

# *Toward multifactorial null models of range contraction in terrestrial vertebrates*

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13   **ABSTRACT**

14   The contraction of a species' distribution range, which results from the extirpation of  
15   local populations, generally precedes its extinction. Therefore, understanding drivers of  
16   range contraction is important for conservation and management. Although there are  
17   many processes that can potentially lead to local extirpation and range contraction, three  
18   main null models have been proposed: demographic, contagion, and refuge. The first  
19   two models postulate that the probability of local extirpation for a given area depends  
20   on its relative position within the range; but these models generate distinct spatial  
21   predictions because they assume either a ubiquitous (demographic) or a clinal  
22   (contagion) distribution of threats. The third model (refuge) postulates that extirpations  
23   are determined by the intensity of human impacts, leading to heterogeneous spatial  
24   predictions potentially compatible with those made by the other two null models. A few  
25   previous studies have explored the generality of some of these null models, but we  
26   present here the first comprehensive evaluation of all three models. Using descriptive  
27   indices and regression analyses we contrast the predictions made by each of the null  
28   models using empirical spatial data describing range contraction in 386 terrestrial  
29   vertebrates (mammals, birds, amphibians, and reptiles) distributed across the World.  
30   Observed contraction patterns do not consistently conform to the predictions of any of  
31   the three models, suggesting that these may not be adequate null models to evaluate  
32   range contraction dynamics among terrestrial vertebrates. Instead, our results support  
33   alternative null models that account for both relative position and intensity of human  
34   impacts. These new models provide a better multifactorial baseline to describe range  
35   contraction patterns in vertebrates. This general baseline can be used to explore how  
36   additional factors influence contraction, and ultimately extinction for particular areas or  
37   species as well as to predict future changes in light of current and new threats.

38     *Keywords:* Border, extinction, habitat loss, historical range, human, land use, range  
39     dynamics.

40 **INTRODUCTION**

41 Species extinctions generally start with the vanishing of particular populations that  
42 continue until no populations remain (Yackulic et al. 2011). In other words, complete  
43 extinction is usually preceded by a contraction of the distribution range that results from  
44 the extirpation of local populations. Local extirpations and contractions are considered  
45 good descriptors of biological capital loss, possibly even preferable to quantifying  
46 extinction itself (Ceballos and Ehrlich 2002, Davis et al. 1998). Therefore,  
47 understanding the general dynamics of range contraction is key for effective  
48 conservation (Safi and Pettorelli 2010). The list of proximate and ultimate causes of  
49 local extinction is long, and taxon-dependent (Cahill et al. 2012, González-Suárez and  
50 Revilla 2014); thus, we may expect a wide variety of range contraction patterns.  
51 Nevertheless, ecologists and conservation biologists have used null models or simple  
52 hypotheses to describe the expected spatial patterns of local extinction and range  
53 contraction, especially when detailed information is not available.

54 Null models are representations based on the simplest and most general  
55 mechanisms, and deliberately focus on a few key factors or processes to provide a  
56 baseline for comparison with empirical observations or with more complex models  
57 (Gotelli 2001). The simplicity of null models can be useful for species for which little  
58 information exists, as well as in theoretical studies (Hanski 1998, Hanski and  
59 Ovaskainen 2000). Generalized patterns of distribution range contraction have been  
60 described in the literature using three different null models: demographic, contagion,  
61 and refuge. These models describe contraction based on distinct mechanisms derived  
62 from theoretical principles in ecology, biogeography, and conservation biology (Hanski  
63 1998, Hemerik et al. 2006); and have been used in empirical studies as baselines to  
64 determine the role of additional factors or to broadly describe observed contraction

65 patterns (Franco et al. 2006, Parmesan 1996, Pomara et al. 2014, Thomas et al. 2004,  
66 Turvey et al. 2015, Yackulic et al. 2011).

67 The demographic null model derives from basic population dynamic principles,  
68 and from the ecological assumption which postulate that environmental conditions and  
69 resources at the center of a distribution range are more suitable than at the border,  
70 resulting in higher population growth rates and thus, higher abundance in central areas  
71 (Brown 1995, Lawton 1993). Because extinction is directly determined by population  
72 abundance (Brown 1971, David et al. 2003, Jones and Diamond 1976, Pimm et al.  
73 1988), when the drivers of extinction (threats) are ubiquitous, central areas would have  
74 lower extinction/extirpation risk (MacArthur and Wilson 1967). Assuming threats are  
75 indeed ubiquitous, this null model then predicts that populations would be first  
76 extirpated along the historical border (where density is lower) and would continue  
77 toward the center, where the last (most dense) population would be found (Fig. 1). The  
78 contagion null model, on the other hand, assumes that the threats have clinal distribution,  
79 with threats spreading across the landscape with distinct directionality, like a contagious  
80 disease (Channell and Lomolino 2000a, Channell and Lomolino 2000b, Lawton 1993).  
81 Based on this clinal threat pattern, the contagion null model predicts that populations  
82 would be first extirpated in the historical border closest to the extinction driver's origin,  
83 and then as the threat spreads across the range, the central areas would become  
84 extirpated until only the historical border located farthest from the initial point remains  
85 (Fig. 1). Finally, the refuge model assumes that more humanized land uses are  
86 associated with higher risk of extinction (Ceballos and Ehrlich 2002, Fisher 2011,  
87 Hoffmann et al. 2010, Laliberte and Ripple 2004, Li et al. 2015, Pomara et al. 2014,  
88 Schipper et al. 2008, Yackulic et al. 2011), and predicts that populations would be first  
89 extirpated in areas that are more modified and heavily used by humans. According to

90 this model, the last population will be located in the least used area, which represents a  
91 final refuge for the species (Fig. 1).

