

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 Corredor Llano

University of Northern British Columbia

Miguel Arias

University of Northern British Columbia

Oscar Venter

University of Northern British Columbia

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1 **Title**

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3

4 **Authors**

5 Juan Pablo Ramírez-Delgado*¹, Moreno Di Marco^{2,3}, James E.M. Watson^{3,4,5}, Chris J. Johnson¹,
6 Carlo Rondinini⁶, Xavier Corredor Llano¹, Miguel Arias¹, Oscar Venter¹

7

8 **Affiliations**

9 ¹*Natural Resources and Environmental Studies Institute, University of Northern British*
10 *Columbia, Prince George V2N 4Z9, Canada.*

11 ²*Department of Biology and Biotechnologies, Sapienza University of Rome, Rome 00185, Italy.*

12 ³*School of Earth and Environmental Sciences, University of Queensland, St Lucia 4072,*
13 *Australia.*

14 ⁴*Centre for Biodiversity and Conservation Science, School of Biological Sciences, The*
15 *University of Queensland, Brisbane 4072, Queensland, Australia.*

16 ⁵*Wildlife Conservation Society, Global Conservation Program, Bronx, NY 20460, USA.*

17 ⁶*Global Mammal Assessment Program, Department of Biology and Biotechnologies, Sapienza*
18 *University of Rome, Rome 00185, Italy.*

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

24 **Abstract**

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

37

38 **Main**

39 Although habitat loss is the leading cause of ongoing biodiversity loss¹⁻⁴, the degree to which
40 habitat fragmentation, defined as the spatial arrangement of remaining habitat for a given amount
41 of habitat loss, influences the loss of biodiversity has remained the focus of considerable debate⁵⁻
42 ¹⁰. Central to the debate has been a persistent uncertainty in disentangling the effects of habitat
43 loss on biodiversity from the effects of fragmentation *per se*, especially relative to the reduction
44 in patch size and the increase in patch isolation^{8,11}. Whereas some studies have challenged the
45 assumption of the impacts of fragmentation^{6,8,9,12}, others have demonstrated that the effects of
46 fragmentation are negative and stronger for local species^{5,7,13,14}, particularly in the tropics¹⁵ and

47 at intermediate (30–60%) levels of habitat amount^{16,17}. Resolving this debate is critical to not just
48 informing efforts to prioritize the protection and management of intact and fragmented
49 landscapes with the same total amount of habitat, but also to better understand the role of the
50 areas surrounding patches of habitat, commonly referred to as the ‘matrix’, in maintaining
51 biodiversity^{10,18,19}.

52
53 The traditional characterization of landscapes, which views patches of habitat as islands
54 embedded in a matrix of non-habitat, as assumed in classical theoretical models^{20,21}, has been
55 strongly criticized^{18,22–24}. This characterization has progressively been relaxed with approaches
56 based on the premise that the matrix should in fact be treated as a heterogeneous mosaic of
57 different land covers (e.g. ‘countryside biogeography’²⁵, and the ‘land-sharing’ and ‘land-
58 sparing’ approaches^{26–30}), as it is recognized that species use different matrices for foraging,
59 dispersing, and reproduction purposes^{31,32}. While high-contrast matrices (e.g. intensive
60 agricultural or built environments) act as movement barriers or ecological traps for many species,
61 with an elevated risk of mortality³³, low-contrast matrices (e.g. secondary forests or shade-grown
62 low-intensive agriculture in forested regions) may act as permeable barriers with a reduced risk
63 of mortality, even for those species typically considered habitat specialists^{25,27}. To date, however,
64 conservation and management assessments across different scales have focused mainly on
65 species’ primary habitat^{34,35}, thus limiting our understanding of their response to the matrix,
66 which may have direct implications for the design of functional landscapes³⁶ and the
67 prioritization of different conservation actions in fragmented landscapes³⁷.

68

69 Comparative extinction risk modelling is an approach for assessing the drivers of extinction risk
70 and its change over time, based on the relationship between species' life histories, the pressure
71 within species geographic ranges, and their threat status³⁸⁻⁴³. Built with readily available data,
72 this approach allows for the prediction of the risk of extinction of a larger number of species
73 compared with that provided by expert-based assessments. This more rapid approach can
74 substantially reduce resource requirements, as well as proactively inform conservation and
75 management strategies^{44,45}. Although the loss^{3,43} and fragmentation^{46,47} of habitat are among the
76 main determinants of species extinction risk, the influence of the matrix condition on the effects
77 of fragmentation and its relationship with species extinction risk has not been well evaluated for
78 any animal taxon at a global scale.

