Matrix condition mitigates the effects of habitat fragmentation on species extinction risk

Juan Ramírez-Delgado (✉ delgado@unbc.ca)
University of Northern British Columbia  https://orcid.org/0000-0003-2673-0741

Moreno Di Marco
Sapienza University of Rome

James Watson
University of Queensland

Chris Johnson
University of Northern British Columbia

Carlo Rondinini
Sapienza University of Rome  https://orcid.org/0000-0002-6617-018X

Xavier Comedor Llano
University of Northern British Columbia

Miguel Arias
University of Northern British Columbia

Oscar Venter
University of Northern British Columbia

Article

Keywords: Habitat Loss, Global Biodiversity Decline, Human Footprint Levels, Conservation Action

DOI: https://doi.org/10.21203/rs.3.rs-340760/v1

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Matrix condition mitigates the effects of habitat fragmentation on species extinction risk

Authors
Juan Pablo Ramírez-Delgado*1, Moreno Di Marco2,3, James E.M. Watson3,4,5, Chris J. Johnson1, Carlo Rondinini6, Xavier Corredor Llano1, Miguel Arias1, Oscar Venter1

Affiliations
1Natural Resources and Environmental Studies Institute, University of Northern British Columbia, Prince George V2N 4Z9, Canada.
2Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy.
3School of Earth and Environmental Sciences, University of Queensland, St Lucia 4072, Australia.
4Centre for Biodiversity and Conservation Science, School of Biological Sciences, The University of Queensland, Brisbane 4072, Queensland, Australia.
5Wildlife Conservation Society, Global Conservation Program, Bronx, NY 20460, USA.
6Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy.

*Correspondence and request for materials should be addressed to J.P.R.-D. (delgado@unbc.ca)
Abstract

Habitat loss is the leading cause of global biodiversity decline, but the influence of human pressure within the matrix surrounding habitat fragments remains poorly understood. Here we measure the relationship between fragmentation, matrix condition (measured as the extent of high human footprint levels), and the change in extinction risk of 4,327 terrestrial mammals. We find that the matrix condition and the fragmentation of habitat are strongly associated with changes in species extinction risk. Importantly, we discover that fragmentation is a stronger predictor of risk than species life-history traits, habitat loss, and habitat amount. Moreover, the importance of fragmentation increases with an increasing deterioration of the matrix condition, highlighting the critical influence matrix quality plays on the effects of fragmentation. These findings suggest that restoration measures in habitat matrices may be an important conservation action for mitigating the effects of fragmentation relative to extinction risk of terrestrial mammals.

Main

Although habitat loss is the leading cause of ongoing biodiversity loss, the degree to which habitat fragmentation, defined as the spatial arrangement of remaining habitat for a given amount of habitat loss, influences the loss of biodiversity has remained the focus of considerable debate. Central to the debate has been a persistent uncertainty in disentangling the effects of habitat loss on biodiversity from the effects of fragmentation per se, especially relative to the reduction in patch size and the increase in patch isolation. Whereas some studies have challenged the assumption of the impacts of fragmentation, others have demonstrated that the effects of fragmentation are negative and stronger for local species, particularly in the tropics.
at intermediate (30–60%) levels of habitat amount\textsuperscript{16,17}. Resolving this debate is critical to not just informing efforts to prioritize the protection and management of intact and fragmented landscapes with the same total amount of habitat, but also to better understand the role of the areas surrounding patches of habitat, commonly referred to as the ‘matrix’, in maintaining biodiversity\textsuperscript{10,18,19}.