92 Some of the assumptions and the predictions of primarily the demographic and  
93 contagion models have been tested by previous studies, which collectively suggest these  
94 models may not be broadly applicable (Ceballos and Ehrlich 2002, Fisher 2011,  
95 Hemerik et al. 2006, Laliberte and Ripple 2004, Sagarin and Gaines 2002, Thomas et al.  
96 2008, Yackulic et al. 2011). However, there has been no comprehensive evaluation of  
97 all three null models; partly because spatial data quantifying range contraction at the  
98 global scale are limited, but also because there are important methodological challenges  
99 including the difficulties in defining a unique center and a relative position within a  
100 species range. In this study we overcome these challenges to simultaneously evaluate  
101 these three null models using a global dataset for 386 terrestrial vertebrates (mammals,  
102 birds, amphibians and reptiles). We first identify the key predictions derived from each  
103 null model and then, using descriptive indices and regression analyses, we evaluate if  
104 empirical range contraction data conform to the models predictions. Our goals are: 1) to  
105 determine which, if any, of the proposed null models represents the most adequate  
106 general baseline to explain range contractions; 2) if necessary, to propose and evaluate  
107 alternative multifactorial null models; and 3) to provide a more consistent framework  
108 regarding the general underlying causes of range contraction dynamics among terrestrial  
109 vertebrates.

110

## 111 **METHODS**

### 112 **Spatial distribution data**

113 We used global distribution data of 386 terrestrial vertebrates (International Union for  
114 Conservation of Nature 2010) with known range contraction (i.e., a distribution with

115 extirpated areas, where the species was present in the past but is no longer found, and  
116 current areas, where the species is currently present, and following the notation of the  
117 International Union for Conservation of Nature 2010; detailed information is provided  
118 in Appendix 1). Since most species distributions are fragmented and have complex  
119 shapes, our analyses were conducted at two different scales. At the range scale, we used  
120 data from the complete historical distribution range of each species ( $N=374$ ), which  
121 often included multiple fragments separated by unoccupied areas. At the fragment scale,  
122 we used data from all individual fragments with observed contraction ( $N=273$ . See  
123 Supplementary materials for additional information in data preparation).

124 Supplementary material Appendix 2, Table A3 and A4, and Fig. A1 provide  
125 descriptive summaries of these data including total area in  $\text{km}^2$  and percentage of  
126 contraction (calculated as the percentage of the historical range area classified as  
127 extirpated) for complete ranges and individuals fragments. For complete ranges we also  
128 summarize the number of fragments present in the historical, extirpated, and current  
129 ranges, as well as the percentage of extirpated fragments (percentage of historical  
130 fragments classified as extirpated). Spatial data were projected into an equal area  
131 projection (Cylindrical Equal Area) and rasterized.

132

### 133 **Analyses**

134 We followed a two-step approach to evaluate the key predictions of each null model  
135 (Fig. 1). First, we defined three indices to visually explore the support of model  
136 predictions by the empirical data. Second, we defined and compared three regression  
137 models that estimate the probability of extirpation based on the key model predictions,  
138 thus providing a quantitative test of support for each null model.

139

140 *Indexes*

141 The demographic and contagion null models both associate the probability of  
142 extirpation with an area's relative position within a range (Fig. 1). Therefore, we  
143 defined a position index based on relative distance to the border. We use the border  
144 instead of the center because identifying meaningful centers is complicated in  
145 complexly shaped and fragmented distributions (Sagarin et al. 2006). For each  
146 distribution range and fragment analyzed, we first estimated the geodetic distance from  
147 each grid cell to the closest historical border cell (Fig. 2, and see Supplementary  
148 material Appendix 2). A geodetic distance is the distance between two unprojected  
149 points on the spheroid of the Earth (using the spheroid World Geodetic System 1984,  
150 WGS84). Distances were standardized dividing species' values by the maximum  
151 distance observed for the range (at range scale) or fragment (at fragment scale) to  
152 facilitate comparison among species with different distribution ranges. Using these  
153 distance values from each cell to the nearest border, we then calculated the variable  
154 *Border* as the arithmetic mean distance to the border from all cells within one area, with  
155 *Border\_ext* representing extirpated areas and *Border\_curr* current areas. Using these  
156 values we defined the *Centrality Index* = *Border\_ext*/*Border\_curr* for each range and  
157 fragment. The demographic null model predicts *Centrality Index* < 1 (extirpated areas  
158 are closer to the border), whereas the contagion model predicts *Centrality Index* < 1 only  
159 for initial stages of contraction (approximately <50% of the historical range  
160 extirpated), and *Centrality Index* > 1 for contractions >50%. Therefore, both the  
161 contagion and demographic null models predict the same values of *Centrality Index* in  
162 early stages of contraction but different values in later stages. The refuge null model  
163 makes no general prediction for the *Centrality Index* (Fig. 1).

164           The second prediction made by the demographic and contagion null models  
165   relates to the directionality in contraction. The demographic null model predicts that  
166   contraction occurs in multiple directions, while the contagion null model states that  
167   contraction occurs along a unique general direction that can be detected as a  
168   predominant contraction angle (Fig. 1). We calculated the geodetic angle of contraction  
169   for each extirpated cell as the azimuth of the direction defined by the vector joining  
170   each extirpated grid cell with its closest current cell (Fig. 2 and Supplementary material,  
171   Appendix 2). Using all angles of contraction for each distribution (complete range or  
172   individual fragment) we calculated the *Directionality Index* as the angular  
173   concentration. *Directionality Index* ranges from 0 to 1 and is the inverse of the  
174   dispersion of the angles (Zar 1999). The demographic null model predicts *Directionality*  
175   *Index* values close to 0 (high angle dispersion) and the contagion null model predicts  
176   values close to 1 (a low angle dispersion). The refuge model makes no prediction for the  
177   *Directionality Index* (Fig. 1).