79
80 Here, we quantify the relationship between changes in the extinction risk of 4,327 terrestrial
81 mammals over a 24-year period (1996-2020), the degree of fragmentation of their suitable
82 habitat, and the levels of human pressure within the associated habitat matrix. Our goal is to test
83 the influence of human pressure within the matrix on the effects of fragmentation for
84 determining changes in species extinction risk globally. We focus on terrestrial mammals as they
85 have been used as a focal taxon in previous extinction risk analyses⁴⁸, they are known to be
86 sensitive to fragmentation⁴⁶, and data are available to delineate levels of suitable habitat and
87 'unsuitable' (i.e. matrix) habitat within their ranges⁴⁹. For each species, we quantify the degree of
88 fragmentation as the average Euclidean distance within patches of suitable habitat from the
89 nearest patch edge, and matrix condition as the extent and change over time of high human
90 pressure levels overlapping with the surrounding matrix. Spatial data representing the condition
91 of the matrix were obtained from the most comprehensive global maps of changing human

92 pressure on the environment⁵⁰, the recently updated human footprint maps⁵¹, which provide a
93 single metric that combines data on human activities, all of which are driving the current
94 biodiversity crisis³. We define a human footprint threshold of ≥ 3 out of 50 to represent the extent
95 of human-modified habitat within the matrix. This threshold was used as it has shown to be the
96 strongest predictor of transitions in extinction risk for terrestrial mammals⁴³. Furthermore, this
97 human footprint threshold is associated with the highest declines in mammalian movements⁵²
98 and chimpanzee behavioral diversity⁵³. Following previous studies^{42,43,54}, we classify species into
99 two groups of extinction risk, low-risk transitions and high-risk transitions (Fig. 1), based on the
100 initial and final Red List category registered between 1996 and 2020. In combination with other
101 predictors of extinction risk (see Table 2 for a description), we quantify the relative predictive
102 importance of habitat fragmentation and the condition of the matrix for determining extinction
103 risk transitions in terrestrial mammals.

104

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

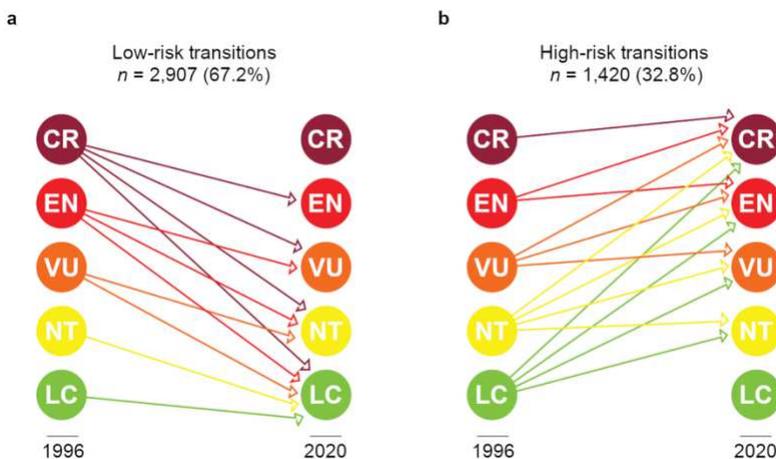
109

110 **Results**

111 **Changes in species extinction risk**

112 When classifying extinction risk transitions with the initial and final Red List categories
113 registered between 1996 and 2020, we found that 2,907 (67.2%) species faced a low-risk
114 transition and 1,420 (32.8%) a high-risk transition (Fig. 1). The proportions of low-risk and high-

115 risk transitions were almost unchanged when applying a different classification routine
116 (Supplementary Fig. 1; Supplementary Note 1).

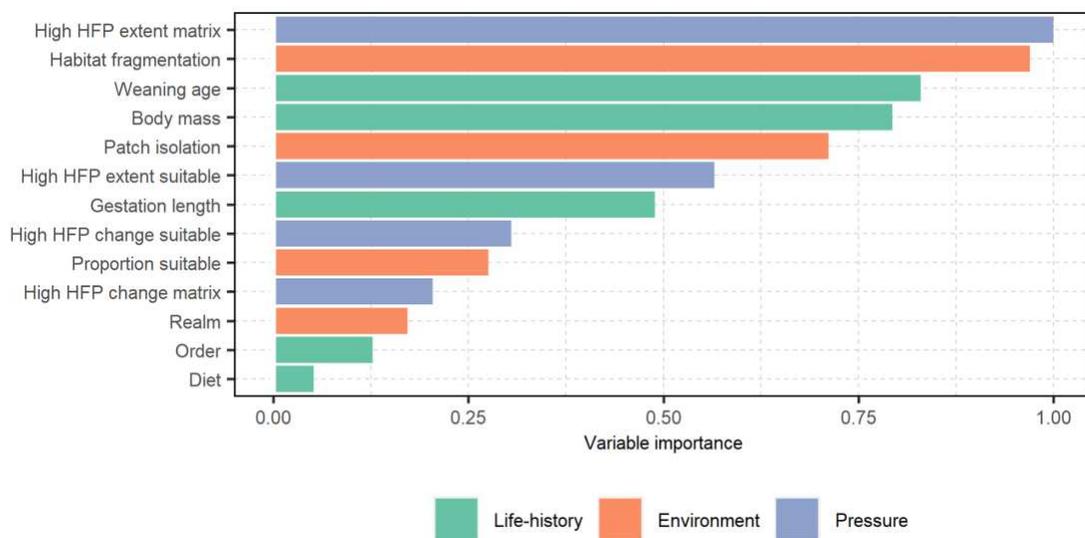


117
118 **Figure 1. Classification of species extinction risk transitions based on past and present**
119 **IUCN Red List categories***. **a** Represents low-risk transitions, which included species that
120 retained a category of least concern, together with those species that moved from any higher
121 category of threat to a lower category between 1996 and 2020. **b** Represents high-risk transitions,
122 which included all species that retained a category of threatened or near threatened, together with
123 those species that moved from any lower category of threat to a higher category between 1996
124 and 2020. *Acronyms refer to the IUCN Red List categories, including Least Concern (LC), Near
125 Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) (figure
126 adapted from Di Marco et al.⁴³).

