

Range area matters, and so does spatial configuration: predicting conservation status in vertebrates

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1 *Title:* Range area matters, and so does spatial configuration: predicting conservation
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15

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29

30 **ABSTRACT**

31 The current rapid loss of biodiversity globally calls for improved tools to predict
32 conservation status. Conservation status varies among taxa and is influenced by intrinsic
33 species' traits and extrinsic factors. Among these predictors, the most consistently
34 recognized and widely available is geographic range area. However, ranges of equal
35 area can have diverse spatial configurations that reflect variation in threatening
36 processes and species' characteristics (e.g., dispersal ability), and can affect local and
37 regional population dynamics. The aim of this study is to assess if and how the spatial
38 configuration of a species' range relates to its conservation status. We obtained range
39 maps and two descriptors of conservation status: extinction risk and population trend,
40 from the IUCN for 11,052 species of amphibians, non-marine birds, and terrestrial
41 mammals distributed across the World. We characterized spatial configuration using
42 descriptors of shape and fragmentation (fragment number and size heterogeneity) and
43 used regression analysis to evaluate their role in explaining current extinction risk and
44 population trend. The most important predictor of conservation status was range area,
45 but our analyses also identified shape and fragmentation as valuable predictors. We
46 detected complex relationships, revealed by multiple interaction terms, e.g. more
47 circular shapes were negatively correlated with population trend, and heterogeneity was
48 positively correlated with extinction risk for small range areas but negatively for bigger
49 ranges. Considering descriptors of spatial configuration beyond size improves our
50 understanding of conservation status among vertebrates. The metrics we propose are
51 relatively easy to define (although values can be sensitive to data quality), and unlike
52 other correlates of status, like species' traits, are readily available for many species (all
53 of those with range maps). We argue that considering spatial configuration predictors is

54 a straightforward way to improve our capacity to predict conservation status and thus,

55 can be useful to promote more effective conservation.

56

57 *Keywords:* conservation, extinction, fragmentation, range, vertebrates

58 INTRODUCTION

59 Anthropogenic activities are causing the loss of many populations and species leading
60 to an important reduction in natural, economic and social capital (CBD 2010). Estimates
61 suggest that current rates of extinction are 3-4 orders of magnitude higher than natural
62 rates (Barnosky et al. 2011). Approximately 20% of extant vertebrate species are
63 classified as Threatened by the International Union for the Conservation of Nature
64 (IUCN, Hoffmann et al. 2010), and future scenarios predict further extinctions and
65 increased risk (Hurt et al. 2011, 2010, Pereira et al. 2010). As a result, there is growing
66 concern regarding how to achieve a significant reduction in future biodiversity loss
67 (CBD 2010, Sala et al. 2000). Predicting which species are at risk is key to achieve that
68 goal and develop more effective conservation management actions (Cardillo and
69 Meijaard 2012, Safi and Pettorelli 2010).

70 The best estimates of extinction risk and population trend are based on
71 Population Viability Analysis (PVA, Beissinger and McCullough 2002). However,
72 PVA generally require long-term and detailed data (Wenger et al. 2017). Thus,
73 estimates of PVA are available for relatively few species and regions. To overcome this
74 limitation, many studies have searched for correlates of conservation status, including
75 morphological, ecological, life history and behavioral species' traits (Cardillo et al.
76 2008, Davidson et al. 2009, Fritz et al. 2009, González-Suárez et al. 2013, González-
77 Suárez and Revilla 2013, Purvis et al. 2000). Among these correlates, the best/more
78 common statistical predictor of status for different taxa, is range area which is a
79 measure of the spatial extent of the geographical space a species occupies (Keith et al.
80 2018). Everything else being equal, larger range areas can host more individuals, and
81 thus, are associated with lower risk of extinction (Cardillo et al. 2008, Cardillo et al.
82 2005, Gaston 1994, Gaston and Fuller 2009, Orzechowski et al. 2015, Runge et al.

83 2015). Species in larger range areas are also at lower risk compared with those small
84 ranges because stochastic threats are less likely to impact the entirety of a large area
85 (Bland et al. 2016, IUCN 2017a).

86 There are several aspects that determine the risk of extinction of a species. The
87 IUCN (IUCN 2012) considers the following criteria to assess the risk of extinction of a
88 given species: the number of individuals, the generation length, the population trend,
89 and the range size and its spatial aggregation (IUCN 2012, Joppa et al. 2016, Keith et al.
90 2018, Murray et al. 2017). While a useful measure of conservation status, a species
91 range size can be difficult to measure (Gaston 1991, 2003, Gaston and Fuller 2009).
92 Gaston (1991) proposed two metrics: (1) the extent of a species occurrence (EEO)
93 defined as the area contained within the shortest continuous imaginary boundary which
94 can be drawn to encompass all the known, inferred or projected sites of present
95 occurrence of a taxon, excluding cases of vagrancy; and (2) the area of occupancy
96 (AOO) defined as the area of the EEO occupied by a taxon (IUCN 2012, 2017a). Both
97 AOO and EEO can be used as criteria to assess extinction risk under criterion B of the
98 IUCN Red List. In addition, the degree of fragmentation including number of locations
99 (the distribution of how the individuals are aggregated in subpopulations with more or
100 less population size and more or less isolated subpopulations), and the number of
101 locations can be used under criteria B and D (Collen et al. 2016, IUCN 2012, 2017b).

102 At the local/population scale, other spatial configuration aspects have been
103 shown to influence extinction risk and population trends (Bascompte and Solé 1998,
104 Crooks et al. 2017, David Tilman and Kareiva 1997, Hanski 1999, Levins 1969,
105 MacArthur and Wilson 1967, Pfeifer et al. 2017). Landscapes are heterogeneous spaces
106 with varying degrees of habitat suitability (Forman 1995, Forman and Godron 1986).
107 Habitat suitability also varies within occupied fragments between the border, where is

108 usually lower, and the core areas, where tends to be higher (Bascompte and Solé 1995).
109 Therefore, for a given area the shape of the fragment is important. Fragments with a
110 greater ratio of border to core tend to have lower habitat suitability and thus, less
111 carrying capacity, than more compact or circular fragments. The viability of spatially
112 structured populations is also influenced by the degree of fragmentation, i.e., the size
113 and number of fragments, of the available habitat (Gyllenberg and Hanski 1992, Hanski
114 and Gyllenberg 1997, Hanski and Gyllenberg 1993). Heterogeneity in fragment size
115 may also influence vulnerability. When heterogeneity is large, with one fragment much
116 larger than the rest, vulnerability is mostly determined by the probability of extinction
117 of this largest fragment, and larger fragments are less likely to become extinct (Hanski
118 et al. 1996). However, if threatening impacts concentrate on that larger patch the risk
119 could be greater with high heterogeneity than if similarly sized fragments (exposed to
120 different risks) existed.

121 Complete species' ranges also show diverse spatial configurations, e.g. multiple
122 fragments of varying sizes, located at different distances, and with diverse shapes that
123 differ in their border to area ratios (Brown 1995, Channell and Lomolino 2000a, b,
124 Gaston 1990, Gaston 1994, Gaston 2003, Gaston 2008, 2009, Lawton 1993). Some of
125 this variation reflects differences in geographic conditions and species' traits (dispersal
126 abilities or habitat specialization). Additionally, variation in spatial configuration can
127 reflect effects of human impacts, such as changes in land use or climate change, which
128 can cause local extinctions leading to area loss, changes in shape and fragmentation, and
129 altered patterns of dispersal and colonization (Albrecht et al. 2017, Turvey et al. 2015).
130 Arguably, ignoring variation in the spatial configuration of species' ranges could lead to
131 over- or under-estimation of conservation status and thus, less effective use of
132 conservation resources. Previous studies have assessed the effects of different spatial

133 metrics on conservation status (Cardillo et al. 2008, Joppa et al. 2016, Keith et al. 2018,
134 Murray et al. 2017), but we lack a comprehensive evaluation covering different taxa and
135 testing multiple descriptors.

136 Here, we evaluate if conservation status, based on assessments of extinction risk
137 and global population trend, correlates with several spatial descriptors of species' ranges
138 related to size, shape and fragmentation (defined by fragment number and size
139 heterogeneity) for three groups of vertebrates: amphibians, non-marine birds, and
140 terrestrial mammals. Our analyses excluded species for which extinction risk
141 assessments were based on spatial criteria to avoid circularity, as well as species from
142 marine systems as information on their range is sparse compared to those in terrestrial
143 areas (Johnston et al. 2015). Although potentially important, we did not consider
144 fragment isolation because it is largely driven by species' dispersal abilities which are
145 not well-described and are distinct within the studied taxonomic groups (so
146 generalizations would be inaccurate). Based on metapopulation theory we predict that,
147 for a given area, conservation status will be worst in ranges with more fragments, higher
148 border to area ratios (irregular shapes), and with more homogeneous (equally sized)
149 fragments (Fig. 1). We also expect these effects of spatial configuration to be
150 particularly relevant for species with small ranges because they presumably have
151 smaller population sizes which are more susceptible to extinction (Hanski 1999).