178           The last index we defined captures the predictions of the refuge model (Fig. 1).  
179   Although human land use has changed over time and past uses likely influenced  
180   observed contraction, data are not available at a global scale to describe past land use.  
181   Therefore, we defined land use based on the 1-km resolution MODIS (MCD12Q1)  
182   Land Cover Product (Oak Ridge National Laboratory Distributed Active Archive  
183   Center 2010). We determined the extent of land classified as covered/used  
184   (henceforward used) by humans for each range or fragment (Supplementary material,  
185   Appendix 2 and Table A5). From these cell values we then calculated the variables  
186   *Land use\_ext* as the proportion of cells used by humans in the extirpated area, and *Land*  
187   *use\_curr* as the proportion of cells used by humans in the current area. Using these  
188   variables, we defined a *Land use Index* which is calculated as *Land use\_ext/ Land*

189    *use\_curr*. If extirpated areas have a greater proportion of human use, then *Land use*  
190    *Index* > 1 as predicted by the refuge null model. The contagion and demographic null  
191    models make no specific predictions regarding the *Land use Index*. We calculated and  
192    investigated the distribution of these three indices for terrestrial vertebrates.

193            Prior to visualizing the empirical data the behavior of the *Centrality* and  
194    *Directionality* indexes was evaluated using simulated scenarios. We sketched three  
195    example distribution range areas (Supplementary material Figure A3) for which we  
196    simulated two patterns: range contraction towards the center (demographic model), and  
197    clinal range contraction (contagion model). For irregularly shaped distributions we  
198    explored two different directions of contraction because distinct clines could influence  
199    results. The indexes were then validated exploring the behavior of values calculated at  
200    seven stages along the contraction process in these simulated scenarios (Supplementary  
201    material Fig. A3).

202

### 203    *Regression analyses*

204    We defined regression models to estimate the probability of extirpation of an area based  
205    on two of the previously defined variables (*Border* and *Land use*) and the percentage of  
206    contraction (*Contraction*). For this approach we excluded distributions (ranges and  
207    fragments) with <10% or >90% contraction (Supplementary material, Appendix 1,  
208    Tables A1 and A2) because at early and late stages of contraction stochastic noise may  
209    confound existing patterns (Yackulic et al. 2011). Under the demographic model, the  
210    probability of extirpation should continuously decrease with the distance to the border  
211    independently of the percentage of contraction. Thus, the probability of extirpation of an  
212    area could be simply defined by the variable *Border* (*Mod\_Demographic*, Table 1). A  
213    key prediction of the contagion null model is that there is directionality in contraction,

214 but the angle of contraction is a relative concept that compares extirpated and current  
215 areas and thus, cannot be estimated for completely extirpated or current areas. Instead,  
216 we evaluated another prediction of this null model, namely that the effect of distance to  
217 the border on the probability of extirpation depends on the percentage of contraction.  
218 We modeled this prediction using an interaction term between the variables *Border* and  
219 *Contraction* (*Mod\_Contagion*, Table 1). Finally, under the refuge null model, the  
220 probability of extirpation should simply depend on the human land use intensity, which  
221 is represented by the variable *Land use* (*Mod\_Refuge*, Table 1). For each of the analysis  
222 scales (range and fragment) we fitted generalized linear mixed regression models  
223 (GLMM) with family binomial and a logit link using the function *glmer* from the *lme4*  
224 package in R (R Development Core Team 2013). All models included taxonomic class,  
225 order, family, and genus as random factors to control for evolutionary non-  
226 independence of the observations. We compared models using an information theoretic  
227 approach based on Akaike Information Criterion, AIC (Burnham and Anderson 2002).

228 Finally, we explored the possibility that the multiple processes postulated by  
229 these null models may occur simultaneously. We fitted two additional models that  
230 combine predictions from compatible null models. *Combined\_1* modelled the  
231 probability of extirpation considering both *Land use* and *Border*, *Combined\_2* included  
232 *Land use* and allowed for the interaction of *Border* with *Contraction* (Table 1).

233

## 234 RESULTS

235 We analyzed spatial data for 386 species (374 species at range scale and 213 at  
236 fragment scale) which represent ~1.6% of the terrestrial vertebrates listed by the IUCN.  
237 The studied distribution ranges and fragments have widely variable areas, with an  
238 observed mean percentage of contraction of 41% for complete ranges and 51% for

239 fragments (Supplementary material Appendix 2, Tables A3 and A4 and Fig. A1).  
240 Distribution ranges are often fragmented with a mean of 6.7 fragments per historical  
241 range.

242 Validation of the indexes showed that as expected, when contraction was  
243 simulated following the demographic model, *Centrality Index* values decreased and  
244 *Directionality Index* values were generally close to 0 (although for irregular shapes  
245 values showed a small increase at high contraction stages). When contraction was  
246 simulated following a cline (as proposed by the contagion model), we detected the  
247 predicted shift in the *Centrality Index* and values for the *Directionality Index* generally  
248 close to 1.

249 Empirical estimates of the three indices did not identify a single best-supported  
250 null model at the range or fragment scale (Fig. 3). *Centrality Index* values show a  
251 tendency to change with the percentage of contraction as predicted by the contagion null  
252 model. However, *Directionality Index* values show no support for either the contagion  
253 or demographic models. The *Land use Index* suggests extirpation has been more likely  
254 in humanized areas as predicted by the refuge null model (median values are  
255 consistently above 1; Fig. 3). However, in many cases current areas are more humanized  
256 than those extirpated. Results were broadly consistent among taxonomic classes  
257 (Supplementary material, Appendix 2, Fig. A4).