127
128 **Predicting transitions in species extinction risk**

129 Using a Random Forest model for classification⁵⁵, we measured the performance of an array of
130 life-history, environmental and pressure variables for the prediction of extinction risk transitions
131 (see Table 2 for a description). We found that the extent of high human footprint values in the

132 matrix and the degree of fragmentation of suitable habitat had higher predictive performance
 133 than life-history traits and other pressure and environmental variables (Fig. 2). When employing
 134 a different classification routine of extinction risk transitions (i.e. when transitions were
 135 classified using the second last and last Red List category instead of the initial and final Red List
 136 categories between 1996 and 2020), these two variables remained as the most important
 137 predictors of extinction risk (Supplementary Fig. 2a), suggesting that these results are robust to
 138 changes in species threat status.



139

140 **Fig. 2. Relative importance of selected variables for the prediction of extinction risk**
 141 **transitions in terrestrial mammals.** Variables are colour-coded according to their broad class
 142 (life-history, environment, and human pressure). The description of each variable can be found in
 143 Table 2. High levels of the human footprint (HFP) included values of 3 or above.
 144

145 Interestingly, our results show that the degree of fragmentation of suitable habitat had higher
 146 predictive performance than the change in high human footprint values (as defined by increases
 147 in high human footprint values through time) within suitable habitat and the proportion of

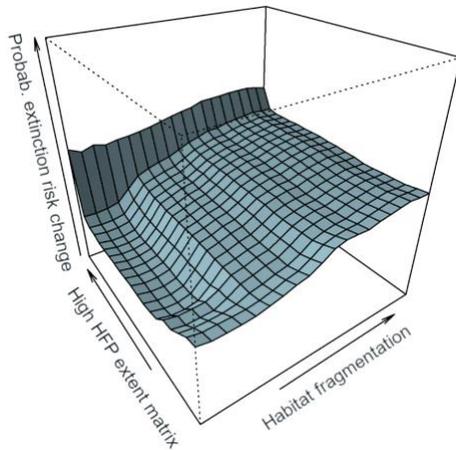
148 suitable habitat (Fig. 2). This result is supported by a sensitivity analysis where a different
149 classification routine of extinction risk transitions and a different combination of the levels of
150 habitat suitability were applied (Supplementary Fig. 2a and 2b). This suggests that habitat
151 fragmentation better predicts changes in species extinction risk than habitat loss and habitat
152 amount at a global scale.

153

154 Our results also show that the predictive importance of the change in high human footprint
155 values within the extent of suitable habitat is greater than that within the extent of the matrix
156 (Fig. 2). This result was confirmed when employing a different classification routine of
157 extinction risk transitions and a different combination of the levels of habitat suitability
158 (Supplementary Fig. 2a and 2b), highlighting the key influence of the extent and change over
159 time of high human pressure levels within species' ranges⁴³.

160

161 When looking at the interaction between the degree of fragmentation of suitable habitat and the
162 condition of the matrix on the probability of changes in species extinction risk (Fig. 3), we found
163 that the probability of high-risk transitions increased with an increasing degree of habitat
164 fragmentation and an increasing extent of high human pressure levels within the matrix. This
165 trend was reversed to an increased probability of low-risk transitions.



166

167 **Fig. 3. Interaction of the degree of habitat fragmentation with the matrix condition on**
 168 **extinction risk transitions in terrestrial mammals.** The plot represents the positive interaction
 169 between the degree of fragmentation of suitable habitat and the matrix condition for high-risk
 170 transition. The interaction between the degree of fragmentation of suitable habitat and the matrix
 171 condition for low-risk species is represented when the plot is inverted. The fragmentation metric
 172 was inverse-coded so high values represent high degree of fragmentation. The extent of high
 173 human footprint values in the matrix was arcsine square-root-transformed to avoid variance
 174 instability when handling proportions close to zero. The description of each variable is given in
 175 Table 2. High levels of the human footprint (HFP) included values of 3 or above.