The traditional characterization of landscapes, which views patches of habitat as islands embedded in a matrix of non-habitat, as assumed in classical theoretical models\textsuperscript{20,21}, has been strongly criticized\textsuperscript{18,22–24}. This characterization has progressively been relaxed with approaches based on the premise that the matrix should in fact be treated as a heterogeneous mosaic of different land covers (e.g. ‘countryside biogeography’\textsuperscript{25}, and the ‘land-sharing’ and ‘land-sparing’ approaches\textsuperscript{26–30}), as it is recognized that species use different matrices for foraging, dispersing, and reproduction purposes\textsuperscript{31,32}. While high-contrast matrices (e.g. intensive agricultural or built environments) act as movement barriers or ecological traps for many species, with an elevated risk of mortality\textsuperscript{33}, low-contrast matrices (e.g. secondary forests or shade-grown low-intensive agriculture in forested regions) may act as permeable barriers with a reduced risk of mortality, even for those species typically considered habitat specialists\textsuperscript{25,27}. To date, however, conservation and management assessments across different scales have focused mainly on species’ primary habitat\textsuperscript{34,35}, thus limiting our understanding of their response to the matrix, which may have direct implications for the design of functional landscapes\textsuperscript{36} and the prioritization of different conservation actions in fragmented landscapes\textsuperscript{37}. 
Comparative extinction risk modelling is an approach for assessing the drivers of extinction risk and its change over time, based on the relationship between species’ life histories, the pressure within species geographic ranges, and their threat status\textsuperscript{38--43}. Built with readily available data, this approach allows for the prediction of the risk of extinction of a larger number of species compared with that provided by expert-based assessments. This more rapid approach can substantially reduce resource requirements, as well as proactively inform conservation and management strategies\textsuperscript{44,45}. Although the loss\textsuperscript{3,43} and fragmentation\textsuperscript{46,47} of habitat are among the main determinants of species extinction risk, the influence of the matrix condition on the effects of fragmentation and its relationship with species extinction risk has not been well evaluated for any animal taxon at a global scale.

Here, we quantify the relationship between changes in the extinction risk of 4,327 terrestrial mammals over a 24-year period (1996-2020), the degree of fragmentation of their suitable habitat, and the levels of human pressure within the associated habitat matrix. Our goal is to test the influence of human pressure within the matrix on the effects of fragmentation for determining changes in species extinction risk globally. We focus on terrestrial mammals as they have been used as a focal taxon in previous extinction risk analyses\textsuperscript{48}, they are known to be sensitive to fragmentation\textsuperscript{46}, and data are available to delineate levels of suitable habitat and ‘unsuitable’ (i.e. matrix) habitat within their ranges\textsuperscript{49}. For each species, we quantify the degree of fragmentation as the average Euclidean distance within patches of suitable habitat from the nearest patch edge, and matrix condition as the extent and change over time of high human pressure levels overlapping with the surrounding matrix. Spatial data representing the condition of the matrix were obtained from the most comprehensive global maps of changing human
pressure on the environment, the recently updated human footprint maps, which provide a
single metric that combines data on human activities, all of which are driving the current
biodiversity crisis. We define a human footprint threshold of ≥ 3 out of 50 to represent the extent
of human-modified habitat within the matrix. This threshold was used as it has shown to be the
strongest predictor of transitions in extinction risk for terrestrial mammals. Furthermore, this
human footprint threshold is associated with the highest declines in mammalian movements
and chimpanzee behavioral diversity. Following previous studies, we classify species into
two groups of extinction risk, low-risk transitions and high-risk transitions (Fig. 1), based on the
initial and final Red List category registered between 1996 and 2020. In combination with other
predictors of extinction risk (see Table 2 for a description), we quantify the relative predictive
importance of habitat fragmentation and the condition of the matrix for determining extinction
risk transitions in terrestrial mammals.

Our analyses reveal that the condition of the matrix plays a major role on the effects of
fragmentation for predicting extinction risk transitions in terrestrial mammals. Our results
suggest that the negative effects of habitat fragmentation may be somewhat mitigated when the
matrix is associated with lower levels of human pressure.

**Results**

**Changes in species extinction risk**

When classifying extinction risk transitions with the initial and final Red List categories
registered between 1996 and 2020, we found that 2,907 (67.2%) species faced a low-risk
transition and 1,420 (32.8%) a high-risk transition (Fig. 1). The proportions of low-risk and high-
risk transitions were almost unchanged when applying a different classification routine (Supplementary Fig. 1; Supplementary Note 1).

**Figure 1. Classification of species extinction risk transitions based on past and present IUCN Red List categories*. a** Represents low-risk transitions, which included species that retained a category of least concern, together with those species that moved from any higher category of threat to a lower category between 1996 and 2020. **b** Represents high-risk transitions, which included all species that retained a category of threatened or near threatened, together with those species that moved from any lower category of threat to a higher category between 1996 and 2020. *Acronyms refer to the IUCN Red List categories, including Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) (figure adapted from Di Marco et al.43).

**Predicting transitions in species extinction risk**

Using a Random Forest model for classification55, we measured the performance of an array of life-history, environmental and pressure variables for the prediction of extinction risk transitions (see Table 2 for a description). We found that the extent of high human footprint values in the
matrix and the degree of fragmentation of suitable habitat had higher predictive performance than life-history traits and other pressure and environmental variables (Fig. 2). When employing a different classification routine of extinction risk transitions (i.e. when transitions were classified using the second last and last Red List category instead of the initial and final Red List categories between 1996 and 2020), these two variables remained as the most important predictors of extinction risk (Supplementary Fig. 2a), suggesting that these results are robust to changes in species threat status.