258 Results from the regression analyses at both scales also failed to clearly identify  
259 a single best null model. At the range scale, both the refuge (*Mod\_Refuge*) and the  
260 contagion (*Mod\_Contagion*) null models received support; whereas at the fragment  
261 scale the only supported model was *Mod\_Refuge* (Table 1). Although overall the refuge  
262 null model received greater support compared to other null models, results at both range  
263 and fragment scales revealed that either of the combined models represents a great

264 improvement (based on AIC) over models based on the unifactorial null models (Table  
265 1). At least for the available data, multiple processes appear to best explain the general  
266 patterns of contraction among terrestrial vertebrates.

267 At the range scale *Combined\_2* was the only supported model (Table 1), which  
268 describes the probability of extirpation as positively correlated with human use (*Land*  
269 *use*) and identifies a contraction-dependent effect of distance to the border. In particular,  
270 at early stages of contraction (up to ~60% contraction, obtained when the  $\partial$ Probability  
271 of Extirpation/ $\partial$ Border is equal to zero) areas near the border are more likely to be  
272 extirpated whereas at later stages the pattern is reversed (Fig. 4a). At the fragment scale,  
273 both combined models were supported (being within 2 AIC units of each other, Table 1)  
274 and show a positive association between the probability of extirpation and *Land use*,  
275 with the best supported model, *Combined\_2*, additionally supports an interaction  
276 between *Border* with *Contraction* with extirpation being generally more likely near the  
277 border, but with a weakening effect as contraction advances. In this model, extirpation  
278 only becomes more likely near the center outside the range of data values used to fit the  
279 model (approximately >98% contraction, obtained when the  $\partial$ Probability of  
280 Extirpation/ $\partial$ Border is equal to zero. Data used to fit the models exclude fragments with  
281 <10% or >90% contraction). The simpler supported model (*Combined\_1*) does not  
282 include an interaction term and suggests that extirpation is consistently more likely near  
283 the border (Figs. 4b and 4c). Thus, at the fragment scale, and considering both  
284 supported models we interpret the results as that in the early stages of contraction areas  
285 close to the border have higher probability of extirpation than central areas. However,  
286 this difference between border and central areas may weaken as contraction progresses.  
287 Separate analyses for data rasterized at different resolutions offered results consistent  
288 with these analyses (Supplementary material, Appendix 2, Table A9)

289

290 **DISCUSSION**

291 The three main null models of range contraction proposed to date make diverse  
292 predictions derived from their theoretical underpinnings. Our evaluation using global  
293 spatial data for terrestrial vertebrates reveals that none of these null models is  
294 sufficiently general to describe contraction range patterns. Even though in the majority  
295 of species extirpated areas are more likely to be heavily humanized, as predicted by the  
296 refuge null model, we also find support for models that incorporate two distinct  
297 mechanisms that likely act together. In addition, the relative position within a range also  
298 appears to influence extirpation probability (independently of human use). For many of  
299 the studied species, extirpation is more likely near the border during early stages of  
300 contraction but during the final stages of contraction extirpation becomes more likely in  
301 central areas, as proposed by the contagion null model. Yet, we also find support for the  
302 demographic model which postulates that the probability of extirpation is always higher  
303 near the border. Future research focused on the final stages of contraction would be  
304 necessary to disentangle these patterns. Nevertheless, our results show that contraction  
305 is better described by multi-process models that consider both human impacts and  
306 relative position, than by the three originally-proposed null models.

307

308 **Contraction and human land use**

309 We find that human use is probably the best single predictor of extirpation probability,  
310 as previously suggested by Yackulic et al. (2011). The key role of human land use  
311 changes in species extinction has been proposed by previous studies that identified  
312 habitat loss due to human land use as the main threat for diverse vertebrate groups  
313 (González-Suárez and Revilla 2014, Hayward 2011, Pekin and Pijanowski 2012,

314 Schipper et al. 2008). In our study, we find that indeed greater extirpation risk is  
315 generally associated with more humanized areas. However, a correlation between  
316 human use and extirpation does not imply a direct causal relationship. Other factors,  
317 such as the presence of invasive species or climate change, could be spatially correlated  
318 with human uses leading to similar patterns of contraction (Franco et al. 2006, Thomas  
319 et al. 2006). The potential role of these other factors could be explored considering our  
320 new proposed baseline that accounts for relative position and human impacts.

321           Although extirpations are generally more common in humanized areas, some  
322 species persist within these regions. Distinct patterns may be due to intrinsic responses;  
323 some species are less sensitive to human impacts than others (Maklakov et al. 2011),  
324 and some even benefit from humanized conditions (Maclean et al. 2011). Additionally,  
325 extirpation may be determined by other drivers of extinction with different spatial  
326 configurations (Clavero et al. 2009, González-Suárez et al. 2013, González-Suárez and  
327 Revilla 2014, Thomas et al. 2006). A caveat of our approach is that our data reflect only  
328 current human land uses, which may not correspond to the past uses potentially  
329 responsible for observed extirpations (Carvalheiro et al. 2013, Plieninger et al. 2006). It  
330 is not clear to us, however, how this could bias our results since we analyzed a large  
331 number of species at a global scale, and the progress of land use changes has been  
332 heterogeneous across the world. While land uses often intensify with time, the rates of  
333 intensification vary by area, and may affect species differently (Bregman et al. 2014,  
334 Gilroy et al. 2014). For example, in some areas of Europe and North America there has  
335 been a reversal toward more natural uses as agricultural land has been abandoned, but  
336 this reversal has not occurred in other areas (Gellrich et al. 2007, MacDonald et al.  
337 2000, Mottet et al. 2006, Strijk 2005). Future studies would be necessary to address  
338 the temporal aspect of land use changes; however, human activities and land use are still

339 likely to be key factors driving range contraction. In fact, they may well play an even  
340 more important and complex role than identified here, e.g., areas with intense  
341 agricultural uses have a greater impact than agri-environmental management areas  
342 (Carvalheiro et al. 2013, Franco et al. 2006).