176

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

181

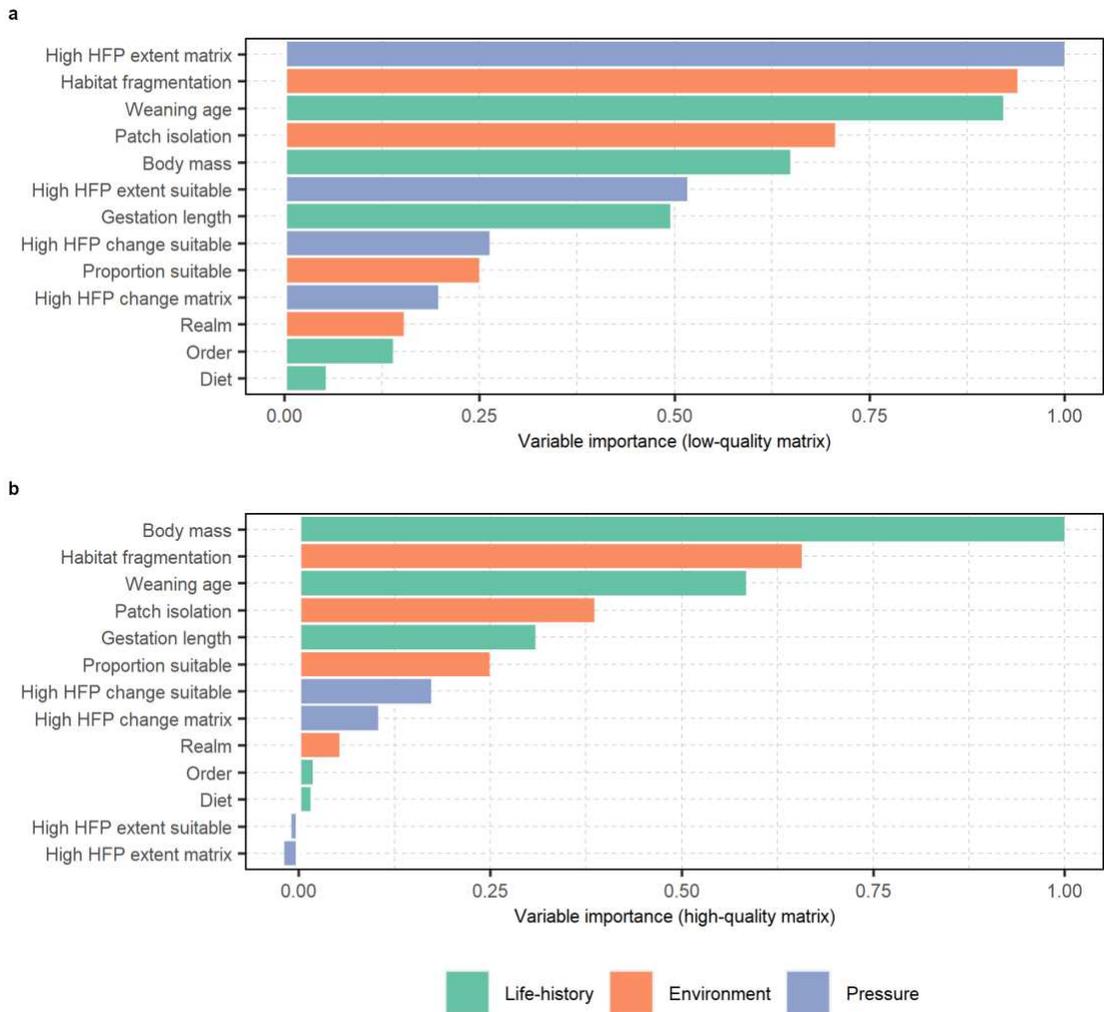
182 The predictive performance of our model did not markedly change compared to the models built
 183 based on a different classification routine of extinction risk transitions and a different

184 combination of the levels of habitat suitability (Supplementary Table 1). Thus, the model is
185 robust to changes in species threat status and in the levels of habitat suitability.

186

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

189 In order to measure the influence of the matrix on the importance of fragmentation for the
190 prediction of extinction risk transitions, we first discretized the extent of high human footprint
191 values within the matrix into two broad levels as a proxy for matrix quality: 'low-quality matrix',
192 representing species with $\geq 50\%$ of the extent of their matrix overlapping with high human
193 footprint values ($n = 2,529$ low-risk species and 1,250 high-risk species); and 'high-quality
194 matrix', representing species with $< 50\%$ of the extent of their matrix overlapping with high
195 human footprint values ($n = 341$ low-risk species and 111 high-risk species). We then built
196 separate Random Forest models for each level of quality of the matrix in order to compare the
197 predictive performance of the degree of fragmentation of suitable habitat between the defined
198 levels of quality of the matrix. We found that the degree of fragmentation had a higher relative
199 predictive performance for species with low-quality matrix (Fig. 4a) than that observed for
200 species with low-quality matrix (Fig. 4b), with a decrease of 30.1%. Notably, the relative
201 predictive importance of the extent of high human footprint values in the matrix was markedly
202 higher for the low-quality matrix model compared with the high-quality matrix model,
203 suggesting that the lower the quality of the matrix, the higher the predictive importance of the
204 matrix.



205

206

Fig. 4. Influence of the matrix condition on the relative importance of selected variables for

207

the prediction of extinction risk transitions in terrestrial mammals. a Shows the relative

208

importance of each predictor with low-quality matrix, which included species with proportions \geq

209

50% of the extent of their matrix overlapping with high human footprint values ($n = 2,529$ low-

210

risk species and 1,250 high-risk species). **b** Shows the relative importance of each predictor with

211

high-quality matrix, which included species with proportions $< 50\%$ of the extent of their matrix

212

overlapping with high human footprint values ($n = 341$ low-risk species and 111 high-risk

213

species). Variables are colour-coded according to their broad class (life-history, environment, and

214 human pressure). The description of each variable is given in Table 2. High levels of the human
215 footprint (HFP) included values of 3 or above.