**Fig. 2. Relative importance of selected variables for the prediction of extinction risk transitions in terrestrial mammals.** Variables are colour-coded according to their broad class (life-history, environment, and human pressure). The description of each variable can be found in Table 2. High levels of the human footprint (HFP) included values of 3 or above.

Interestingly, our results show that the degree of fragmentation of suitable habitat had higher predictive performance than the change in high human footprint values (as defined by increases in high human footprint values through time) within suitable habitat and the proportion of
suitable habitat (Fig. 2). This result is supported by a sensitivity analysis where a different classification routine of extinction risk transitions and a different combination of the levels of habitat suitability were applied (Supplementary Fig. 2a and 2b). This suggests that habitat fragmentation better predicts changes in species extinction risk than habitat loss and habitat amount at a global scale.

Our results also show that the predictive importance of the change in high human footprint values within the extent of suitable habitat is greater than that within the extent of the matrix (Fig. 2). This result was confirmed when employing a different classification routine of extinction risk transitions and a different combination of the levels of habitat suitability (Supplementary Fig. 2a and 2b), highlighting the key influence of the extent and change over time of high human pressure levels within species’ ranges\(^{43}\).

When looking at the interaction between the degree of fragmentation of suitable habitat and the condition of the matrix on the probability of changes in species extinction risk (Fig. 3), we found that the probability of high-risk transitions increased with an increasing degree of habitat fragmentation and an increasing extent of high human pressure levels within the matrix. This trend was reversed to an increased probability of low-risk transitions.
**Fig. 3. Interaction of the degree of habitat fragmentation with the matrix condition on extinction risk transitions in terrestrial mammals.** The plot represents the positive interaction between the degree of fragmentation of suitable habitat and the matrix condition for high-risk transition. The interaction between the degree of fragmentation of suitable habitat and the matrix condition for low-risk species is represented when the plot is inverted. The fragmentation metric was inverse-coded so high values represent high degree of fragmentation. The extent of high human footprint values in the matrix was arcsine square-root-transformed to avoid variance instability when handling proportions close to zero. The description of each variable is given in Table 2. High levels of the human footprint (HFP) included values of 3 or above.

Our model showed good overall classification ability during cross-validation, with 82% of species correctly classified. The accuracy in predicting high-risk transitions (sensitivity = 61.7%) was lower than the accuracy in predicting low-risk transitions (specificity = 84.4%), with a true skill statistic of 0.5.

The predictive performance of our model did not markedly change compared to the models built based on a different classification routine of extinction risk transitions and a different
combination of the levels of habitat suitability (Supplementary Table 1). Thus, the model is
robust to changes in species threat status and in the levels of habitat suitability.

The influence of the matrix condition on the importance of habitat fragmentation for
predicting extinction risk transitions

In order to measure the influence of the matrix on the importance of fragmentation for the
prediction of extinction risk transitions, we first discretized the extent of high human footprint
values within the matrix into two broad levels as a proxy for matrix quality: 'low-quality matrix’,
representing species with ≥ 50% of the extent of their matrix overlapping with high human
footprint values (n = 2,529 low-risk species and 1,250 high-risk species); and ‘high-quality
matrix’, representing species with < 50% of the extent of their matrix overlapping with high
human footprint values (n = 341 low-risk species and 111 high-risk species). We then built
separate Random Forest models for each level of quality of the matrix in order to compare the
predictive performance of the degree of fragmentation of suitable habitat between the defined
levels of quality of the matrix. We found that the degree of fragmentation had a higher relative
predictive performance for species with low-quality matrix (Fig. 4a) than that observed for
species with low-quality matrix (Fig. 4b), with a decrease of 30.1%. Notably, the relative
predictive importance of the extent of high human footprint values in the matrix was markedly
higher for the low-quality matrix model compared with the high-quality matrix model,
suggesting that the lower the quality of the matrix, the higher the predictive importance of the
matrix.
Fig. 4. Influence of the matrix condition on the relative importance of selected variables for the prediction of extinction risk transitions in terrestrial mammals. a Shows the relative importance of each predictor with low-quality matrix, which included species with proportions ≥ 50% of the extent of their matrix overlapping with high human footprint values (n = 2,529 low-risk species and 1,250 high-risk species). b Shows the relative importance of each predictor with high-quality matrix, which included species with proportions < 50% of the extent of their matrix overlapping with high human footprint values (n = 341 low-risk species and 111 high-risk species). Variables are colour-coded according to their broad class (life-history, environment, and...
human pressure). The description of each variable is given in Table 2. High levels of the human footprint (HFP) included values of 3 or above.