343

344 **Contraction and relative position within the range: different patterns at different  
345 scales**

346 In addition to the importance of human land use, our analyses show that the relative  
347 position of an area also influences its probability of extirpation (Brown 1995, Channell  
348 and Lomolino 2000a, Channell and Lomolino 2000b, Lawton 1993). At the range scale  
349 our results indicate that the probability of extirpation near the border (or the center)  
350 depends on the contraction stage. This pattern can be caused by directional threats as  
351 proposed by Channell & Lomolino (2000a, 2000b). For example, climate change can  
352 create latitudinal and altitudinal clines (Parmesan 1996, Parmesan and Yohe 2003).

353 However, there are alternative mechanisms that can also lead to this observed pattern.

354 Climatic and biotic factors generally define range limits (Araújo and Rozenfeld 2014),  
355 but some boundaries are due to abrupt ecosystem changes or physical barriers, such as  
356 mountain chains or the transition from land to ocean. In these cases, border areas may  
357 actually represent optimal habitat and thus, be the most populated (Caughley et al. 1988,  
358 Gaston 2003, Sagarin and Gaines 2002). When optimal habitat occurs in a range border,  
359 a directional pattern of contraction could simply occur due to intrinsic population  
360 dynamics, as less dense populations are more likely to go extinct.

361 At the fragment scale we found support for two apparently contrasting models.

362 The simplest model predicts that the probability of extirpation is always higher near the  
363 border, while the best model suggests that the probability of extirpation near the border

364 depends on the contraction level. However, the predicted shift from higher extirpation  
365 risk near the border to higher near the center occurs at the very final stages of  
366 contraction (which lay beyond the range of values analyzed, >90% contraction). In  
367 comparison, at the range scale this shift is predicted at ~60% contraction. Therefore, we  
368 interpret these results as supporting a higher probability of extirpation near fragment  
369 borders in early stages with a potential weakening of this effect as contraction  
370 progresses.

371 There are various possible reasons that could explain the discrepancy in the  
372 results between range and fragment scales. First, different factors and process influence  
373 dynamics at different scales, e.g., climate acts at broader scale while biotic interactions  
374 are more relevant locally (Araújo and Rozenfeld 2014, Pearson and Dawson 2003,  
375 Whittaker et al. 2001). Second, the meaning and identification of relative positions in  
376 complexly shaped distributions is complicated and this may confound results. For  
377 example, the border area in a fragment located near other fragments has a greater  
378 probability of receiving migrants than a “true border”, and thus, could have a lower  
379 probability of extirpation. Null models are commonly defined based on idealized  
380 distributions that largely fail to represent reality. Most species distributions are  
381 complex, often formed by multiple fragments with different shapes that change over  
382 time (Gaston 2003, Wilson et al. 2004). To study range dynamics we need to embrace  
383 this complexity, considering all types of ranges and not only those that conform to some  
384 theoretical or idealized depictions. Importantly, as shown here, we must evaluate  
385 predictions at different scales because results and inferences may differ (Thomas *et. al.*  
386 2008).

387

388 **A new baseline to understand range contraction: multifactorial null models**

389      Earlier null models of range contraction have focused on single processes –basic  
390      population rules and simple threat dynamics (Brown and Kodricbrown 1977, Brown  
391      1995, Channell and Lomolino 2000a, Channell and Lomolino 2000b, Lawton 1993).  
392      Here we show that these null models are not adequate baselines, at least for terrestrial  
393      vertebrates. Species persistence may be influenced by multiple external threats and  
394      intrinsic processes (González-Suárez et al. 2013, Yackulic et al. 2011). To partly  
395      account for this complexity, Yackulic *et al.* (2011) proposed multifactorial models  
396      (including biome, human impacts, and relative position) to explain range contraction in  
397      large mammals. Here, we generalized the importance of multifactorial models for a  
398      wide range of terrestrial vertebrates.

399           Understanding range contraction is important for conservation and management,  
400      particularly if we hope to accurately predict future range changes and assess the effects  
401      of new threats (Newbold et al. 2014, Peters et al. 2014, Selwood et al. 2014, Stanton et  
402      al. 2014, Thomas et al. 2004, Thomas et al. 2011). Our global study based on data from  
403      four different groups of vertebrates reveals the need to develop more realistic null  
404      models to use as baselines. Without departing from the objective of simplicity, we  
405      propose to combine simple key elements already identified as relevant to define new  
406      multi-process null models of range contraction. We realize that data at this scale could  
407      have their own limitations, but we feel that these models can offer a more realistic  
408      baseline to evaluate the role of additional factors, such as the effect of different types of  
409      range borders, the role of environmental conditions, additional human and natural  
410      threats, as well as how intrinsic species' traits influence contraction range dynamics.