216

217 When looking at the difference in the degree of fragmentation for low-risk and high-risk species,
218 we found that those classified as high-risk had higher degrees of fragmentation, with a difference
219 that was significant for each of the levels of quality of the matrix (p -values < 0.001 ; Wilcoxon
220 signed rank test, one-sided). When it comes to the effect size of the degree of fragmentation
221 between low-risk and high-risk species, we found that such an effect was slightly lower for those
222 species with matrices of high-quality habitat (Cohen's $d = 0.15$; Supplementary Fig. 3a)
223 compared to those with matrices of low-quality habitat (Cohen's $d = 0.16$; Supplementary Fig.
224 3b).

225

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

230

231 **Table 1. Cross-validation results of the Random Forest models for the prediction of**
232 **extinction risk transitions in terrestrial mammals with low- and high-quality matrix.** The
233 cross-validation was performed in terms of proportion of correctly classified species (accuracy),
234 proportion of correctly classified high-risk species (sensitivity), proportion of correctly classified
235 low-risk species (specificity), and the true skill statistic (TSS = sensitivity + specificity – 1).
236 Low-quality matrix included species with proportions $\geq 50\%$ of the extent of their matrix

237 overlapping with high human footprint values ($n = 2,529$ low-risk species and 1,250 high-risk
 238 species). High-quality matrix included species with proportions $< 50\%$ of the extent of their
 239 matrix overlapping with high human footprint values ($n = 341$ low-risk species and 111 high-risk
 240 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

241

242 **Discussion**

243 Understanding the external conditions under which a species is likely to face an increased risk of
 244 extinction are necessary to inform conservation policies and management strategies⁴². We found
 245 that the condition of the matrix, as defined by the extent of high human footprint values between
 246 patches of suitable habitat, strongly influenced the effects of fragmentation on extinction risk
 247 transitions of terrestrial mammals. Specifically, we found that when predicting changes in the
 248 risk of extinction of terrestrial mammals, matrices of high-quality habitat decreased the relative
 249 predictive importance of the degree of habitat fragmentation by $\sim 30\%$ compared with low-
 250 quality matrices. To the best of our knowledge, this finding is the first to demonstrate
 251 consistently whether and how much human pressure within the matrix alters the importance of
 252 habitat fragmentation as a predictor of extinction risk change. This finding is consistent with
 253 previous studies showing that the use of the matrix is among the main determinants of the

254 vulnerability of mammalian populations to local extinction in fragmented landscapes^{25,56,57}, and
255 supports recent findings demonstrating that species living in forested landscapes with a low-
256 quality matrix (in terms of plant biomass) are more vulnerable to extinction than those living in
257 forested landscapes with a higher quality matrix⁵⁸.

258

259 Our results showed that species with greater fragmentation and lower quality matrix within their
260 ranges tended to be at greater risk of extinction. As reported by others⁴⁸, this might indicate that
261 species at a lower risk of extinction are able to exploit a greater number of habitats and resources
262 compared to species in the high-risk group. This result might be related to the fact that species
263 occurring in regions with low rates of historical disturbance are more likely to be sensitive to
264 fragmentation¹⁵, and thus more likely to face an increased risk of extinction. That would suggest
265 that those species within the high-risk group are mainly concentrated in the tropics, particularly
266 in forested landscapes, where deforestation continues at a rapid rate^{59,60}. In fact, ~33%, ~34%,
267 and ~45% of all species restricted to the Neotropical, Afrotropical, and Indo-Malay
268 biogeographic realms, respectively, were facing an increased risk of extinction between 1996 and
269 2020, which is consistent with these findings.

270

271 In our extinction risk model, some variables had higher predictive performance than others. For
272 example, the extent of high human footprint values in the matrix was the most important
273 predictor of changes in species extinction risk. This result contrasts with the findings from
274 previous extinction risk modelling exercises for mammals, where the predictive importance of
275 human pressure was found to be lower than life-history traits or environmental conditions^{48,61,62}.
276 However, it helps confirm the findings of one recent extinction risk modelling exercise for

277 mammals⁴³, where the extent of high human footprint values within species' ranges had higher
278 predictive importance than environmental conditions, life-history traits, and other measures of
279 human pressure. This result may, in part, be explained by the fact that species are increasingly
280 exposed to anthropogenic land covers^{63,64}, especially in the matrix where higher contrast (i.e.
281 lower quality habitat) likely prevents their movement⁵² and elevates their mortality³³ (e.g. by
282 roadkill⁶⁵ or increasing predation by feral animals⁶⁶).

283

284 The degree of fragmentation of suitable habitat was also found to be a key correlate of change in
285 extinction risk. This finding is in line with previous extinction risk modelling showing that the
286 inclusion of habitat fragmentation as a predictor increases the explanatory power of the
287 models^{46,47}. In particular, this result supports previous findings showing that terrestrial mammals
288 with higher fragmentation have smaller ranges, lower proportions of suitable habitat and are at
289 greater risk of extinction⁴⁶.