When looking at the difference in the degree of fragmentation for low-risk and high-risk species, we found that those classified as high-risk had higher degrees of fragmentation, with a difference that was significant for each of the levels of quality of the matrix ($p$-values < 0.001; Wilcoxon signed rank test, one-sided). When it comes to the effect size of the degree of fragmentation between low-risk and high-risk species, we found that such an effect was slightly lower for those species with matrices of high-quality habitat (Cohen’s $d = 0.15$; Supplementary Fig. 3a) compared to those with matrices of low-quality habitat (Cohen’s $d = 0.16$; Supplementary Fig. 3b).

Our results show that the model for species with matrices of low-quality habitat had higher predictive performance than the model for species with matrices of high-quality habitat (Table 1). However, it is important to note that this result is related to the fact that the latter showed a larger imbalance between low-risk and high-risk species than that showed by the former.

Table 1. Cross-validation results of the Random Forest models for the prediction of extinction risk transitions in terrestrial mammals with low- and high-quality matrix. The cross-validation was performed in terms of proportion of correctly classified species (accuracy), proportion of correctly classified high-risk species (sensitivity), proportion of correctly classified low-risk species (specificity), and the true skill statistic (TSS = sensitivity + specificity − 1). Low-quality matrix included species with proportions ≥ 50% of the extent of their matrix.
overlapping with high human footprint values \((n = 2,529\) low-risk species and \(1,250\) high-risk species). High-quality matrix included species with proportions < 50\% of the extent of their matrix overlapping with high human footprint values \((n = 341\) low-risk species and \(111\) high-risk species). High human footprint included values of 3 or above.

| Model                        | Accuracy (\%) | Sensitivity (\%) | Specificity (\%) | TSS |
|------------------------------|---------------|------------------|------------------|-----|
| Extinction risk transitions ~ Low-quality matrix | 81.5 | 62.8 | 84.1 | 0.5 |
| Extinction risk transitions ~ High-quality matrix | 81.7 | 34.8 | 83.7 | 0.2 |

**Discussion**

Understanding the external conditions under which a species is likely to face an increased risk of extinction are necessary to inform conservation policies and management strategies\(^{42}\). We found that the condition of the matrix, as defined by the extent of high human footprint values between patches of suitable habitat, strongly influenced the effects of fragmentation on extinction risk transitions of terrestrial mammals. Specifically, we found that when predicting changes in the risk of extinction of terrestrial mammals, matrices of high-quality habitat decreased the relative predictive importance of the degree of habitat fragmentation by \(~30\%\) compared with low-quality matrices. To the best of our knowledge, this finding is the first to demonstrate consistently whether and how much human pressure within the matrix alters the importance of habitat fragmentation as a predictor of extinction risk change. This finding is consistent with previous studies showing that the use of the matrix is among the main determinants of the
vulnerability of mammalian populations to local extinction in fragmented landscapes, and supports recent findings demonstrating that species living in forested landscapes with a low-quality matrix (in terms of plant biomass) are more vulnerable to extinction than those living in forested landscapes with a higher quality matrix.

Our results showed that species with greater fragmentation and lower quality matrix within their ranges tended to be at greater risk of extinction. As reported by others, this might indicate that species at a lower risk of extinction are able to exploit a greater number of habitats and resources compared to species in the high-risk group. This result might be related to the fact that species occurring in regions with low rates of historical disturbance are more likely to be sensitive to fragmentation, and thus more likely to face an increased risk of extinction. That would suggest that those species within the high-risk group are mainly concentrated in the tropics, particularly in forested landscapes, where deforestation continues at a rapid rate. In fact, ~33%, ~34%, and ~45% of all species restricted to the Neotropical, Afrotropical, and Indo-Malay biogeographic realms, respectively, were facing an increased risk of extinction between 1996 and 2020, which is consistent with these findings.