152

153 **METHODS**

154 **Data**

155 Species maps were downloaded from the International Union for Conservation of
156 Nature (IUCN 2015) for all available species of amphibians, non-marine birds, and
157 terrestrial mammals. Reptile and fish data are only available for particular clades

158 (assessments are ongoing) and thus, these vertebrate groups were not considered for this
159 general study. IUCN spatial maps are not perfect representations of each species
160 distribution but are the best possible map assessors can make considering the available
161 information (IUCN 2018). These maps are depicted as polygons, and each polygon has
162 information about several attributes including presence, origin, and seasonality (IUCN
163 2018). Ideally, polygons for these maps should be drawn by assessors using occurrence
164 data, but the methods and the quality and quantity of the occurrence data can vary
165 across assessment. Using occurrence data a species EOO can be directly calculated
166 linking locations by a minimum convex polygon, and AOO can be estimated by the
167 overlap of species occurrences with a grid with a standard cell size (Lee et al 2019).
168 However, the IUCN provides only the polygons defined by the assessor, not the
169 occurrence data. Given this limitation we estimated range size here using the approach
170 taken by most previous studies (Cardillo et al. 2008, Purvis et al. 2000): adding the area
171 of polygons classified as native or reintroduced in origin, with extant or probably extant
172 presence, and seasonality values of resident, breeding season, or non-breeding season
173 for birds, and all seasonality values for amphibians and mammals (IUCN 2018; Table
174 A1). This estimate approximates AOO in many cases, but could be larger (approaching
175 EOO) for species in which species maps were defined with poor quality data or making
176 broad assumptions about occupancy. We projected the selected polygons using the
177 Winkel tripel projection, which aims to minimize the three kinds of distortions: area,
178 direction and distance and with the Cylindrical equal area projection which maintain the
179 area.

180 From each of the projected maps we used ArcMap 9.3 (ESRI 2008) to measure
181 geometries and R 3.1.2 (R Development Core Team 2017) to process the information,
182 we calculated four variables: range size (*Area*), fragment shape (*Circularity*), number of

183 fragments (*N_frag*), and fragment size heterogeneity (*Heterogeneity*; definitions in Fig.
184 1). To minimize the error in our variables due to distortions from projections, we used
185 Cylindrical equal area to calculate *Area*, *N_frag* and *Heterogeneity*, and Winkel tripel to
186 calculate *Circularity*. To better evaluate the role of fragmentation we limited our
187 analyses to ranges with >1 distinct fragments (the minimum required to estimate
188 *Heterogeneity*; Table A1). We tested the correlation among variables for each class and
189 type analysis using Spearman correlation (Tables A2 and A3). In addition, because we
190 expected spatial descriptors could be affected by *Area* (e.g., heterogeneity may be more
191 likely in widely distributed species) we also explored how *Circularity*, *N_frag* and
192 *Heterogeneity* vary with *Area* with correlation plots (Fig. A1) and fitting generalized
193 linear mixed models for each variable (Table A4) with *Area* as the predictor and
194 including taxonomic information (order, family, and genus) as random factors to control
195 for evolutionary non-independence of the observations following González-Suárez and
196 Revilla (2013), using the function *lmer* from the “lme4” package (Bolker 2018) in R.

197 To define conservation status we used two different metrics from the IUCN
198 (IUCN 2015). First, we considered extinction risk as described by the Red List Status,
199 an ordinal variable with levels (from low to high risk): Least Concern, Near Threatened,
200 Vulnerable, Endangered and Critically Endangered. Because we used species with
201 current ranges only, no species in our data were classified as Extinct in the Wild or
202 Extinct. Second, we considered population trend using the Population Trend categories,
203 which are an indication of recent change in total abundance of the species, with
204 categories: Increasing, Stable, Decreasing, or unknown. In our analyses population
205 trend categories were considered as ordinal levels (decreasing, stable, and increasing).
206 Species with Data Deficient Status or Unknown Population Trend were not included in
207 our analyses.

208

209 **Analyses**

210 To avoid circularity in our analyses of extinction risk (based on Red List Status) caused
211 by using predictors that had been used to define the response, we excluded species
212 classified as threatened based on criteria B and/or D (small geographic range or area of
213 occupancy and possibly fragmented and few locations, respectively; Table A1). We
214 defined generalized linear mixed regression multinomial models that aimed to predict
215 conservation status (modelled as Red List Status ordinal categories or Population Trend
216 ordinal categories) as a function of *Area*, *Circularity*, *N_frag*, and *Heterogeneity*.

217 Because our objective was to assess if additional descriptors of spatial configuration
218 may affect the conservation status, we look if these descriptors resulted in improved
219 models, using as our null model a regression including *Area* as the single predictor.

220 Increasingly complex models that incorporated the other variables describing shape
221 and/or fragmentation (Table 1) were compared to this null model using an information
222 theoretic approach based on AICc (Burnham and Anderson 2002). Because we
223 hypothesized that spatial configuration may have different effects depending on the
224 range size, and because we found correlations between *Area* and the other variables
225 (Table A4), we also defined models including interaction terms between *Area* and shape
226 (*Circularity*) and/or fragmentation (*N_frag* and *Heterogeneity*). Inferences were based
227 on the best supported model, defined as the one with the lowest AICc. If there were
228 several supported models (models within two AICc units of the best model) these were
229 considered and discussed. Because models included interaction terms we could not use
230 model averaging techniques (Burnham and Anderson 2002). We fitted separate models
231 for each taxonomic class because of their distinct characteristics in dispersal and life-
232 history.

233 Extinction risk models were fitted as multivariate GLMM with cumulative logits
234 for ordered multinomial data and random intercepts using the function `clmm` from the
235 “ordinal” package (Christensen 2015) in R. Models included taxonomic information
236 (order, family, and genus) as random factors to control for evolutionary non-
237 independence of the observations following González-Suárez and Revilla (2013). To
238 illustrate results we plotted predicted marginal probabilities for both Red List Status and
239 Population Trend exploring the observed range of *Heterogeneity* values in combination
240 with two possible values for *Area*, *N_frag* and *Circularity* based on percentiles of the
241 observed data (Supplementary material Appendix 1, Table A5 for values). We also
242 tested the predictability of the models (Mac Nally et al. 2017) using Nagelkerke pseudo
243 R^2 calculated with the `nagelkerke` function from the “rcompanion” package in R
244 (Mangiafico 2017). We report conditional R^2 (representing both fixed and random
245 effects), marginal R^2 (fixed effects only), and the change in R^2 compared to our null
246 (*Area* only) model.

247

248 **RESULTS**

249 The final database for extinction risk analysis (based on Red List status) included data
250 for 11,052 species (55% of the recognized diversity of the three taxonomic classes
251 considered) representing 1,482 amphibians, 7,147 birds, and 2,423 mammals (23%,
252 69% and 46% of each group’s diversity respectively. For a summary by Red List Status
253 category see Table A6). The database available to predict Population Trend included
254 10,495 species (47% of the recognized diversity) representing 1,676 amphibians, 6,979
255 birds, and 1,840 mammals (26%, 67% and 35% of each group’s diversity respectively.
256 For a summary by trend category see Table A7). Initial descriptive analyses of these
257 data showed that species with higher risk of extinction and decreasing population trend

258 generally had smaller ranges, with more circular shapes and possibly fewer, more
259 evenly-sized fragments (Figs. A2 and A3). We found *Area* was associated with all other
260 descriptors of spatial configuration (Table A4, Fig. A1) with smaller range sizes
261 associated with higher values of *Circularity*, lower values of *Heterogeneity*, and fewer
262 fragments (*N_frag*).

263

264 **Spatial Configuration and Extinction Risk**

265 Models that included descriptors of shape and/or fragmentation were identified as
266 improvements over the null (*Area* only models) based on AICc and R^2 for all taxonomic
267 groups, although the particular descriptors included in the best model varied among
268 groups (Figs. 1 and 2, Tables 1 and 2). For all three analyzed groups an increase in the
269 range area (*Area*) was associated with a decrease in extinction risk, and distinctly-sized
270 fragments (*Heterogeneity*) were associated with lower extinction risk in larger ranges,
271 but higher risk for small ranges (Figs. 1 and 2, Table 2). For birds and amphibians both
272 shape and fragmentation were revealed as important, but with different associations. In
273 amphibians, more circular shapes and fewer fragments were positively correlated with
274 risk of extinction; for birds, more circular shapes, particularly for larger ranges, were
275 also associated with slightly higher risk, and when many fragments existed distinctly-
276 sized fragments generally reduced risk (Figs. 1 and 2, Table 2).