411

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426

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- 557

558 **SUPPLEMENTARY MATERIAL**

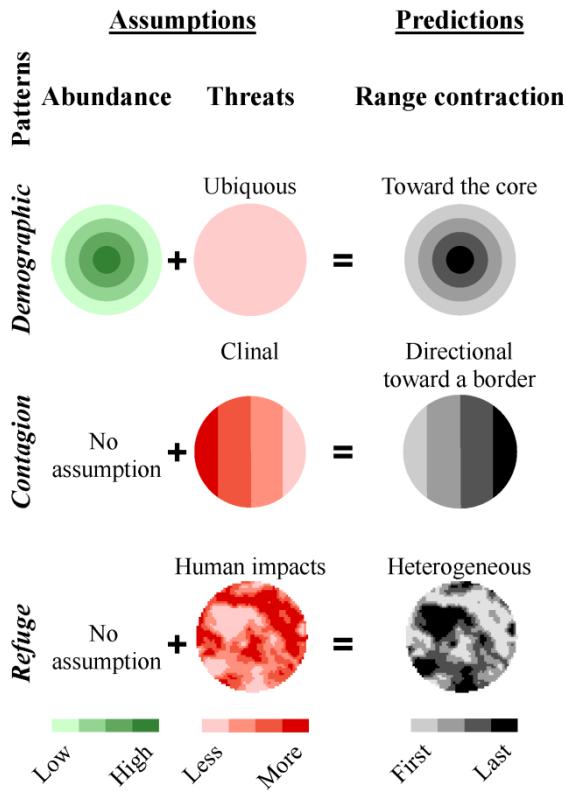
559 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

560 Appendices 1-2.

561    **TABLES**

562    **Table 1.** Results from the regression analyses based on regression models (GLMM) to evaluate the three main null models of range contraction  
563    (demographic, contagion and refuge) and two combined models that incorporate multiple processes. *Combined\_1* proposes that the probability of  
564    extirpation of an area is determined by the proportion of human use in the area (variable *Land use*) and the distance to the historical border  
565    (variable *Border*). *Combined\_2* proposes that the probability of extirpation depends on *Land use* and the interaction of *Border* and *Contraction*  
566    (reflecting the expectation that as range contraction progresses the risk associated with being near the border changes). All models were fitted at  
567    two scales: complete historical range and historical fragment. We report model coefficients (best estimates and their SE), AIC,  $\Delta\text{AIC}$  (difference  
568    in AIC with the best model comparing all five models), and  $\Delta\text{AIC}_{\text{sm}}$  (difference in AIC comparing only the three models derived from the main  
569    proposed null models). Dashes indicate variables not included in the model.

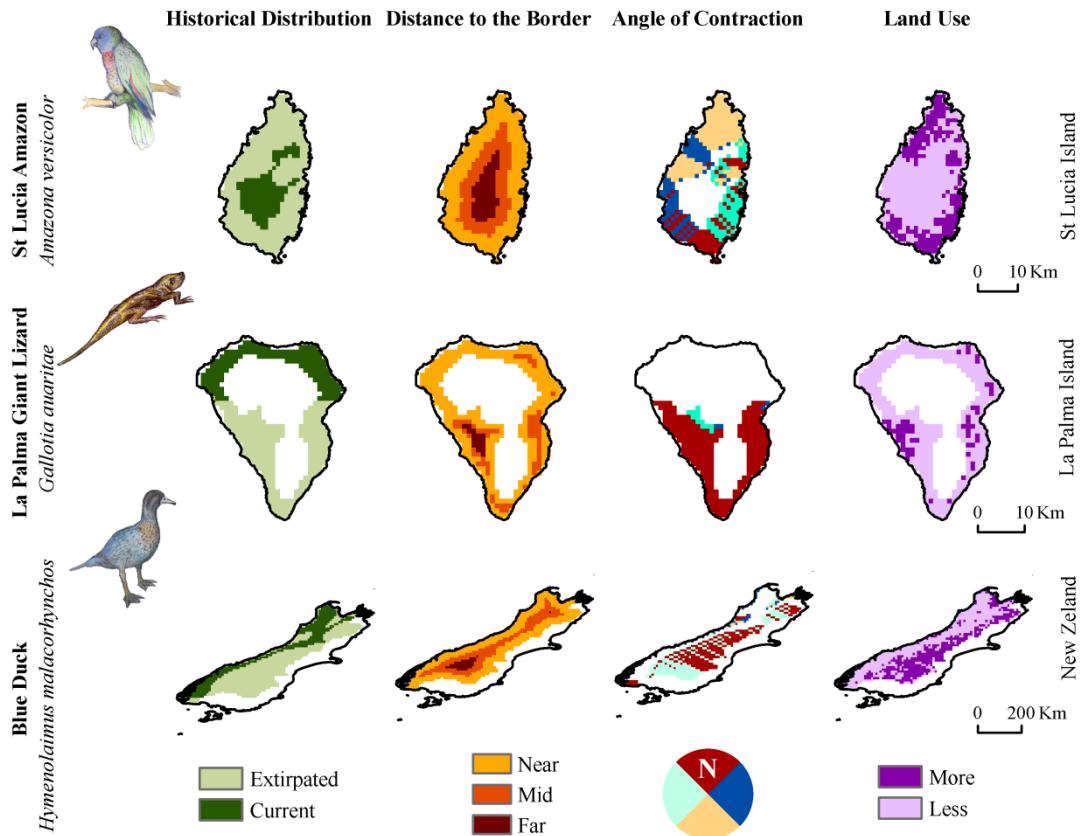
Model	Coefficients				Model comparison		
	<i>Land use</i>	<i>Border</i>	<i>Contraction</i>	<i>Border*Contraction</i>	<i>AIC</i>	$\Delta AIC$	$\Delta AIC_{sm}$
<b>Range scale (N=457, 229 species)</b>							
<i>Combined_2</i>	2.13 (0.466)*	-9.74 (2.145)*	-2.66 (0.688)*	15.86 (3.699)*	605.21	0.00	
<i>Combined_1</i>	2.03 (0.443)*	-1.78 (0.919)†	-	-	621.33	16.13	
<i>Mod_Refuge</i>	2.02 (0.441)*	-	-	-	623.15	17.94	0.00
<i>Mod_Contagion</i>	-	-9.81 (2.110)*	-2.23 (0.664)*	15.74 (3.650)*	625.49	20.28	2.34
<i>Mod_Demographic</i>	-	-1.74 (0.887)†	-	-	641.64	36.43	18.49
<b>Fragment scale (N=362, 142 species)</b>							
<i>Combined_2</i>	2.73 (0.541)*	-9.15 (2.497)*	-2.03 (0.977)*	9.35 (4.131)*	468.09	0.00	
<i>Combined_1</i>	2.62 (0.527)*	-4.16 (1.008)*	-	-	469.35	1.26	
<i>Mod_Refuge</i>	2.57 (0.514)*	-	-	-	486.24	18.14	0.00
<i>Mod_Contagion</i>	-	-8.30 (2.430)*	-1.22 (0.927)	7.65 (3.975)†	494.30	26.21	8.06
<i>Mod_Demographic</i>	-	-3.98 (0.952)*	-	-	494.72	26.62	8.48