290

291 Conflicting results on the effects of fragmentation *per se* on biodiversity have arisen from studies
292 attempting to separate 'independent' effects of habitat loss from those of habitat fragmentation¹¹.
293 Some studies have argued that the effects of habitat loss are greater and more negative
294 (e.g.^{6,8,9,12}), while others have demonstrated that the effects due to fragmentation, such as
295 declining patch size, increasing habitat isolation, and increasing edge effects, are essentially
296 negative and lasting (e.g.^{5,7,13,14}). However, in real landscapes, habitat loss inevitably causes
297 habitat fragmentation, and both act in synergy with other threats to biodiversity^{67,68}. Thus, there
298 is little practical value in attempting to separate the effects of habitat loss and fragmentation^{7,69–}
299 ⁷¹. Our study does not attempt to resolve the current debate as to whether and how habitat

300 fragmentation *per se* (i.e. the spatial arrangement of remaining habitat for a given amount of
301 habitat loss) influences biodiversity⁵⁻¹⁰, but the results showed that the degree of fragmentation
302 of suitable habitat was more important than the change in high human footprint values (as
303 represented by increases in high human pressure levels over time) within suitable habitat and the
304 proportion of suitable habitat. This suggests that changes in species extinction risk are primarily
305 determined by the fragmentation of habitat, and secondarily by the loss and the amount of habitat
306 within species' ranges. However, there is also the possibility that the loss of most suitable habitat
307 patches had already occurred before the beginning of the study period, resulting in fragmentation
308 being a more important predictor of extinction risk than habitat loss and habitat amount.

309

310 Our models were better at correctly classifying low-risk transitions than high-risk transitions.
311 This suggests that the external conditions leading to a high-risk transition might be more difficult
312 to identify than those leading to a low-risk transition, as also indicated in previous studies⁴¹⁻
313 ^{43,62,72}. However, it is important to acknowledge that the exclusion of other variables associated
314 with pressure (such as overhunting, disease, invasive species, and climate change) and life-
315 history traits (such as rarity, dispersal mode, and ranging behavior) could have increased the
316 uncertainty of our predictions, and thus influenced the ability of our models to correctly classify
317 high-risk transitions.

318

319 Our modelling framework can be used to proactively inform conservation and management
320 strategies seeking to minimize the number of species that are facing or will face an increased risk
321 of extinction. This includes species that are currently classified as threatened and those that are
322 likely to become so if human activities continue to expand and intensify into the future. An

323 important next step will be to create a global map that captures the matrix condition for the
324 world's terrestrial mammals. This will require weighting the extent of the matrix of all terrestrial
325 mammals with the human footprint as a proxy for matrix quality within species' geographic
326 distributions. If species threat statuses are considered, this could have the potential to identify
327 where conservation actions are needed to be improved. For example, in those locations where
328 species with an increased risk of extinction show a low-quality habitat within their matrix, a
329 land-sparing approach could be effective as it maximizes conservation actions on the remaining
330 patches of suitable habitat while concentrating agriculture production elsewhere^{26,28-30}.

331 Alternatively, in those locations where species with an increased risk of extinction show a high-
332 quality habitat within their matrix, a land-sharing approach would work better as it minimizes the
333 impact of agriculture production by maintaining or restoring the conservation value of the land
334 already farmed²⁷⁻³⁰.

335

336 Our results indicate that species suffering from greater pressure in their matrix require particular
337 conservation attention. Among these species, those with smaller ranges require careful
338 management of the areas surrounding their suitable habitat, especially in light of the current and
339 future effects of climate and land-use change⁷³. Our results also highlight the potential of high-
340 quality matrices to mitigate the effects of fragmentation on species extinction risk, thus
341 suggesting that in addition to efforts to maintain remaining suitable habitat^{32,35,74}, there is a need
342 for restoration of habitats in the matrix.

343

344

345

346 **Methods**

347 **Habitat suitability models**

348 We used habitat suitability models developed by Rondinini et al.⁴⁹ to represent the extent of
349 suitable habitat patches and the extent of the matrix of 4,327 out of 5,722 extant terrestrial
350 mammals, corresponding to 76% of all species in the group⁷⁵. These models were built for the
351 year 2000 at a spatial resolution of 300 m, based on species' elevation range and other habitat
352 affinities, including preferred land cover types and relationship to water bodies. Data for each
353 species were extracted from the International Union for Conservation of Nature (IUCN) datasets,
354 and using expert information combined with spatial data on habitat variables. The models
355 include three levels of habitat suitability: (i) high, representing primary habitat or preferred
356 habitat where the species can persist; (ii) medium, representing secondary habitat where the
357 species can occur but not persist without nearby high suitable habitat; and (iii) 'unsuitable',
358 representing locations where the species is expected to occasionally or never be found.

359

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

366

367 In this analysis, we combined high and medium habitat suitability to represent the extent of
368 suitable habitat patches, and use the level of 'unsuitable' habitat to represent the extent of the

369 matrix of each species. We also applied a different combination of the levels of habitat suitability
370 when representing the extent of suitable habitat patches (high suitability instead of high and
371 medium suitability combined) and the extent of the matrix (medium suitability and ‘unsuitable’
372 combined instead of ‘unsuitable’ habitat) of each species.

