fragmentation was deemed a plausible threat by assessors, criterion B should be applied, even in the presence of uncertainty. Because of the relationship between range size and fragmentation (*Results and Discussion*, Fig. 2, and Fig. S1), we decided to adopt a conservative approach to account for potential circularity and exclude all species categorized because of range restriction (i.e., under any combination of subcriteria of criterion B, representing 46.8% of threatened species). We then used phylogenetic generalized linear models and AIC to compare models with all combinations of fragmentation, body mass, and range size as predictors of binary extinction risk. As above, we used two classification schemes to model extinction risk, assuming Near Threatened species (*i*) face no immediate extinction risk or (*ii*) face some extinction risk. For each model, we compared Least Concern/Near Threatened species to those threatened species not listed under criterion B.

We also evaluated how our fragmentation metric related to body mass and range size. We first conducted simple correlation analyses, corrected for phylogeny, relating fragmentation to body mass and also to range size. We then evaluated these relationships further with a phylogenetic generalized least-squares regression (64) that assessed the relative influence of body mass and range size on the fragmentation metric; we used AIC to compare models with all combinations of body mass, range size, and their interaction as predictors of habitat fragmentation. For our generalized least-squares regressions, we assumed that the continuous covariates evolved randomly after a speciation event (65), so we used a Brownian-motion model to define the structure of the correlation among species.

In addition to the macroecological variables, we also conducted two additional phylogenetic generalized least-squares regressions relating fragmentation to proportion of high-suitability habitat within the range and to proportion of protected high-suitability habitat within the range. Prior work has demonstrated that prevalence of remaining suitable habitat within the geographic range, or conversely the proportion of unsuitable human-affected land cover, is predictive of threat status in mammals (10, 14, 16) and other taxa (66, 67). We also conducted separate phylogenetic generalized linear models to evaluate the relative importance of fragmentation versus proportion of suitable habitat as sole predictors of extinction risk. These tests thus helped distinguish between the effects of habitat loss per se (as assessed by proportion of suitable habitat remaining in the range) from how remaining suitable habitat was distributed into intact, core habitat patches (as assessed by our fragmentation metric).

Mapping Fragmentation Hotspots. We generated global maps of fragmentation by summing the fragmentation metric at each 300 × 300-m cell for all terrestrial mammal species worldwide. Because we summed metrics for all species within a given area (Fig. 3), degree of fragmentation in part reflects global patterns of species distribution and richness. Thus, we also generated global maps displaying an average fragmentation index that was corrected for species richness (for details, see *Supporting Information*).

Our fragmentation analyses are based on the extent and geometry of high-suitability habitat and do not distinguish as to whether fragmentation is caused by natural factors (e.g., elevational or hydrological barriers) or anthropogenic disturbances (e.g., human development). To further identify the sources of fragmentation, we generated another map that highlighted anthropogenic

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).

ACKNOWLEDGMENTS. We thank L. Angeloni, T. Caro, and D. Wilcove for comments on earlier drafts of this manuscript. We also thank F. Chiozza, the International Union for Conservation of Nature, and the Global Mammal Assessment data contributors and workshop facilitators who enabled the creation of the habitat suitability models.