571 **FIGURES**

572

573 **Figure 1.** Assumptions and predicted range contraction patterns for each of the three  
 574 null models. The demographic null model assumes higher density in the center of the  
 575 range and a ubiquitous threat pattern. As a result, contractions are predicted to occur  
 576 toward the core in multiple directions. The contagion null model assumes that threats  
 577 are distributed in a cline resulting in a directional contraction along this cline. The  
 578 refuge null model assumes that the extirpation is determined by human land use and  
 579 predicts a heterogeneous range contraction pattern with less used areas being less likely  
 580 to become extirpated.

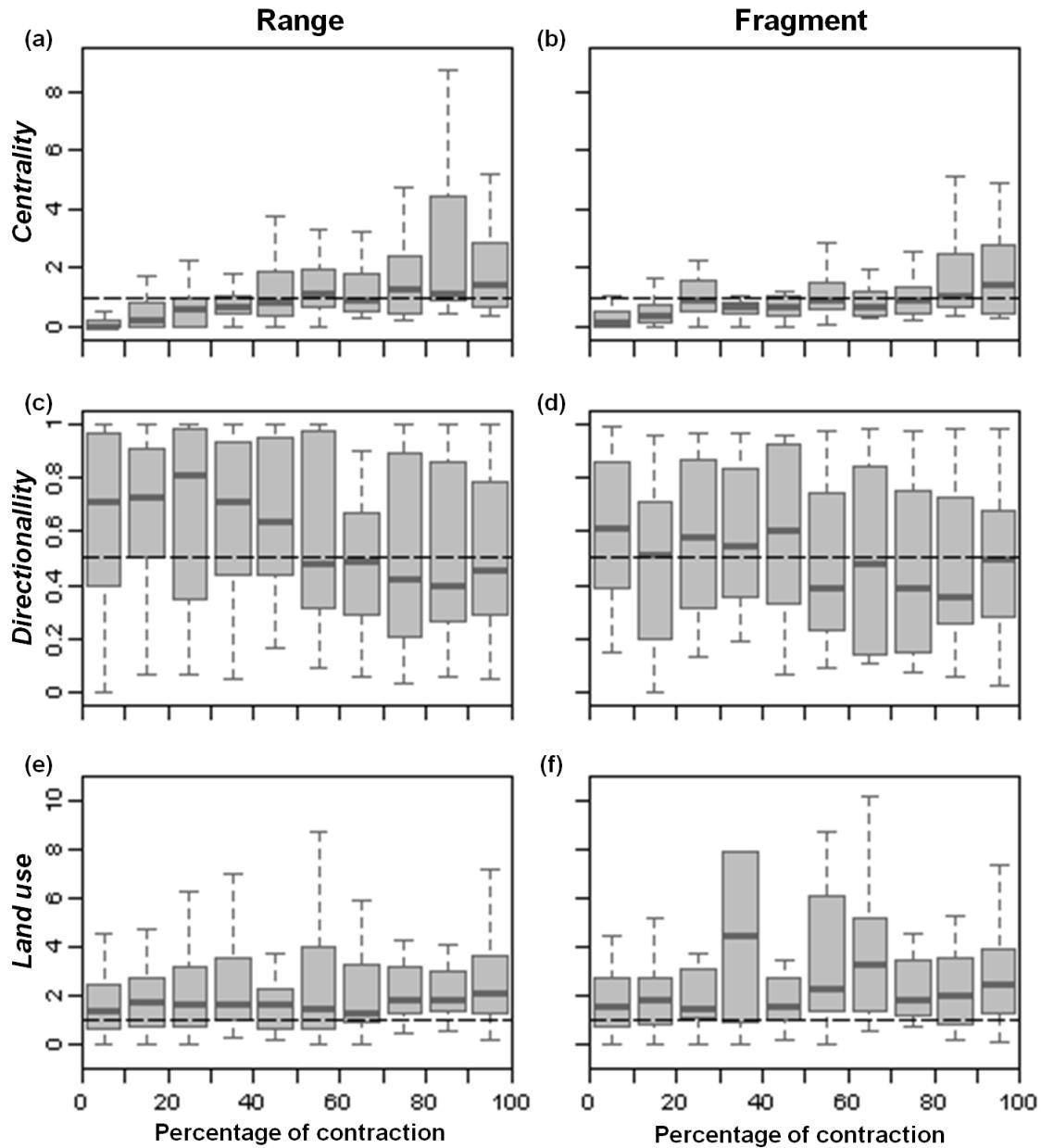
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582