277 For mammals there were two additional supported models (falling within a range
278 of 2AICc, Table 1; Fig. A4, and Table A8). In both, model *Mammals (1)* and model
279 *Mammals (2)*, having more fragments was associated with lower risk of extinction,
280 especially for small areas. In model *Mammals (2)* in addition *Heterogeneity* was
281 associated with higher extinction risk especially for species with many fragments.

282

283 **Spatial Configuration and Population trend**

284 Analyses of population trend also supported the importance of additional spatial
285 configuration descriptors (Tables 1 and 2). The best models for birds and mammals
286 were largely consistent with extinction risk analyses; although for amphibians the best
287 model was simpler. For the three analyzed taxonomic groups, an increase in the range
288 area (*Area*) was associated with a decline in population trend. In contrast to results
289 based on extinction risk, effects were generally more noticeable for larger ranges. For
290 example, for the three taxonomic groups more regular shapes (*Circularity*) were
291 associated with increasing population trends especially those species with bigger range
292 areas. For birds and mammals, greater *Heterogeneity*, in more fragmented areas with
293 more irregular shapes, was associated with increasing population trend (Figs. 1 and 2,
294 Table 2). For amphibians, we had a second supported model (falling within a range of
295 2AICc, Table 1; Fig. A5, and Table A8) that suggests lower values of distinctly-sized
296 fragments (*Heterogeneity*), fewer fragments and more regular shapes were associated
297 with decreasing population trend.

298

299 **DISCUSSION**

300 The spatial configuration of terrestrial vertebrate ranges varies by orders of magnitude
301 in total area of occupancy and in the number, size and shape of their fragments. This
302 heterogeneity is caused by natural and anthropogenic processes that define range
303 boundaries and that vary in space and time (Gaston 2003, Lucas et al. 2016). This
304 complexity is often considered when studying local extinction processes (Pfeifer et al.
305 2017), and it is acknowledged in the global assessments of the IUCN (IUCN 2012,
306 2015). However, it has been largely overlooked in comparative studies of species'
307 extinction risk (Arbetman et al. 2017, Cardillo et al. 2008). As previously reported, the

308 best descriptor of conservation status is the area of the range, likely due to its direct
309 association with total population size: all else been equal, larger ranges should have
310 lower risks (Bielby et al. 2008, Davidson et al. 2009, Giam et al. 2011, Harris and Pimm
311 2008, Joppa et al. 2016, Keith et al. 2018). In addition, the better conservation status of
312 large range areas could be associated to a buffer effect against stochastic impacts. It is
313 less probable that a big range would be entirely affected by a stochastic impact, while a
314 catastrophe could affect a whole small range (Bland et al. 2016, Murray et al. 2017).

315 The area of the range is also associated with some species traits which may
316 explain some of the observed patterns. Species with broad ecological niches can occupy
317 and maintain populations in a greater number of habitats and use a wider range of food
318 resources which can reduce the impact of habitat loss and community changes
319 (González-Suárez et al. 2013). Dispersal ability of the species is also determinant, with
320 bigger areas associated with high dispersal and for extension high dispersal with a better
321 conservation status (McCauley et al. 2014). Therefore, the observed reduced risk in
322 wider ranges may reflect the benefits of habitat and diet generalism and dispersal
323 capacity, in addition to the more direct effects of population size and reduced stochastic
324 risk discussed above.

325 Beyond the known role of area, here we show that other descriptors of the spatial
326 configuration of species' ranges, namely shape, number of fragments, and heterogeneity
327 in fragment size, can improve our understanding of the conservation status of the
328 species. We discuss below the different mechanisms that may be behind these
329 relationships.

330

331 **Range shape and conservation status**

332 Metapopulation and island biogeography theory predict that higher border to core ratios
333 should increase extinction risk at the population level, because individuals living near
334 the edge due to edge effects are likely to have lower expected fitness (Brown 1984,
335 Brown et al. 1995, Gaston 1990, Hanski 1999, Murray et al. 2017). However, at the
336 much larger spatial scale of ranges, we found the opposite, a higher extinction risk in
337 amphibians, birds and mammals (the latter only for Population Trend) with ranges with
338 more circular shapes, particularly in larger ranges. It is possible that for global range
339 maps, current circular shapes actually reflect past large scale human impacts rather than
340 edge-effect risks. Through the process of range contraction, local extinctions change the
341 spatial configuration of ranges, resulting in more context-specific spatial configurations,
342 determined by the interaction between the distribution of impacts, species abundance
343 and the stage of range contraction (Channell and Lomolino 2000a, b, Lucas et al. 2016).
344 Border areas are more prone to be extirpated (Brown 1995, Channell and Lomolino
345 2000a, b, Lawton 1993, Lucas et al. 2016) and thus, initially irregularly shaped ranges,
346 may increase their circularity as border areas become extirpated (Mehlman 1997, Smale
347 and Wernberg 2013). Indeed, as we would expect if this was true, we found that smaller
348 ranges tended to have more circular shapes. Therefore, there may be a link between the
349 mechanistic prediction of metapopulation theory and our results but only through an
350 increase in local extinction in areas with more edge areas, which is not directly
351 detectable at the whole range scale. Fully testing this hypothesis would require long-
352 term data reflecting temporal variation in distribution ranges, which currently are
353 available only for a few species.

354

355 **A role for range fragmentation: number of fragments and size heterogeneity**

356 A priori, and based on the predictions of population ecology and metapopulation theory,
357 we expected a higher extinction risk for species with more fragmented ranges and with a
358 more homogeneous distribution of fragments size (Gaston 1994, Gaston and Fuller
359 2009, Hanski 1998, MacArthur and Wilson 1967, Tormod Vaaland Burkey 1997). We
360 found an association between the number of fragments and conservation status for all
361 taxonomic classes, especially when describing Population Trends, but with an effect
362 contrary to our expectations. Species with better conservation status had more
363 fragmented ranges, with a more marked effect for those with small ranges. Range
364 fragmentation is common among species suffering contraction (Hooftman et al. 2016,
365 Riordan et al. 2016, Turvey et al. 2015). However, the process of range contraction also
366 leads to the extirpation of small fragments so that the total number of fragments may not
367 actually increase but be stable or even decrease. For example, Rodriguez and Delibes
368 (2002) showed that the Iberian lynx *Lynx pardinus* range suffered an important
369 contraction in which the largest fragments were fragmented, but also the smallest
370 fragments were lost such that at the end, the total number of populations/fragments
371 barely changed. At the other extreme, species with lower extinction risk, often more
372 abundant, are likely to have higher dispersal rates which allow to colonize new areas
373 leading to an overall more fragmented ranges (McCauley et al. 2014, Wiegand et al.
374 2005). Dispersal also favors that species escape from habitat destruction and/or tracking
375 climate so these species are expected to be less affected by impacts and would be
376 associated with species with lower extinction risk (Sunday et al. 2015).

377 Moreover, there are situations in which extinction risk may not increase with the
378 number of fragments. If the primarily causes of extinction are environmental stochastic
379 processes, even large populations are vulnerable to extinction, e.g. in the spread of
380 invasive species there is a positive spatial autocorrelation (Veran et al. 2016), thus

381 multiple fragments (subject to independent environmental processes), could act as a
382 buffer against perturbations (Gilarranz et al. 2017), reducing the overall risk (Quinn and
383 Hastings 1987). This buffer effect mechanism could be explaining why for amphibians,
384 a class where the risk of extinction in many species is associated to a contagious disease
385 (Hoffmann et al. 2010, O’Hanlon et al. 2018, Stuart et al. 2004), more fragmented
386 ranges are associated with less risk of extinction.

387 Populations with a fragmented range but with most area located in a single
388 fragment (continent-island system) would have a substantially lower extinction
389 probability when compared with populations with a more homogeneous distribution of
390 fragment areas (Hanski et al. 1996, Thomas and Kunin 1999, Wiegand et al. 2005). If
391 the population is divided into multiple fragments the heterogeneity of the network can
392 reduce risk favoring rescue effects (Gilarranz and Bascompte 2012, Hanski et al. 1996).
393 If we consider that connectivity of a fragment is positively correlated with its size, a
394 range with high heterogeneity in its area would have a high heterogeneity in its
395 connectivity and less risk of extinction. How the range area was distributed among the
396 existing fragments was also a relevant descriptor of conservation status with an effect
397 that often depended on the total area of the range. As expected, for big range sizes, high
398 heterogeneity was generally associated with lower extinction risk, as the overall species
399 extinction risk is directly linked to the risk of the largest fragment, and because large
400 continuous fragments suffer less edge effects (Murray et al. 2017). As the size of the
401 largest fragment is the main limiting factor, species with small ranges cannot show a
402 large effect of the heterogeneity of fragment size. Indeed, heterogeneity and number of
403 fragments increased with range area. In birds, the effect was most noticeable in species
404 with ranges with many fragments for which the potential for higher heterogeneity is
405 greater. On the other hand, increased extinction risk in ranges with more

406 homogeneously-sized fragments may be a consequence of the dynamics of range
407 contraction and expansion. Range contraction may lead to range collapse and a high
408 fragmentation at the end of the process (Riordan et al. 2016, Rodríguez and Delibes
409 1992, 2002, 2003). During contraction, fragments may split into smaller fragments, thus
410 reducing maximum fragment size. However, minimum fragment size is constrained by
411 the minimum size that can support a population in the short term. Therefore, the final
412 stages of range contraction may lead to more homogeneously-sized areas (Rodríguez
413 and Delibes 2003).