In our extinction risk model, some variables had higher predictive performance than others. For example, the extent of high human footprint values in the matrix was the most important predictor of changes in species extinction risk. This result contrasts with the findings from previous extinction risk modelling exercises for mammals, where the predictive importance of human pressure was found to be lower than life-history traits or environmental conditions. However, it helps confirms the findings of one recent extinction risk modelling exercise for...
mammals\textsuperscript{43}, where the extent of high human footprint values within species’ ranges had higher predictive importance than environmental conditions, life-history traits, and other measures of human pressure. This result may, in part, be explained by the fact that species are increasingly exposed to anthropogenic land covers\textsuperscript{63,64}, especially in the matrix where higher contrast (i.e. lower quality habitat) likely prevents their movement\textsuperscript{52} and elevates their mortality\textsuperscript{33} (e.g. by roadkill\textsuperscript{65} or increasing predation by feral animals\textsuperscript{66}).

The degree of fragmentation of suitable habitat was also found to be a key correlate of change in extinction risk. This finding is in line with previous extinction risk modelling showing that the inclusion of habitat fragmentation as a predictor increases the explanatory power of the models\textsuperscript{46,47}. In particular, this result supports previous findings showing that terrestrial mammals with higher fragmentation have smaller ranges, lower proportions of suitable habitat and are at greater risk of extinction\textsuperscript{46}.

Conflicting results on the effects of fragmentation \textit{per se} on biodiversity have arisen from studies attempting to separate ‘independent’ effects of habitat loss from those of habitat fragmentation\textsuperscript{11}. Some studies have argued that the effects of habitat loss are greater and more negative (e.g.\textsuperscript{6,8,9,12}), while others have demonstrated that the effects due to fragmentation, such as declining patch size, increasing habitat isolation, and increasing edge effects, are essentially negative and lasting (e.g.\textsuperscript{5,7,13,14}). However, in real landscapes, habitat loss inevitably causes habitat fragmentation, and both act in synergy with other threats to biodiversity\textsuperscript{67,68}. Thus, there is little practical value in attempting to separate the effects of habitat loss and fragmentation\textsuperscript{7,69–71}. Our study does not attempt to resolve the current debate as to whether and how habitat
fragmentation *per se* (i.e. the spatial arrangement of remaining habitat for a given amount of
habitat loss) influences biodiversity\textsuperscript{5–10}, but the results showed that the degree of fragmentation
of suitable habitat was more important than the change in high human footprint values (as
represented by increases in high human pressure levels over time) within suitable habitat and the
proportion of suitable habitat. This suggests that changes in species extinction risk are primarily
determined by the fragmentation of habitat, and secondarily by the loss and the amount of habitat
within species’ ranges. However, there is also the possibility that the loss of most suitable habitat
patches had already occurred before the beginning of the study period, resulting in fragmentation
being a more important predictor of extinction risk than habitat loss and habitat amount.

Our models were better at correctly classifying low-risk transitions than high-risk transitions.
This suggests that the external conditions leading to a high-risk transition might be more difficult
to identify than those leading to a low-risk transition, as also indicated in previous studies\textsuperscript{41–
43,62,72}. However, it is important to acknowledge that the exclusion of other variables associated
with pressure (such as overhunting, disease, invasive species, and climate change) and life-
history traits (such as rarity, dispersal mode, and ranging behavior) could have increased the
uncertainty of our predictions, and thus influenced the ability of our models to correctly classify
high-risk transitions.

Our modelling framework can be used to proactively inform conservation and management
strategies seeking to minimize the number of species that are facing or will face an increased risk
of extinction. This includes species that are currently classified as threatened and those that are
likely to become so if human activities continue to expand and intensify into the future. An
important next step will be to create a global map that captures the matrix condition for the world’s terrestrial mammals. This will require weighting the extent of the matrix of all terrestrial mammals with the human footprint as a proxy for matrix quality within species’ geographic distributions. If species threat statuses are considered, this could have the potential to identify where conservation actions are needed to be improved. For example, in those locations where species with an increased risk of extinction show a low-quality habitat within their matrix, a land-sparing approach could be effective as it maximizes conservation actions on the remaining patches of suitable habitat while concentrating agriculture production elsewhere\textsuperscript{26,28–30}.

Alternatively, in those locations where species with an increased risk of extinction show a high-quality habitat within their matrix, a land-sharing approach would work better as it minimizes the impact of agriculture production by maintaining or restoring the conservation value of the land already farmed\textsuperscript{27–30}.