373

374 **Habitat fragmentation as a predictor of extinction risk transitions**

375 For each species, we measured the degree of habitat fragmentation by quantifying the average
376 Euclidean distance of all the pixels within patches of suitable habitat from the nearest patch
377 edge⁷⁷. Large values of the average Euclidean distance represented low degrees of habitat
378 fragmentation, whereas small values represented high degrees of habitat fragmentation.

379 Additionally, we calculated the average Euclidean distance between patches of suitable habitat
380 through the surrounding matrix (i.e., the average Euclidean distance of all the pixels within
381 ‘unsuitable’ habitat from the nearest edge) to account for patch isolation (after⁴⁶). Here, large
382 values of the average Euclidean distance represented low degrees of patch isolation, and small
383 values represented high degrees of patch isolation. The average Euclidean distance was
384 considered because this metric does not require a predetermined distance threshold of what
385 constitutes an edge, accounts for different shapes of fragments and landscapes patterns and
386 arrangements, accounts for the distribution of habitat area⁷⁸, is comparable across landscapes of
387 different extents, and provides stable and readily interpretable information⁷⁶. Moreover, average
388 Euclidean distance has been shown to be singularly valuable in quantifying the relationship
389 between habitat fragmentation and extinction risk of the world’s terrestrial mammals⁴⁶, which
390 made it highly suitable for our analyses.

391

392 **The matrix condition as a predictor of extinction risk transitions**

393 Spatially explicit data on the condition of the matrix, as represented by the extent and change
394 over time of high human pressure levels overlapping with the area of ‘unsuitable’ habitat
395 surrounding patches of suitable habitat (after⁴³), was obtained from the recently updated global
396 human footprint maps⁵¹. These maps represent the most comprehensive global distribution of
397 changing human pressure on the environment at 1 km resolution between 2000 and 2013, based
398 on eight pressure layers⁵⁰: (i) built environments; (ii) intensive agriculture; (iii) pasture land; (iv)
399 human population density; (v) night-time lights; (vi) roads; (vii) railways; and (viii) navigable
400 waterways, all of which are driving the current extinction crisis³. Each human footprint map
401 provides a single pressure metric ranging from 0 to 50, where a value of 0 represents areas free
402 of any human influence (e.g., terrestrial remaining wilderness), values of 4 or below represent
403 areas of low human pressure (e.g., pasture lands), and values above 20 represent areas with very
404 high pressure levels (e.g., densely populated semi-urban and urban environments).

405

406 In this analysis, we measured the current extent of high human footprint values and their change
407 over time (between 2000 and 2013) in areas of ‘unsuitable’ habitat, using a defined human
408 footprint threshold of 3 or above. This threshold was used as it is the strongest predictor of
409 extinction risk transitions in terrestrial mammals⁴³, and is associated with the highest declines in
410 mammalian movements⁵² and chimpanzee behavioral diversity⁵³. Based on previous studies^{43,79},
411 we considered high human footprint values as the extent and change over time of high pressure
412 levels within species’ ranges have shown to be more sensitive to predict extinction risk than
413 using mean pressure levels. We also considered the changes in the extent of high human
414 footprint values after discarding areas where the human footprint was lower in 2013 than in 2000

415 (assuming no change in these particular areas), as decreases in human pressure levels are likely
416 to take time before having a measurable effect on species threat status, particularly for species
417 with a long generation time period⁴³.

418

419 **Changes in species extinction risk**

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

430

431 In this analysis, we classified species into the two extinction risk groups (low-risk transitions and
432 high-risk transitions) based on the initial and final Red List category registered between 1996
433 and 2020. In order to test the sensitivity of this classification, we also classified all species into
434 the two extinction risk groups based on the last two Red List assessments registered between
435 1996 and 2020 (i.e. the second last and last Red List categories registered between 1996 and
436 2020). We excluded species without a defined threat status (Data Deficient), and those already
437 extinct at the beginning of the study period.

438 **Predicting extinction risk transitions**

439 We used a multivariate Random Forest model to predict extinction risk transitions of terrestrial
440 mammals (Fig. 1). Random Forest is a non-parametric, tree based, machine-learning technique
441 that produces multiple decision trees using a randomly selected subset of training samples and
442 variables to make a prediction^{55,81}. Due to its limited assumptions on data distributions, its high
443 classification stability and performance, and its ability to cope well with a large number of
444 potentially correlated predictors and non-linear responses, Random Forest is a highly suitable
445 technique for species threat status classification⁶². Furthermore, Random Forest modelling has
446 shown to have the highest performance among several machine learning techniques tested for the
447 prediction of global extinction risk of terrestrial mammals⁷².