414

415 **Future directions**

416 We found clear patterns of association between extinction risk and the spatial
417 configuration of species' ranges. These effects can be interpreted as emergent properties
418 of population dynamics at smaller spatial scales. In principle, they can be used to
419 complement the role of range size in categorizing risk of extinction. Current data
420 availability, quality and practice call for some caution in doing so (Hurlbert and Jetz
421 2007, Maréchaux et al. 2017). The spatial configuration of ranges is very sensitive to
422 the method employed to define it. A range delineated by experts, using minimum
423 convex polygon or a kernel method on the same dataset would look very different
424 (Joppa et al. 2016). The large biases in sampling effort across the globe, with large areas
425 with few data available also precludes obtaining good quality ranges (González-Suárez
426 et al. 2012). We need more systematically and transparently built ranges that can offer
427 better information over time, including patterns of range expansion and contraction.
428 Current efforts compiling information at large scales and in big numbers, often with the
429 aid of citizen science, could help in improving the quality of the ranges. Improved
430 ranges would allow future work considering how species' traits, distinct threatening

431 processes, and local environmental conditions may affect range dynamics and extinction
432 risk. To advance from correlations between spatial pattern of ranges and risk of
433 extinction/population trend to mechanisms, we need long-term data reflecting temporal
434 variation in distribution ranges with different levels and combination of impacts.
435 Looking to the past biodiversity responses to climate and human impacts will
436 importantly help to fill this gap (Fordham et al. 2016, Nogués-Bravo et al. 2018).

437

438 **Conclusions**

439 Most species ranges are spatially complex, often formed by multiple fragments with
440 diverse shapes which change over time (Gaston 2003, Wilson et al. 2004). We show
441 that using different spatial measures describing this complexity improves our
442 understanding of extinction risk, which can in turn help policy makers and managers to
443 prioritize actions (Cardillo and Meijaard 2012, Mace et al. 2008). Our study does not
444 aim at improving extinction risk assessments, just determine and quantify new factors
445 that may affect the conservation of species. While the area of occupancy (*Area*)
446 contributed most to explain variation in the data, including additional descriptors
447 improved model fit and suggested hypotheses regarding the spatial consequences of
448 range expansion and contraction. In population biology it is widely accepted that spatial
449 complexity affects extinction probability. To our knowledge, this is the first time these
450 relationships have been quantified at biogeographical scales on a large set of species.
451 Our selected variables have a clear ecological basis, are simple to calculate, and can be
452 used at different scales and taxonomic groups. These descriptors are defined from the
453 same ranges maps used to estimate area, thus, do not require additional datasets.
454 Admittedly, there are limitations associated to range map quality and uncertainty, but
455 these also affect area estimates (Hurlbert and Jetz 2007, Maréchaux et al. 2017). Under

456 the current biodiversity crisis we believe these caveats should not stop us from
457 considering these new factors to predict what species are more prone to extinction risk
458 allowing more effective conservation policies.

459

460

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667

668 **SUPPLEMENTARY MATERIAL**

669 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

670 Appendix 1.

671 **TABLES**

672 **Table 1.** Results of the GLMM analyses aimed to predict extinction risk as a function of
 673 several descriptors of range spatial configuration. We report $\Delta AICc$ (difference in AICc
 674 with the best model. Lower values of $\Delta AICc$ represent stronger support) and sample
 675 sizes for each model. Models in bold are the best supported within each category, with
 676 the best overall model in bold and underlined. *Het* = *Heterogeneity*.

Model	$\Delta AICc$ (AICc)					
	Red List Status			Population Trend		
	Amphi bians (n=1,4 82)	Bird s (n=7, 147)	Mam mals (n=2, 423)	Amphi bians (n= 1,676)	Bird s (n=6, 979)	Mam mals (n=1, 840)
<hr/>						
Size	<hr/>					
<i>Area (Null model)</i>	30.13	55.50	12.81	34.13	101.1 3	15.80
<hr/>						
Size and Shape (<i>Circularity</i>)	<hr/>					
<i>Area+Circularity</i>	15.17	54.42	13.55	15.07	92.41	7.09
<i>Area*Circularity</i>	10.37	25.32	15.22	<u>1.69</u>	33.61	4.19
<hr/>						
Size and Fragmentation	<hr/>					
<i>Area+N_frag</i>	26.48	57.33	14.35	24.42	103.1 2	15.58
<i>Area*N_frag</i>	27.94	58.57	15.27	26.44	94.98	15.74
<i>Area+Het</i>	31.69	45.32	10.84	35.65	68.83	14.73
<i>Area*Het</i>	18.51	25.90	<u>0.21</u>	34.71	61.87	10.87

<i>Area*Het+ Area*N_frag</i>	11.91	28.39	<u>0.00</u>	21.54	57.00	6.43
<i>Area*Het+ Area*N_frag+</i>	13.14	20.55	<u>1.44</u>	22.69	50.55	5.84
<i>Het*N_frag</i>						
<hr/>						
Size, Fragmentation and Shape						
<hr/>						
<i>Area*</i>	<u>0.00</u>	—	—	<u>0.00</u>	—	<u>0.00</u>
<i>Circularity+Area*Het+Area*N_</i>						
<i>frag</i>						
<i>Area*Circularity+Area*Het+A</i>	—	<u>0.00</u>	—	—	<u>0.00</u>	—
<i>rea*N_frag+N_frag*Het</i>						
<hr/>						

677

678 **Table 2.** T-values (coefficient/SE) and Nagelkerke pseudo R^2 of the best overall
679 GLMM models predicting extinction risk as a function of several descriptors of range
680 spatial configuration. Models selection results are shown in table 1. We modeled the
681 probability of increase in Red List Status (higher risk) and Population Trend (more
682 declining trend). A dash (-) indicates variables not included in the best models. *Het* =
683 *Heterogeneity*. Sample sizes (n) indicate the number of species included in each model.
684 Conditional R^2 represents the overall (fixed and random effects) fit of the models,
685 marginal R^2 represents fixed effects, and improvement in R^2 is the change in R^2 from
686 the *Area* only null model.

Variables	T-values (coefficient/SE) Red			T-values (coefficient/SE)		
	List Status			Population Trend		
	Amphibia	Birds	Mamma	Amphibia	Birds	Mamma
	ns	(n=7,14	ls	ns	(n=6,97	ls
	(n= 1,482)	7)	(n=2,423	(n= 1,676)	9)	(n=1,840
))
<i>Area</i>	-0.43	-6.745	-3.44	-7.39	-5.84	-2.36
<i>Circularity</i>	0.28	-4.21	-	-2.16	-6.08	-1.17
<i>Heterogeneity</i>	2.49	2.24	3.09	-	0.08	0.80
<i>N_frag</i>	-1.45	0.30	-	-	1.06	-2.23
<i>Area*</i>	0.66	4.69	-	3.94	6.91	1.86
<i>Circularity</i>						
<i>Area*</i>	0.93	1.65	-	-	0.94	2.00
<i>N_frag</i>						

<i>Area*</i>	-2.91	-1.67	-3.54	-	0.16	-1.31
<i>Heterogeneity</i>						
<i>N_frag*</i>	-	-2.93	-	-	-3.22	-
<i>Heterogeneity</i>						
Conditional R^2	0.34	0.30	0.41	0.38	0.18	0.34
Marginal R^2	0.18	0.21	0.35	0.17	0.05	0.18
Incremental R^2	0.04	0.02	0.01	0.04	0.02	0.02