Our results indicate that species suffering from greater pressure in their matrix require particular conservation attention. Among these species, those with smaller ranges require careful management of the areas surrounding their suitable habitat, especially in light of the current and future effects of climate and land-use change\textsuperscript{73}. Our results also highlight the potential of high-quality matrices to mitigate the effects of fragmentation on species extinction risk, thus suggesting that in addition to efforts to maintain remaining suitable habitat\textsuperscript{32,35,74}, there is a need for restoration of habitats in the matrix.
**Methods**

**Habitat suitability models**

We used habitat suitability models developed by Rondinini et al.\textsuperscript{49} to represent the extent of suitable habitat patches and the extent of the matrix of 4,327 out of 5,722 extant terrestrial mammals, corresponding to 76% of all species in the group\textsuperscript{75}. These models were built for the year 2000 at a spatial resolution of 300 m, based on species’ elevation range and other habitat affinities, including preferred land cover types and relationship to water bodies. Data for each species were extracted from the International Union for Conservation of Nature (IUCN) datasets, and using expert information combined with spatial data on habitat variables. The models include three levels of habitat suitability: (i) high, representing primary habitat or preferred habitat where the species can persist; (ii) medium, representing secondary habitat where the species can occur but not persist without nearby high suitable habitat; and (iii) ‘unsuitable’, representing locations where the species is expected to occasionally or never be found.

When delineating the levels of habitat suitability for each species, small contiguous groups of pixels (\(< 4\) adjacent pixels of the same level of habitat suitability) were removed and replaced with the pixel value of the largest neighbor of the contiguous groups of pixels, setting eight neighboring pixels. This reduced the influence of isolated groups of pixels of the same level of habitat suitability, and improved the computational efficiency of the analysis, as also reported in other studies\textsuperscript{46,76}.

In this analysis, we combined high and medium habitat suitability to represent the extent of suitable habitat patches, and use the level of ‘unsuitable’ habitat to represent the extent of the
matrix of each species. We also applied a different combination of the levels of habitat suitability when representing the extent of suitable habitat patches (high suitability instead of high and medium suitability combined) and the extent of the matrix (medium suitability and ‘unsuitable’ combined instead of ‘unsuitable’ habitat) of each species.

Habitat fragmentation as a predictor of extinction risk transitions

For each species, we measured the degree of habitat fragmentation by quantifying the average Euclidean distance of all the pixels within patches of suitable habitat from the nearest patch edge. Large values of the average Euclidean distance represented low degrees of habitat fragmentation, whereas small values represented high degrees of habitat fragmentation. Additionally, we calculated the average Euclidean distance between patches of suitable habitat through the surrounding matrix (i.e., the average Euclidean distance of all the pixels within ‘unsuitable’ habitat from the nearest edge) to account for patch isolation (after). Here, large values of the average Euclidean distance represented low degrees of patch isolation, and small values represented high degrees of patch isolation. The average Euclidean distance was considered because this metric does not require a predetermined distance threshold of what constitutes an edge, accounts for different shapes of fragments and landscapes patterns and arrangements, accounts for the distribution of habitat area, is comparable across landscapes of different extents, and provides stable and readily interpretable information. Moreover, average Euclidean distance has been shown to be singularly valuable in quantifying the relationship between habitat fragmentation and extinction risk of the world’s terrestrial mammals, which made it highly suitable for our analyses.
The matrix condition as a predictor of extinction risk transitions

Spatially explicit data on the condition of the matrix, as represented by the extent and change over time of high human pressure levels overlapping with the area of ‘unsuitable’ habitat surrounding patches of suitable habitat (after), was obtained from the recently updated global human footprint maps. These maps represent the most comprehensive global distribution of changing human pressure on the environment at 1 km resolution between 2000 and 2013, based on eight pressure layers: (i) built environments; (ii) intensive agriculture; (iii) pasture land; (iv) human population density; (v) night-time lights; (vi) roads; (vii) railways; and (viii) navigable waterways, all of which are driving the current extinction crisis. Each human footprint map provides a single pressure metric ranging from 0 to 50, where a value of 0 represents areas free of any human influence (e.g., terrestrial remaining wilderness), values of 4 or below represent areas of low human pressure (e.g., pasture lands), and values above 20 represent areas with very high pressure levels (e.g., densely populated semi-urban and urban environments).

In this analysis, we measured the current extent of high human footprint values and their change over time (between 2000 and 2013) in areas of ‘unsuitable’ habitat, using a defined human footprint threshold of 3 or above. This threshold was used as it is the strongest predictor of extinction risk transitions in terrestrial mammals, and is associated with the highest declines in mammalian movements and chimpanzee behavioral diversity. Based on previous studies, we considered high human footprint values as the extent and change over time of high pressure levels within species’ ranges have shown to be more sensitive to predict extinction risk than using mean pressure levels. We also considered the changes in the extent of high human footprint values after discarding areas where the human footprint was lower in 2013 than in 2000.
(assuming no change in these particular areas), as decreases in human pressure levels are likely to take time before having a measurable effect on species threat status, particularly for species with a long generation time period\(^\text{43}\).