583 **Figure 2.** Examples of the three variables defined to represent the key predictors of the  
 584 three null models: *Distance to the Border (Border)*: average distance to border from  
 585 each cell; *Angle of contraction*: geodetic angle of contraction (from each extirpated cell  
 586 to the closest current cell), and *Human Use (Land use)*: proportion of human use in the  
 587 cell. Examples represent the Saint Lucia amazon (*Amazona versicolor*) which illustrates  
 588 the pattern of contraction predicted by the demographic null model (also partly  
 589 congruent with the refuge null model); the La Palma giant lizard (*Gallotia auaritae*)  
 590 illustrates contraction from a border to the opposite border in a unique direction as  
 591 predicted by the contagion null model (and is also partly congruent with the refuge null  
 592 model); and the blue duck (*Hymenolaimus malacorhynchos*) which adjusts to the refuge  
 593 null model prediction.

594



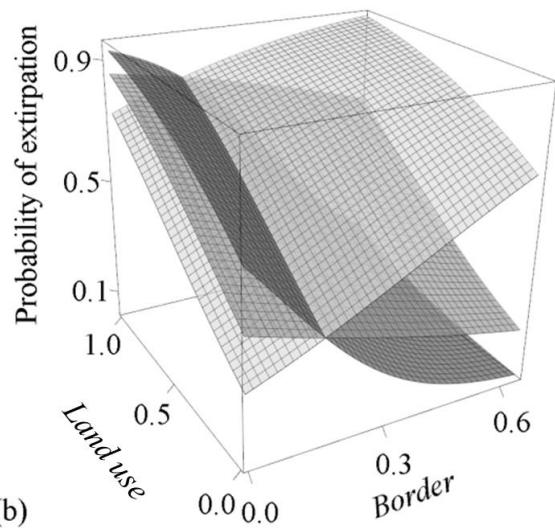
595

596 **Figure 3.** The distribution of three indices at the range (a, c, e) and fragment scale (b, d, 597 f). For initial stages of contraction (< 50% contraction) both demographic and contagion 598 null model predict *Centrality Index* < 1. For higher stages of contraction (> 50% 599 contraction) *Centrality Index* < 1 supports the demographic null model while *Centrality* 600 *Index* > 1 supports the contagion null model (a, b). *Directionality Index* close to 0 is 601 predicted by the demographic null model, whereas values close to 1 support the 602 contagion null model (c, d). *Land use Index* > 1 is predicted by the refuge null model (e, 603 f). Ends of the whiskers represent the lowest datum still within the 1.5 interquartile

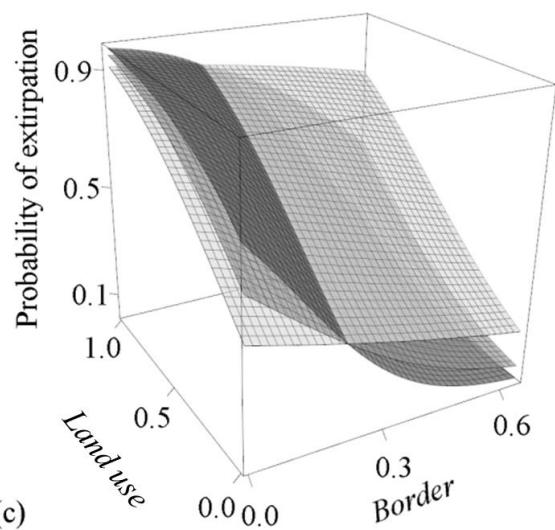
604 range (IQR) of the lower quartile, and the highest datum still within the 1.5 IQR of the  
605 upper quartile (Tukey boxplot).

606

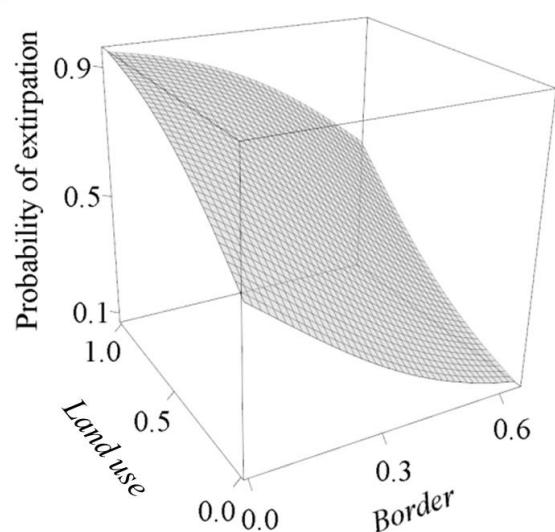
(a)



(b)



(c)



608   **Figure 4.** Predictions of the supported regression models explaining probability of  
609   extirpation of an area as a function of its distance to the historical border (*Border*) and  
610   its human land use (*Land use*) with a possible interaction of *Land use* and the  
611   percentage of contraction (*Contraction*). At the range scale, panel (a), Model  
612   *Combined\_2* (including the interaction) was the single supported model (Table 1). At  
613   the fragment scale both Model *Combined\_2* (b) and Model *Combined\_1* (c, no  
614   interaction) were supported. To visualize the effect of the interaction between *Border*  
615   and *Contraction* (a, b), we represent predictions at three levels of contraction: 20% in  
616   darker grey, 50% in medium dark grey, and 80% in light grey.