687

FIGURE LEGENDS

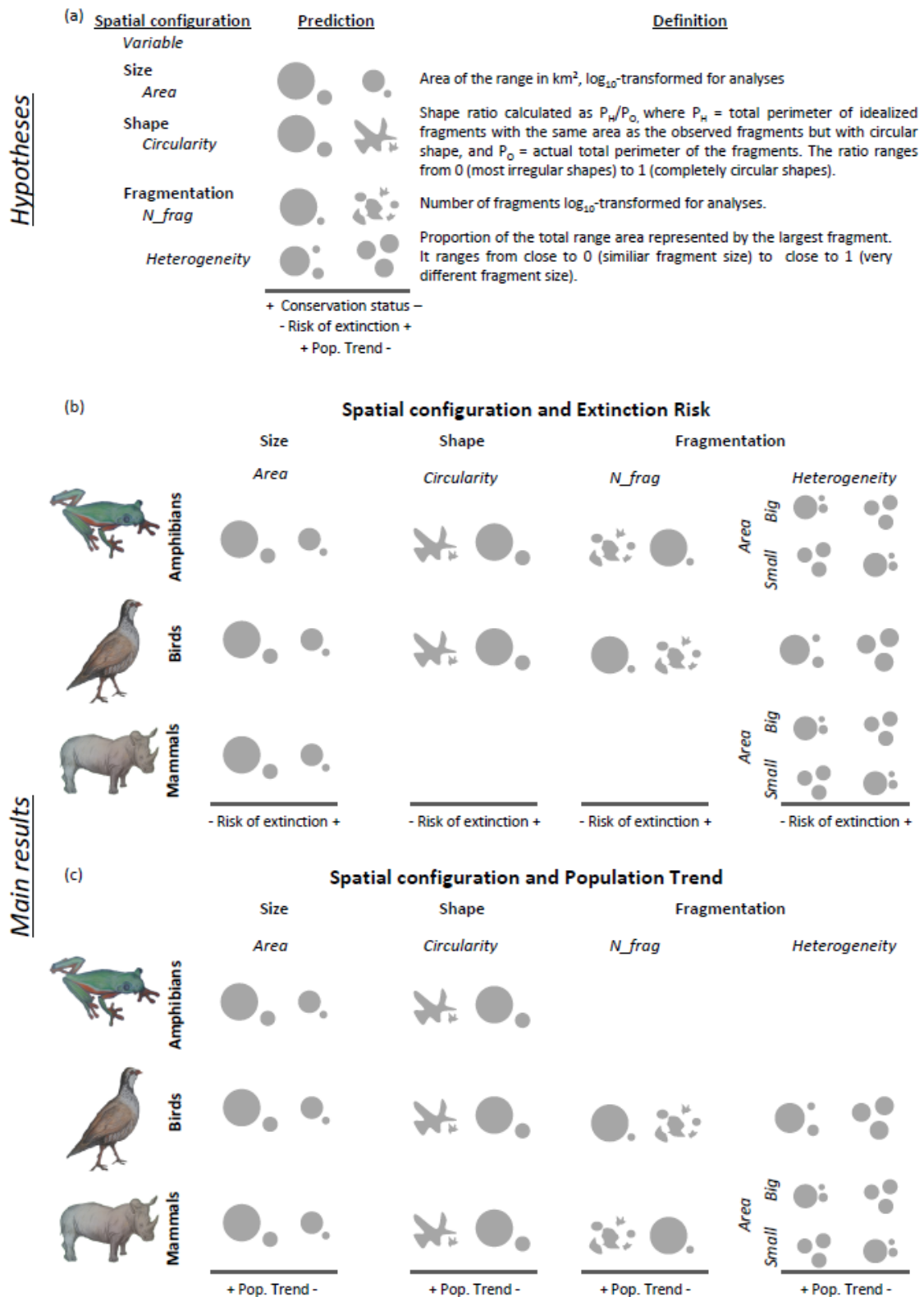


Figure 1. Hypotheses and description of the studied spatial configuration variables with illustrative examples of values, predicted association with increased vulnerability to

extinction based on metapopulation and island biogeography theory, and their definition. *Note that threats acting on borders can increase circularity (a). Main results (not including all interactions) for the analysis of spatial configuration and extinction risk, based on the best models for each class showed in Tables 1 and 2 (b). Main results (not including all interactions) for the analysis of spatial configuration and population trend, based on the best models for each class showed in Tables 1 and 2 (c). For a more detailed description and understanding of the interaction effects between different variables consult Figs. 2 and 3.

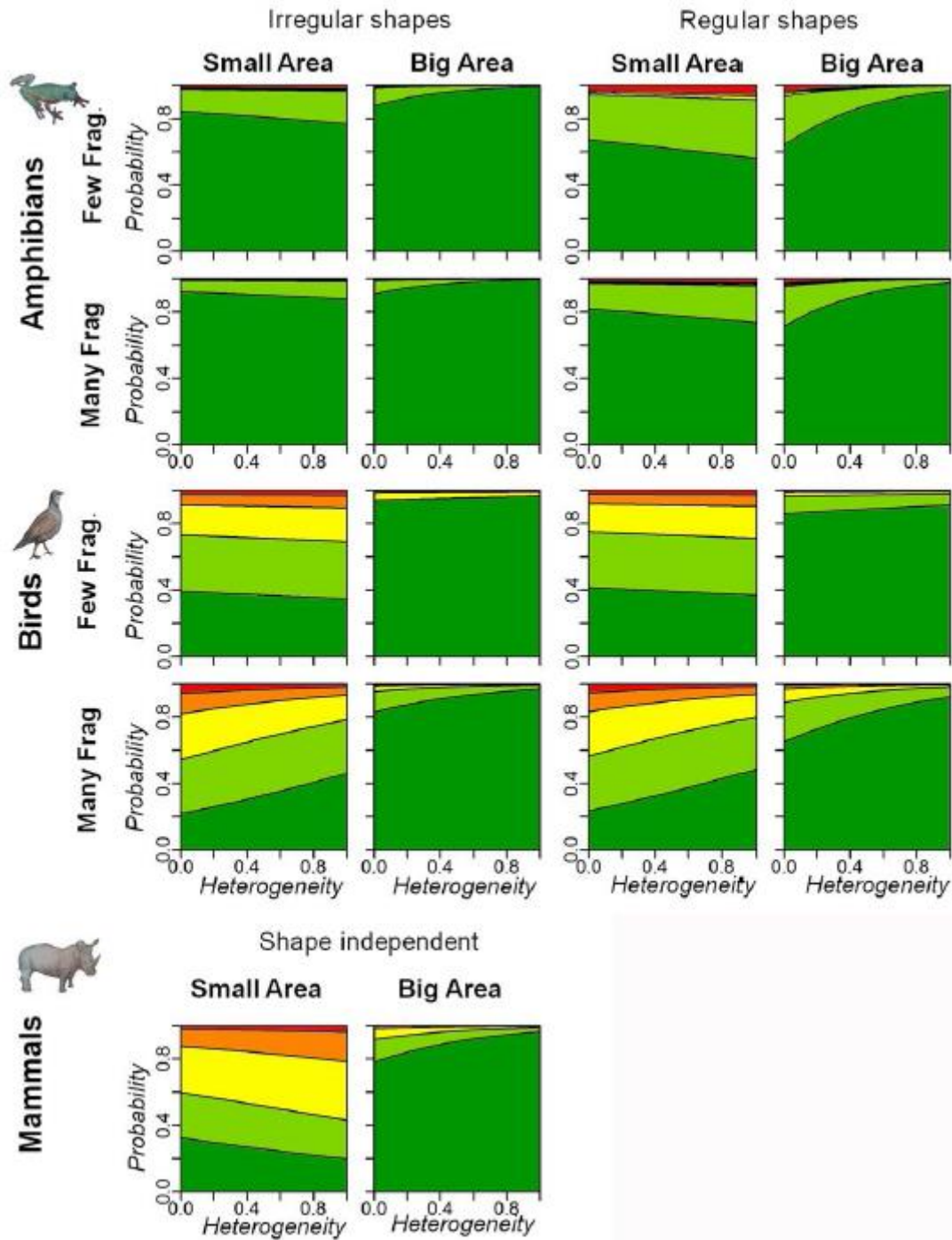


Figure 2. Predicted marginal probabilities for each Red List Status (Table A6), with dark green for Least Concern (LC), light green for Near Threatened (NT), yellow for Vulnerable (VU), orange for Endangered (EN) and red for Critically Endangered species (CR), based on the best models for each class (Tables 1 and 2). In some plots, the probability associated to some threat categories was low or zero, partly reflecting the relatively small number of species in these categories (see lower right panel). To show

interaction effects we explored predictions for the observed the range of *Heterogeneity* values with two possible values for *N_frag* and *Circularity* based on percentiles of the observed data (table A5 for values).