**Changes in species extinction risk**

We used the IUCN Red List of Threatened Species\(^\text{75,80}\), the retrospective Red List Assessments published in Hoffman et al.\(^\text{54}\), and the IUCN list of genuine changes in the conservation status of mammal species (https://www.iucnredlist.org/resources/summary-statistics) to represent trends in extinction risk of terrestrial mammals. Following the classification of extinction risk transitions developed by Di Marco et al.\(^\text{42,43}\), we classified the species into two main groups, low-risk transitions and high-risk transitions (Fig. 1). The low-risk group includes species that retain a category of least concern, together with those species that move from any higher category of threat to a lower category assessment period. The high-risk group includes all species that retain a category of threatened or near threatened, together with those species that move from any lower category of threat to a higher category over time.

In this analysis, we classified species into the two extinction risk groups (low-risk transitions and high-risk transitions) based on the initial and final Red List category registered between 1996 and 2020. In order to test the sensitivity of this classification, we also classified all species into the two extinction risk groups based on the last two Red List assessments registered between 1996 and 2020 (i.e. the second last and last Red List categories registered between 1996 and 2020). We excluded species without a defined threat status (Data Deficient), and those already extinct at the beginning of the study period.
We used a multivariate Random Forest model to predict extinction risk transitions of terrestrial mammals (Fig. 1). Random Forest is a non-parametric, tree based, machine-learning technique that produces multiple decision trees using a randomly selected subset of training samples and variables to make a prediction\textsuperscript{55,81}. Due to its limited assumptions on data distributions, its high classification stability and performance, and its ability to cope well with a large number of potentially correlated predictors and non-linear responses, Random Forest is a highly suitable technique for species threat status classification\textsuperscript{62}. Furthermore, Random Forest modelling has shown to have the highest performance among several machine learning techniques tested for the prediction of global extinction risk of terrestrial mammals\textsuperscript{72}.

In combination with previously identified variables (Table 2), predictors included the degree of fragmentation of suitable habitat and the extent and change over time of high human footprint values in the matrix within species’ ranges. Because mammals of greater body size usually move farther\textsuperscript{82}, and diet may influence their movements as a result of differences in availability of resource types and foraging cost\textsuperscript{83,84}, we decided to include body size and dietary breadth as life-history predictors. We also included the reproductive traits weaning age and the gestation length. Other life-history traits were broadly captured by representing taxonomic orders of each species. To avoid potential circularity in the estimation of changes in extinction risk, we did not include species’ range size as a predictor\textsuperscript{38}. 


Table 2. Description of the selected variables to predict extinction risk transitions in terrestrial mammals.

| Class          | Variable                                      | Description                                                                                                                                                                                                 | Source |
|----------------|-----------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------|
| Pressure       | High human footprint extent in the matrix     | Proportion of the area of ‘unsuitable’ habitat overlapping with high human footprint values in 2000.                                                                                                         | 49,51  |
|                | High human footprint extent in patches of suitable habitat | Proportion of suitable habitat overlapping with high human footprint values in 2000.                                                                                                                         | 49,51  |
|                | High human footprint change in the matrix     | Difference in the proportion overlap between the area of ‘unsuitable’ habitat and high human footprint values during 2000 and 2013.                                                                            | 49,51  |
|                | High human footprint change in patches of suitable habitat | Difference in the proportion overlap between the area of suitable habitat and high human footprint values during 2000 and 2013.                                                                            | 49,51  |
| Environment    | Habitat fragmentation                         | Average Euclidean distance within patches of suitable habitat from the nearest patch edge.                                                                                                                   | 49,77  |
| Life-history | Patch isolation | Proportion of suitable habitat | Realm | Life-history | Body mass | Diet | Weaning age | Gestation length | Order |
|--------------|----------------|-------------------------------|-------|--------------|----------|------|-------------|-----------------|-------|
|              | Average Euclidean distance within the area of ‘unsuitable’ habitat from the nearest edge. | Proportion of suitable habitat within species’ ranges. | Biogeographic realm. | A generic proxy of species life history and energetic requirements. | Dietary categories: vertebrate carnivore (> 90% vertebrate matter ingested), invertebrate carnivore (> 90% invertebrate matter ingested), omnivore (10-90% animal matter ingested or 10-90% plant matter ingested), herbivore (> 90% plant matter ingested). | A proxy of species reproductive timing. | A proxy of species reproductive output. | Species taxonomic order. | After\textsuperscript{46} | 49 | 75,80 | 85–89 | 89–91 | 86,87 | 86,87 | 80 |
We measured the predictive importance of each variable using the Actual Impurity Reduction Importance metric. This metric is unbiased with regard to the number of categories in the variables, and it computes reliable importance estimates without the extra computing cost of permutations. We then calculated the relative predictive importance of each variable using the model improvement ratio (MIR) metric. Unlike the raw importance scores, the MIR metric is comparable among models. MIR is calculated as \( \frac{I_n}{I_{\text{max}}} \), where \( I_n \) is the importance of a given variable, and \( I_{\text{max}} \) is the maximum model improvement score. We reported the overall performance of the Random Forest model through cross-validation in terms of proportion of correctly classified species, proportion of correctly classified high-risk species (sensitivity), proportion of correctly classified low-risk species (specificity), and the true skill statistic (TSS = sensitivity + specificity – 1).