- IUCN (2010) *IUCN Red List of Threatened Species* (IUCN, Gland, Switzerland).
- Schipper J, et al. (2008) The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* 322:225–230.
- Wilson MC, et al. (2016) Habitat fragmentation and biodiversity conservation: Key findings and future challenges. *Landsc Ecol* 31:219–227.
- Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121:161–170.
- Crooks KR, Sanjayan MA (2006) *Connectivity Conservation* (Cambridge Univ Press, Cambridge, UK).
- Didham RK, Tylianakis JM, Gemmill NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol Evol* 22:489–496.
- Krosby M, Tewksbury J, Haddad NM, Hoekstra J (2010) Ecological connectivity for a changing climate. *Conserv Biol* 24:1686–1689.
- Haddad NM, et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1:e1500052.
- Tracewski Ł, et al. (2016) Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conserv Biol* 30:1070–1079.
- Rondinini C, et al. (2011) Global habitat suitability models of terrestrial mammals. *Philos Trans R Soc Lond B Biol Sci* 366:2633–2641.
- Ripple WJ, Bradshaw GA, Spies TA (1991) Measuring forest landscape patterns in the cascade range of Oregon. *Biol Conserv* 57:73–88.
- Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos Trans R Soc Lond B Biol Sci* 366:2642–2651.
- IUCN (2001) *IUCN Red List Categories and Criteria* (IUCN, Gland, Switzerland).
- Cardillo M, et al. (2008) The predictability of extinction: Biological and external correlates of decline in mammals. *Proc Biol Sci* 275:1441–1448.
- Di Marco M, Santini L (2015) Human pressures predict species' geographic range size better than biological traits. *Glob Change Biol* 21:2169–2178.
- Di Marco M, et al. (2014) Drivers of extinction risk in African mammals: The interplay of distribution state, human pressure, conservation response and species biology. *Philos Trans R Soc Lond B Biol Sci* 369:20130198.
- Bland LM, Collen B, Orme CDL, Bielby J (2015) Predicting the conservation status of data-deficient species. *Conserv Biol* 29:250–259.
- Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecol Lett* 9:1136–1145.
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279.
- Williams SE, et al. (2009) Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. *Proc Natl Acad Sci USA* 106:19737–19741.
- McKinney ML (1997) Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annu Rev Ecol Syst* 28:495–516.
- Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: Evidence for climate driven homogenization in avian communities. *Glob Ecol Biogeogr* 21:568–578.
- Henle K, Davies KF, Kleyer M, Margules S, Settele J (2004) Predictors of species sensitivity to fragmentation. *Biodivers Conserv* 13:207–251.
- Charette NA, Cleary DF, Mooers AO (2006) Range-restricted, specialist Bornean butterflies are less likely to recover from ENSO-induced disturbance. *Ecology* 87:2330–2337.
- Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G (2009) Multiple ecological pathways to extinction in mammals. *Proc Natl Acad Sci USA* 106:10702–10705.
- Cardillo M, Mace GM, Gittleman JL, Purvis A (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proc Natl Acad Sci USA* 103:4157–4161.
- Di Marco M, Collen B, Rondinini C, Mace GM (2015) Historical drivers of extinction risk: Using past evidence to direct future monitoring. *Proc Biol Sci* 282:20150928.
- Butchart SHM, Bird JP (2010) Data deficient birds on the IUCN Red List: What don't we know and why does it matter? *Biol Conserv* 143:239–247.
- Theobald DM (2013) A general model to quantify ecological integrity for landscape assessments and US application. *Landsc Ecol* 28:1859–1874.
- McCain CM, King SR (2014) Body size and activity times mediate mammalian responses to climate change. *Glob Change Biol* 20:1760–1769.
- Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob Change Biol* 17:990–996.
- UNEP-WCMC; IUCN (2016) *Protected Planet Report 2016* (UNEP-WCMC and IUCN, Cambridge, UK).
- Butchart SHM, et al. (2015) Shortfalls and solutions for meeting national and global conservation area targets. *Conserv Lett* 8:329–337.
- Laurance WF, et al. (2001) Environment. The future of the Brazilian Amazon. *Science* 291:438–439.
- Soares-Filho BS, et al. (2006) Modelling conservation in the Amazon basin. *Nature* 440:520–523.
- Hansen MC, et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.
- Murray KA, Verde Arregoitia LD, Davidson A, Di Marco M, Di Fonzo MMI (2014) Threat to the point: Improving the value of comparative extinction risk analysis for conservation action. *Glob Change Biol* 20:483–494.
- Orme CDL, et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019.
- Ceballos G, Ehrlich PR (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proc Natl Acad Sci USA* 103:19374–19379.
- Smith RJ, Verissimo D, Leader-Williams N, Cowling RM, Knight AT (2009) Let the locals lead. *Nature* 462:280–281.
- Thornton D, et al. (2016) Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecol Appl* 26:1112–1124.
- Schultz PW (2011) Conservation means behavior. *Conserv Biol* 25:1080–1083.
- Dickman AJ (2010) Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. *Anim Conserv* 13:458–466.
- Kansky R, Kidd M, Knight AT (2016) A wildlife tolerance model and case study for understanding human wildlife conflicts. *Biol Conserv* 201:137–145.
- Wilson DE, Reeder DM (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference* (Johns Hopkins Univ Press, Baltimore), 3rd Ed.
- IUCN; UNEP (2010) *The World Database on Protected Areas (WDPA)* (UNEP-WCMC, Cambridge, UK).
- Di Marco M, et al. (2012) A novel approach for global mammal extinction risk reduction. *Conserv Lett* 5:134–141.
- Li B-L, Archer S (1997) Weighted mean patch size: A robust index for quantifying landscape structure. *Ecol Modell* 102:353–361.
- Whitmee S, Orme CDL (2013) Predicting dispersal distance in mammals: A trait-based approach. *J Anim Ecol* 82:211–221.
- Santini L, et al. (2013) Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix* 24:181–186.
- Schloss CA, Nuñez TA, Lawler JJ (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc Natl Acad Sci USA* 109:8606–8611.
- Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv Ecol* 4:16.
- Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Bininda-Emonds ORP, et al. (2007) The delayed rise of present-day mammals. *Nature* 446:507–512.
- Bininda-Emonds ORP, et al. (2008) The delayed rise of present-day mammals. *Nature* 456:274.
- Paradis E, Claude J, Strimmer K (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Ho Ls, Ané C (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst Biol* 63:397–408.
- Jones KE, et al. (2009) PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.
- Smith FA, et al. (2003) Body mass of late quaternary mammals. *Ecology* 84:3403.
- Nowak RM (1999) *Walker's Mammals of the World* (Johns Hopkins Univ Press, Baltimore), 6th Ed.
- Anderson DR (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence* (Springer Science & Business Media, New York).
- Burnham KP, Anderson DR (2003) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York).
- Grafen A (1989) The phylogenetic regression. *Philos Trans R Soc Lond B Biol Sci* 326:119–157.
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Lee TM, Jetz W (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proc Biol Sci* 278:1329–1338.
- Ficetola GF, Rondinini C, Bonardi A, Baisero D, Padoa-Schioppa E (2015) Habitat availability for amphibians and extinction threat: A global analysis. *Divers Distrib* 21:302–311.
- Pesaresi M, et al. (2013) A global human settlement layer from optical HR/VHR RS data: Concept and first results. *IEEE J Sel Top Appl Earth Obs Remote Sens* 6:2102–2131.
- ESA (2010) European Space Agency (ESA) Climate Change Initiative (CCI) Land Cover dataset. Available at <https://www.esa-landcover-cci.org/?q=node/169>. Accessed March 1, 2016.
- NOAA (2013) *National Oceanic and Atmospheric Agency (NOAA) Visible Infrared Imaging Radiometer Suite (VIIRS)*. Available at ngdc.noaa.gov/eog/viirs.html. Accessed March 1, 2016.
- CIESIN (2010) *Center for International Earth Science Information Network (CIESIN) Global Roads Open Access Data Set, Version 1 (gROADSv1)*. Available at sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1. Accessed March 1, 2016.
- Bonham-Carter G (1994) *Geographic Information Systems for Geoscientists: Modelling with GIS* (Elsevier, Pergamon, Turkey).