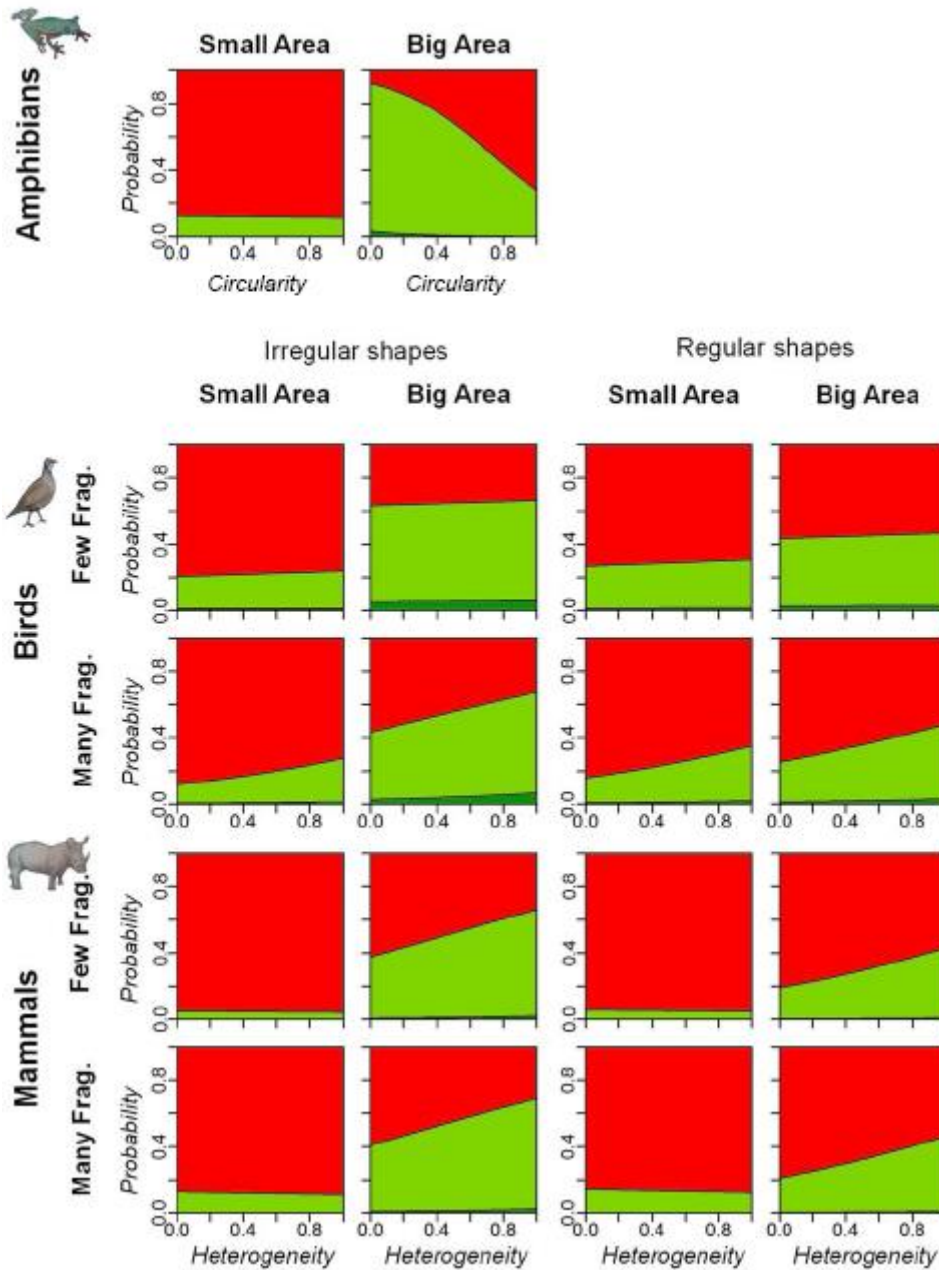


Figure 3. Predicted marginal probabilities for each category of Population Trend (Table A7), with dark green for Increasing, light green for Stable, and red for Decreasing trends, based on the best models with descriptors of spatial configuration for each class (coefficients in table 2). Note that in some plots the predicted probably of Increasing

trend was very small or zero, partly reflecting the small number of species in that category. To show interaction effects we explored predictions for the observed the range of *Heterogeneity* values with two possible values for *N_frag* and *Circularity* based on percentiles of the observed data (table A5 for values).

Supplementary material

Appendix 1.

Table A1. Number of species after each filter by class and percentage from the described number of species (in brackets). Described in the IUCN database refers to the number of species that include the IUCN database as species; IUCN spatial database refers to the number of species which are included in the spatial database of the IUCN (Include Extinct species); Systems refers to the number of species selected after select species living only in terrestrial systems for Birds, for Mammals we directly selected the spatial information which include only terrestrial species as defined by the IUCN. Categorized refers to the species categorized in the IUCN red list. Excluded (Excl.) by B&D criteria and unknown Population trend refers to the number of listed species in the IUCN Red List excluding species categorized by B&D criteria and excluding species categorized by unknown population trend. Multifragment refers to the number of species after select only species with a minimum of two fragment in its distribution.

	Described	Spatial data	Systems	Categories	Excl. by B&D criteria; unknown Pop. Trend	Multifragment <u>Extinction risk; Population trend</u>
Amphibians	6,414	6,277 (97.86)	-	4,744 (73.96)	3,014 (46.99); 3764 (58.68)	1,482 (23.11); 1,676 (26.13)
Birds	10,425	10,424 (99.99)	9,400 (90.17)	9,347 (89.66)	7,529 (72.22); 8669 (83.16)	7,147 (68.56); 6,979 (66.94)
Mammals	5,408	5,269 (97.43)	-	4,499 (83.19)	3,823 (70.69); 2975 (55.01)	2,423 (44.80); 1,840 (34.02)

Table A2. Spearman correlation between the variables used in the analysis of extinction risk. *Area* and shape (*Circularity*) and/or fragmentation (*N_frag* and *Heterogeneity*).

		<i>Area</i>	<i>Circularity</i>	<i>N_frag</i>	<i>Heterogeneity</i>
Amphibians	<i>Area</i>	1.00	-0.46	0.23	0.46
	<i>Circularity</i>		1.00	-0.24	-0.35
	<i>N_frag</i>			1.00	-0.28
	<i>Heterogeneity</i>				1.00
Birds	<i>Area</i>	1.00	-0.20	0.50	0.27
	<i>Circularity</i>		1.00	-0.31	-0.19
	<i>N_frag</i>			1.00	-0.14
	<i>Heterogeneity</i>				1.00
Mammals	<i>Area</i>	1.00	-0.39	0.27	0.30
	<i>Circularity</i>		1.00	-0.27	-0.24
	<i>N_frag</i>			1.00	-0.36
	<i>Heterogeneity</i>				1.00

Table A3. Spearman correlation between the variables used in the analysis with Population Trend. *Area* and shape (*Circularity*) and/or fragmentation (*N_frag* and *Heterogeneity*).

		<i>Area</i>	<i>Circularity</i>	<i>N_frag</i>	<i>Heterogeneity</i>
Amphibians	<i>Area</i>	1.00	-0.63	0.34	0.52
	<i>Circularity</i>		1.00	-0.25	-0.50
	<i>N_frag</i>			1.00	-0.22
	<i>Heterogeneity</i>				1.00
Birds	<i>Area</i>	1.00	-0.23	0.51	0.28
	<i>Circularity</i>		1.00	-0.32	-0.20
	<i>N_frag</i>			1.00	-0.13
	<i>Heterogeneity</i>				1.00
Mammals	<i>Area</i>	1.00	-0.52	0.34	0.34
	<i>Circularity</i>		1.00	-0.30	-0.30
	<i>N_frag</i>			1.00	-0.32
	<i>Heterogeneity</i>				1.00

Table A4. Results of the univariable LMM analyses aimed to predict each variable (*Circularity*, *N_frag* and *Heterogeneity*) as a function of *Area* to test if there was a significative correlation. Models, in the same way as we included in the analysis of extinction risk/population trend, include taxonomic information (order, family, and genus) as random factors to control for evolutionary non-independence of the observations following González-Suárez and Revilla (2013). We report T-values (coefficient/SE).

Variable	T-values (coefficient/SE) Red List Status			T-values (coefficient/SE) Population Trend		
	Amphibians	Birds	Mammals	Amphibians	Birds	Mammals
	(n= 1,482)	(n=7,147)	(n=2,423)	(n= 1,676)	(n=6,979)	(n=1,840)
<i>Circularity</i>	-22.07*	-26.85*	-22.66*	-31.46*	-30.85*	-28.75*
<i>Heterogeneity</i>	17.29*	21.55*	15.54*	19.59*	21.9*	14.74*
<i>N_frag</i>	10.43*	48.87*	14.23*	14.87*	47.32*	16.86*

* p < 0.05

Table A5. Values of *Area* (in km²), number of fragments (*N_frag*) and shape (*Circularity*) used to define predicted values for main text figures 2, 3, and supplementary figures A4 and A5.