Assessing the influence of the matrix on the importance of fragmentation for predicting extinction risk transitions

To measure the influence of the matrix on the importance of fragmentation for the prediction of extinction risk transitions, we first defined two broad levels of quality of the matrix (low and high), and then built separate Random Forest models for species restricted to such levels based on the proportion of high human footprint values in the matrix of each species. When defining the two levels of quality of the matrix, the extent of high human footprint values in the matrix of each species was discretized into two intervals using an equal width discretization method. Using the Actual Impurity Reduction Importance metric and the MIR metric, we measured the relative predictive performance of fragmentation, including the other selected variables (Table 2), from the built Random Forest models. We used cross-validated measures of sensitivity,
specificity, and the true skill statistic to evaluate the overall performance of the models\textsuperscript{94}. We also used Wilcoxon rank sum tests to test for statistical differences in the degree of fragmentation between low-risk and high-risk species restricted to the defined levels of quality of the matrix. To determine the effect size of the degree of habitat fragmentation between low-risk and high-risk species for each of the levels of quality of the matrix, we used Cohen’s d statistic\textsuperscript{95}.

Sensitivity testing

To test the sensitivity of our model, we built additional Random Forest models based on the last two Red List assessments registered between 1996 and 2020 (i.e. the second last and last Red List categories registered during this period), and a different combination of the levels of habitat suitability to represent the extent of suitable habitat patches (high suitability instead of high and medium suitability combined) and the extent of the matrix (medium suitability and ‘unsuitable’ combined instead of ‘unsuitable’ habitat). From these models, the relative importance of each variable was quantified using the Actual Impurity Reduction Importance metric\textsuperscript{92} and the MIR metric\textsuperscript{93}. The overall performance of these models was reported through cross-validation in terms of sensitivity, specificity, and the true skill statistic\textsuperscript{94}.

All spatial analyses were performed in python using the ArcPy processing module from ArcGIS Pro 2.5.0\textsuperscript{96}. Statistical analyses were performed in R\textsuperscript{97}, using the packages ‘randomforest’\textsuperscript{98}, ‘caret’\textsuperscript{99}, ‘ranger’\textsuperscript{100}, ‘plotmo’\textsuperscript{101}, and ‘effsize’\textsuperscript{102}. 
Data availability

The Human Footprint dataset used in this study is available for download at https://doi.org/10.5061/dryad.3tx95x6d9. Habitat suitability models for the world’s terrestrial mammals are available upon request from the model developers (see https://globalmammal.org/habitat-suitability-models-for-terrestrial-mammals/). The raw data on extinction risk categories is available in R\textsuperscript{97}, using the package ‘rredlist’\textsuperscript{103}. The other datasets that support the findings of this study derive from published sources, cited in the Methods section and listed in Table 2.

Code Availability

All relevant codes used in this work are available upon request from the corresponding author (J.P.R.-D.).

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Acknowledgements

We thank Michelle Venter, Kristen Kieta and Rajeev Pillay for comments on earlier drafts of this manuscript.

Author contributions

J.P.R.-D. and O.V. conceived the study; J.P.R.-D. collected and analyzed all the data under advice of O.V., M.D., C.R., X.C.Ll., and M.A.; J.P.R.-D. led the writing of the manuscript with input from O.V., M.D., C.J.I., and C.R.

Additional information

Supplementary information accompanies this paper as a separate file.

Competing interest: The authors declare not competing interest.
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