448

449 In combination with previously identified variables (Table 2), predictors included the degree of
450 fragmentation of suitable habitat and the extent and change over time of high human footprint
451 values in the matrix within species' ranges. Because mammals of greater body size usually move
452 farther⁸², and diet may influence their movements as a result of differences in availability of
453 resource types and foraging cost^{83,84}, we decided to include body size and dietary breadth as life-
454 history predictors. We also included the reproductive traits weaning age and the gestation length.
455 Other life-history traits were broadly captured by representing taxonomic orders of each species.
456 To avoid potential circularity in the estimation of changes in extinction risk, we did not include
457 species' range size as a predictor³⁸.

458

459

460 **Table 2. Description of the selected variables to predict extinction risk transitions in**
 461 **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

	Patch isolation	Average Euclidean distance within the area of 'unsuitable' habitat from the nearest edge.	After ⁴⁶
	Proportion of suitable habitat	Proportion of suitable habitat within species' ranges.	49
	Realm	Biogeographic realm.	75,80
Life-history	Body mass	A generic proxy of species life history and energetic requirements.	85-89
	Diet	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).	89-91
	Weaning age	A proxy of species reproductive timing.	86,87
	Gestation length	A proxy of species reproductive output.	86,87
	Order	Species taxonomic order.	80

463 We measured the predictive importance of each variable using the Actual Impurity Reduction
464 Importance metric⁹². This metric is unbiased with regard to the number of categories in the
465 variables, and it computes reliable importance estimates without the extra computing cost of
466 permutations. We then calculated the relative predictive importance of each variable using the
467 model improvement ratio (MIR) metric⁹³. Unlike the raw importance scores, the MIR metric is
468 comparable among models. MIR is calculated as $[I_n/I_{max}]$, where I_n is the importance of a given
469 variable, and I_{max} is the maximum model improvement score. We reported the overall
470 performance of the Random Forest model through cross-validation in terms of proportion of
471 correctly classified species, proportion of correctly classified high-risk species (sensitivity),
472 proportion of correctly classified low-risk species (specificity), and the true skill statistic (TSS =
473 sensitivity + specificity - 1)⁹⁴.

474

475 **Assessing the influence of the matrix on the importance of fragmentation for predicting** 476 **extinction risk transitions**

477 To measure the influence of the matrix on the importance of fragmentation for the prediction of
478 extinction risk transitions, we first defined two broad levels of quality of the matrix (low and
479 high), and then built separate Random Forest models for species restricted to such levels based
480 on the proportion of high human footprint values in the matrix of each species. When defining
481 the two levels of quality of the matrix, the extent of high human footprint values in the matrix of
482 each species was discretized into two intervals using an equal width discretization method. Using
483 the Actual Impurity Reduction Importance metric⁹² and the MIR metric⁹³, we measured the
484 relative predictive performance of fragmentation, including the other selected variables (Table
485 2), from the built Random Forest models. We used cross-validated measures of sensitivity,

486 specificity, and the true skill statistic to evaluate the overall performance of the models⁹⁴. We
487 also used Wilcoxon rank sum tests to test for statistical differences in the degree of
488 fragmentation between low-risk and high-risk species restricted to the defined levels of quality of
489 the matrix. To determine the effect size of the degree of habitat fragmentation between low-risk
490 and high-risk species for each of the levels of quality of the matrix, we used Cohen's d statistic⁹⁵.

491

492 **Sensitivity testing**

493 To test the sensitivity of our model, we built additional Random Forest models based on the last
494 two Red List assessments registered between 1996 and 2020 (i.e. the second last and last Red
495 List categories registered during this period), and a different combination of the levels of habitat
496 suitability to represent the extent of suitable habitat patches (high suitability instead of high and
497 medium suitability combined) and the extent of the matrix (medium suitability and 'unsuitable'
498 combined instead of 'unsuitable' habitat). From these models, the relative importance of each
499 variable was quantified using the Actual Impurity Reduction Importance metric⁹² and the MIR
500 metric⁹³. The overall performance of these models was reported through cross-validation in
501 terms of sensitivity, specificity, and the true skill statistic⁹⁴.

502

503 All spatial analyses were performed in python using the ArcPy processing module from ArcGIS
504 Pro 2.5.0⁹⁶. Statistical analyses were performed in R⁹⁷, using the packages 'randomforest'⁹⁸,
505 'caret'⁹⁹, 'ranger'¹⁰⁰, 'plotmo'¹⁰¹, and 'effsize'¹⁰².

506

507

508

509 **Data availability**

510 The Human Footprint dataset used in this study is available for download at
511 <https://doi.org/10.5061/dryad.3tx95x6d9>. Habitat suitability models for the world's terrestrial
512 mammals are available upon request from the model developers (see
513 <https://globalmammal.org/habitat-suitability-models-for-terrestrial-mammals/>). The raw data on
514 extinction risk categories is available in R⁹⁷, using the package 'rredlist'¹⁰³. The other datasets
515 that support the findings of this study derive from published sources, cited in the Methods
516 section and listed in Table 2.

517

518 **Code Availability**

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

521

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756 **Author contributions**

757 J.P.R.-D. and O.V. conceived the study; J.P.R.-D. collected and analyzed all the data under advice
758 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
759 from O.V., M.D., C.J.J., and C.R.

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761 **Additional information**

762 **Supplementary information** accompanies this paper as a separate file.

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764 **Competing interest:** The authors declare not competing interest.

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