Descriptor	Size/quantity (percentile)	Amphibians		Birds		Mammals	
		Red List	Pop Trend	Red List	Pop Trend	Red List	Pop Trend
<i>Area</i>	Small (10)	3,224	391	20,447	7,903	10,613	1,047*
	Large (80)	723,374	1,146,874	4,143,878	3,970,727	3,654,382	3,187,561
<i>N_frag</i>	Few (20)	2	-	4	4	-	2
	Many (80)	8	-	160	150	-	16
<i>Circularity</i>	Irregular (10)	0.255	-	0.264	0.265	-	0.261
	Regular (90)	0.821	-	0.635	0.653	-	0.782

* percentile 5

Table A6. Number of species used in the regression analysis by Red list category.

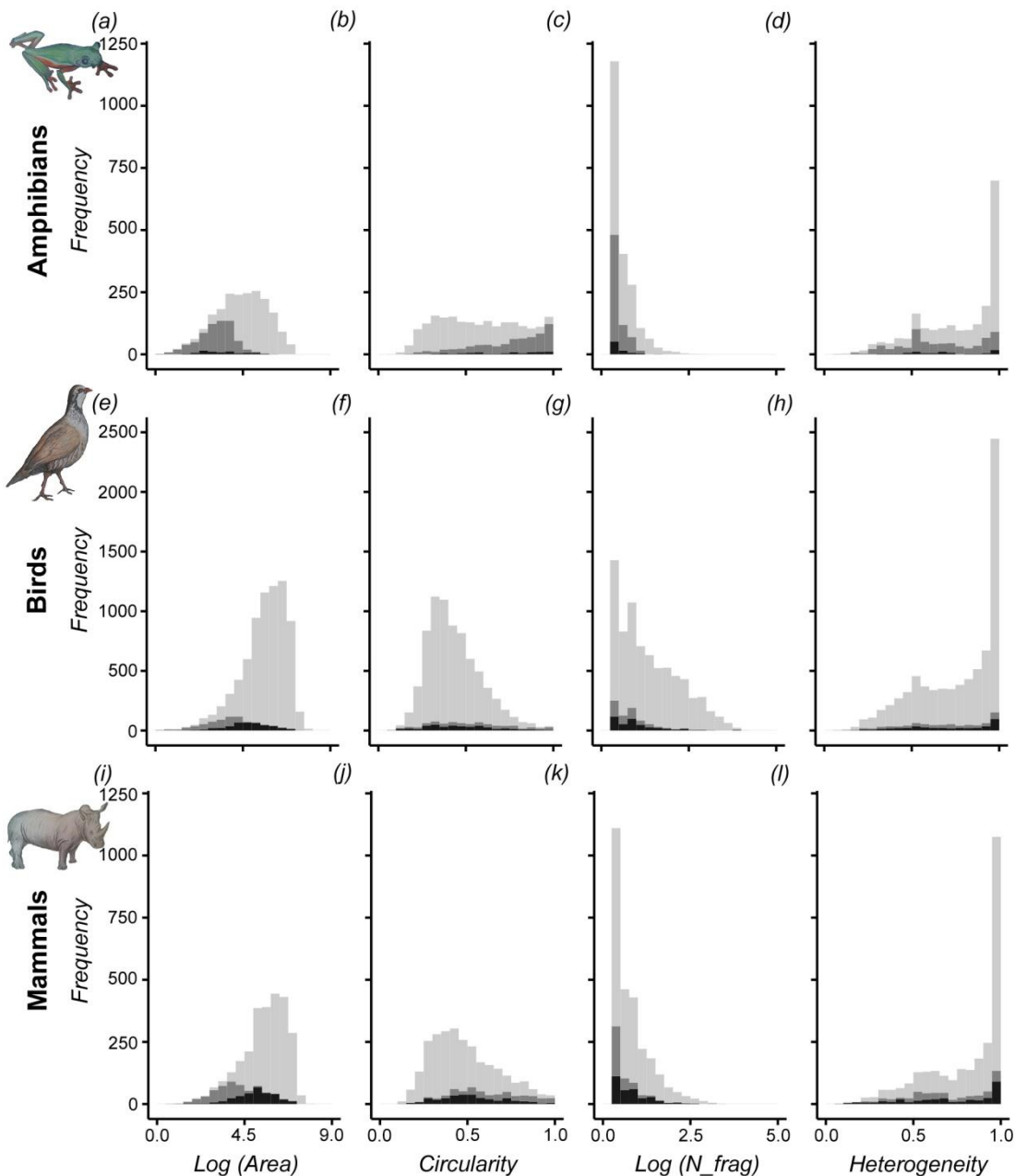
Class	Red List Status				
	LC	NT	VU	EN	CR
Amphibians	1,211	192	13	10	56
Birds	6,069	649	276	99	54
Mammals	1,916	194	159	99	55

Table A7. Number of species used in the regression analysis by Population Trend category.

Class	Population trend		
	Decreasing	Stable	Increasing
Amphibians	931	726	19
Birds	3,195	3,312	472
Mammals	961	830	49

Table A8. T-values (coefficient/SE) of the best alternative overall GLMM models predicting conservation status as a function of several descriptors of distribution spatial configuration. Models selection results are shown in table 1. We modeled the probability of increase in Red List Status (higher risk) and Population Trend (more declining trend). A dash (-) indicates variables not included in the best models. *Het* = *Heterogeneity*. Sample sizes (n) indicate the number of species included in each model.

Variables	T-values (coefficient/SE) Red		T-values
	List Status		(coefficient/SE)
			Population Trend
	Mammals		Amphibians
	(n=2,423)		(n= 1,676)
	Mammals (1)	Mammals (2)	
<i>Area</i>	-2.90	-2.39	-2.98
<i>Circularity</i>	-	-	-1.78
<i>Heterogeneity</i>	2.64	2.67	-0.17
<i>N_frag</i>	-1.10	-1.23	-2.31
<i>Area* Circularity</i>	-	-	3.01
<i>Area* N_frag</i>	0.76	0.54	1.79
<i>Area* Heterogeneity</i>	-3.31	-3.36	-0.19
<i>N_frag* Heterogeneity</i>	-	0.76	-



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Figure A2. Frequency distributions for the variables *Area*, *Circularity*, *N_frag* and *Heterogeneity* for multi-fragment ranges of amphibians, panels a, b, c, d respectively, mammals, panels e, f, g, h respectively, and birds, panels i, j, k, l respectively. Non-threatened species (Least Concern and Near Threatened Status) are in light grey (1,403 species of amphibians, 6,718 species of birds and 2,110 species of mammals which were included in our regression analyses), threatened (Vulnerable, Threatened and Critically Endangered) species classified based on criterion B and D (608 species of amphibians, 382 species of birds and 291 species of mammals which were not included in our regression analyses) are in medium grey, and all other threatened species (79

17 species of amphibians, 429 species of birds and 313 species of mammals which were
18 included in our regression analyses, table S2) are in dark grey.

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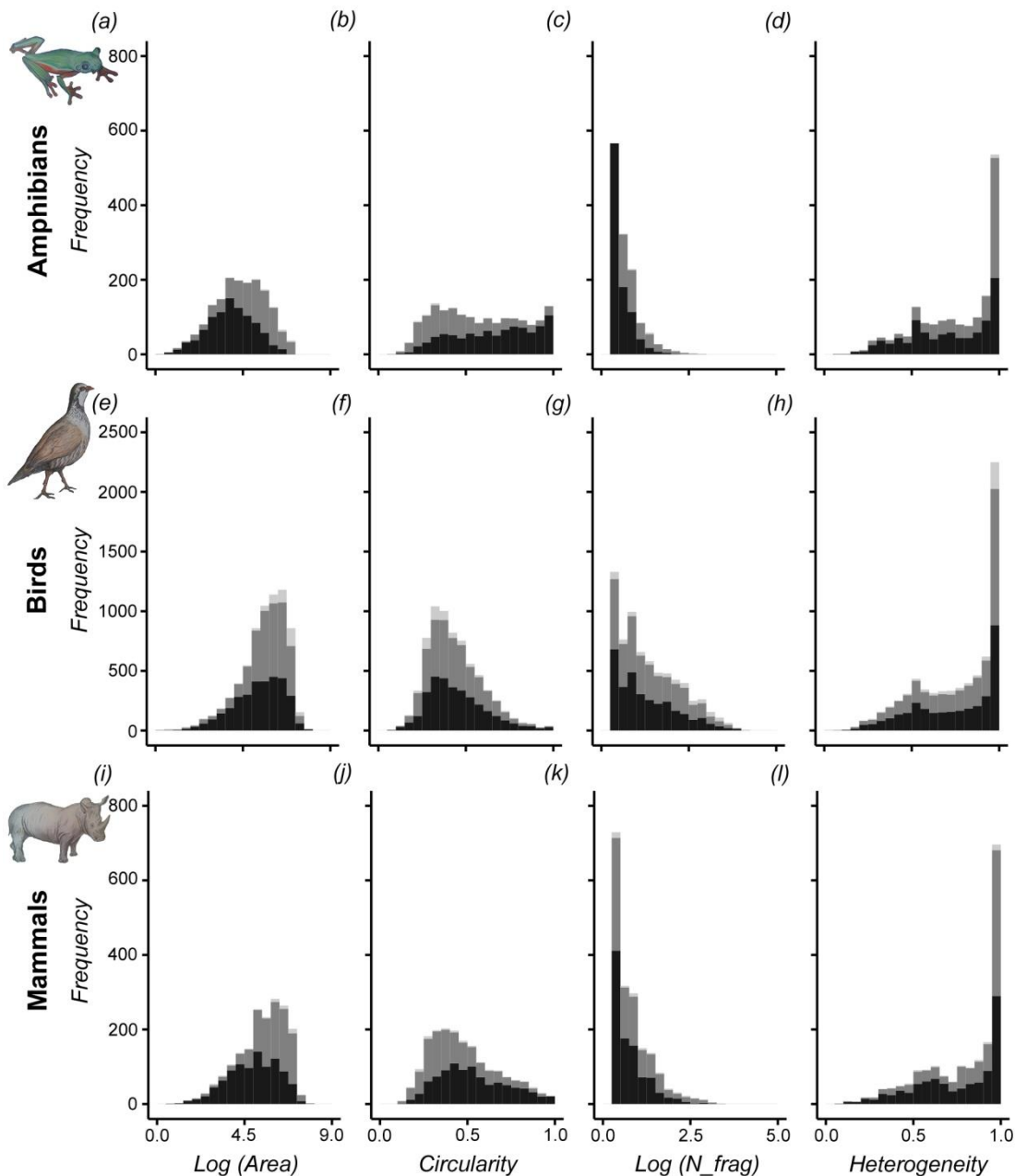
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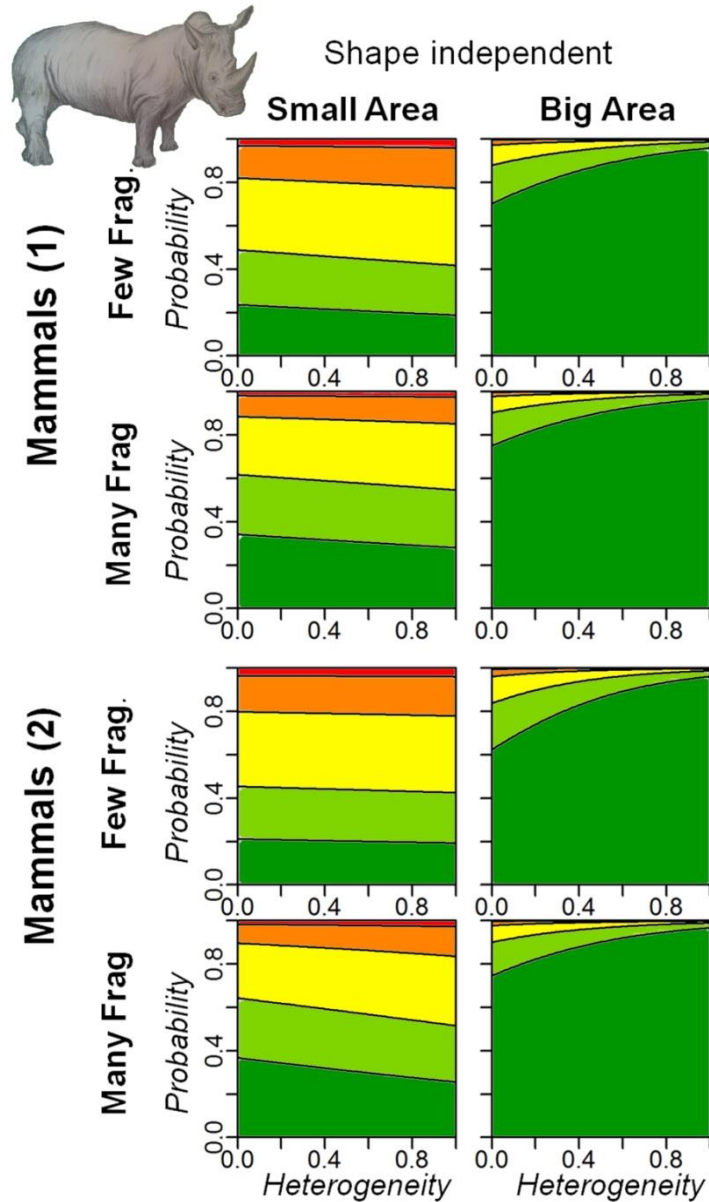
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29 **Figure A3.** Frequency distributions for the variables *Area*, *Circularity*, *N_frag* and
 30 *Heterogeneity* for multi-fragment ranges of amphibians, panels a, b, c, d respectively,
 31 mammals, panels e, f, g, h respectively, and birds, panels i, j, k, l respectively. Species
 32 within increasing Population Trend are in light grey (19 species of amphibians, 472
 33 species of birds and 49 species of mammals; generally few species and thus, sometimes
 34 not clearly visible), stable Population Trend are in medium grey (726 species of
 35 amphibians, 3,312 species of birds and 830 species of mammals), and decreasing
 36 Population Trend are in dark grey (931 species of amphibians, 3,195 species of birds and
 37 961 species of mammals which were included in our regression analyses, table S3).

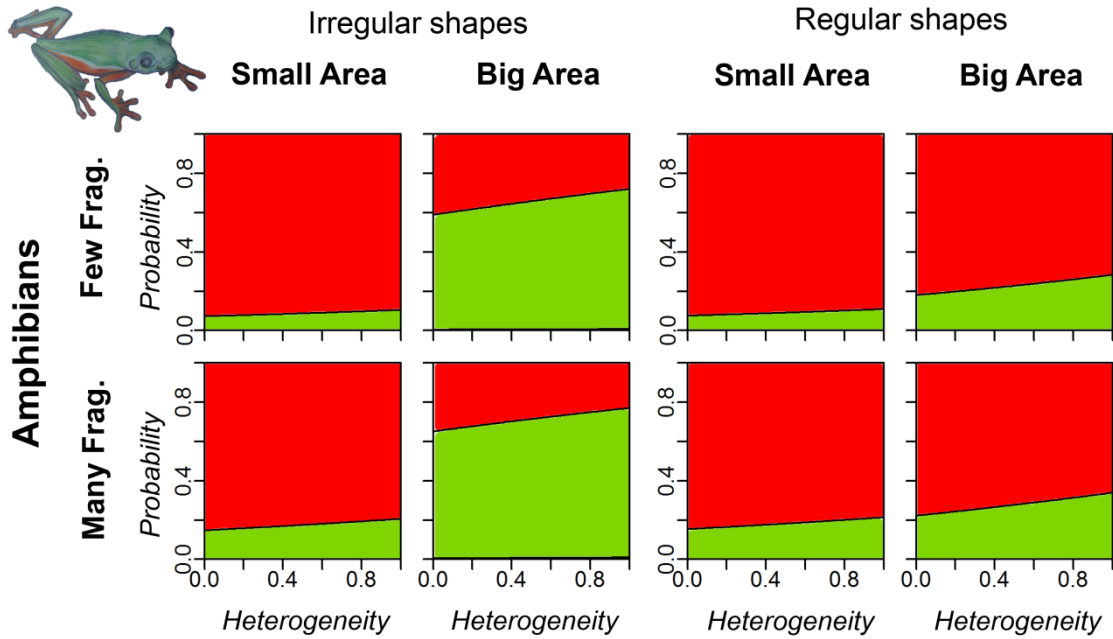
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40 **Figure A4.** Predicted marginal probabilities for each Red List Status (Table S2), with
 41 dark green for Least Concern (LC), light green for Near Threatened (NT), yellow for
 42 Vulnerable (VU), orange for Endangered (EN) and red for Critically Endangered
 43 species (CR), based on the two best alternative models, Mammals (1) and Mammals (2),
 44 for mammal class (Tables 1 and A6). In some plots, the probability associated to some
 45 threat categories was low or zero, partly reflecting the relatively small number of
 46 species in these categories (see lower right panel). To show interaction effects we
 47 explored predictions for the observed range of *Heterogeneity* values with two
 48 possible values for *N_frag* and *Circularity* based on percentiles of the observed data
 49 (see table S1 for values).

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52 **Figure A5.** Predicted marginal probabilities for each category of Population Trend
 53 (Table S3), with dark green for Increasing, light green for Stable, and red for
 54 Decreasing trends, based on the best alternative model, for amphibian class (Tables 1
 55 and A6). Note that in some plots the predicted probably of Increasing trend was very
 56 small or zero, partly reflecting the small number of species in that category. To show
 57 interaction effects we explored predictions for the observed the range of *Heterogeneity*
 58 values with two possible values for *N_frag* and *Circularity* based on percentiles of the
 59 observed data (see table S1 for values).

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