



Toward multifactorial null models of range contraction in terrestrial vertebrates

Article

Accepted Version

Lucas, P. M., Gonzalez-Suarez, M. and Revilla, E. (2016) Toward multifactorial null models of range contraction in terrestrial vertebrates. *Ecography*, 39 (11). 1100- 1108. ISSN 0906-7590 doi: <https://doi.org/10.1111/ecog.01819> Available at <http://centaur.reading.ac.uk/51589/>

It is advisable to refer to the publisher's version if you intend to cite from the work.

Published version at: <http://dx.doi.org/10.1111/ecog.01819>

To link to this article DOI: <http://dx.doi.org/10.1111/ecog.01819>

Publisher: Wiley

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online



1 *Title:* Toward multifactorial null models of range contraction in terrestrial
2 vertebrates

3 *Running title:* Null models of range contraction

4 *List of authors:* Pablo M. Lucas¹, Manuela González-Suárez^{1,2}, Eloy Revilla¹

5 *Institute of origin:*

6 ¹Department of Conservation Biology, Estación Biológica de Doñana EBD-CSIC

7 Calle Americo Vespucio s/n 41092 Seville Spain

8 ²Ecology and Evolutionary Biology, School of Biological Sciences, University of

9 Reading, Whiteknights, Reading RG6 6AS, UK

10 *Corresponding author:* PML, Tel: (+34) 954 466700 (Ext. 1125), Fax: (+34) 954

11 621125, lucas.pablo.2010@gmail.com

12 *Category of article:* Original research

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 treats 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 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 ∂ Probability
271 of Extirpation/ ∂ 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 ∂ Probability of
280 Extirpation/ ∂ 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 (Carvalho 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, Strijker 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 (Carvalho 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

412 **ACKNOWLEDGEMENTS**

413 We are sincerely grateful to Kevin Gaston, Thomas Wilson, Miguel Delibes, Miguel
414 Ángel Olalla, the members of the Spatial Ecology Lab (University of Queensland), the
415 members of the Department of Conservation Biology (EBD-CSIC) and the personal
416 from the Geographic Information System Laboratory (LAST-EBD-CSIC) for their help
417 with technical aspects and helpful suggestions about the manuscript. We are also in debt
418 to Ángel Lucas for the artwork in Figure 2. We also thank two anonymous reviewers for
419 helpful comments that improved earlier drafts of the article. This work was funded by
420 the Spanish Ministry of Economy and Competitiveness (CGL2009-07301/BOS and
421 CGL2012-35931/BOS co-funded by FEDER, and the FPI grant BES-2010-034151), by
422 the European Community's Seventh Framework Programme (FP7/2007-2013) under
423 grant agreement no 235897, and by a Juan de la Cierva post-doctoral fellowship (JCI-
424 2011-09158). We also acknowledge funding from the Spanish Severo Ochoa Program
425 (SEV-2012-0262).

426

427 **REFERENCES**

- 428 Araújo, M. B. and Rozenfeld, A. 2014. The geographic scaling of biotic interactions. -
429 *Ecography* 37: 406–415.
- 430 Bregman, T. P. et al. 2014. Global patterns and predictors of bird species responses to
431 forest fragmentation: implications for ecosystem function and conservation. - *Biol.*
432 *Conserv.*
- 433 Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. -
434 *Am. Nat.* 467-478.
- 435 Brown, J. H. and Kodricbrown, A. 1977. Turnover rates in insular biogeography: effect
436 of immigration on extinction¹. - *Ecology* 58: 445-449.
- 437 Brown, J. H. 1995. *Macroecology*. - University of Chicago Press, Chicago.

438 Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference:
439 A Practical Information-Theoretic Approach. - Springer, New York.

440 Cahill, A. E. et al. 2012. How does climate change cause extinction? - Proc. R. Soc.
441 Lond., Ser. B: Biol. Sci. 280: 1-9.

442 Carvalheiro, L. G. et al. 2013. Species richness declines and biotic homogenisation have
443 slowed down for NW-European pollinators and plants. - Ecol. Lett. 16: 870-878.

444 Caughley, G. et al. 1988. The edge of the range. - The Journal of Animal Ecology

445 Ceballos, G. and Ehrlich, P. R. 2002. Mammal population losses and the extinction
446 crisis. - Science 296: 904-907.

447 Channell, R. and Lomolino, M. V. 2000a. Dynamic biogeography and conservation of
448 endangered species. - Nature 403: 84-86.

449 Channell, R. and Lomolino, M. V. 2000b. Trajectories to extinction: spatial dynamics of
450 the contraction of geographical ranges. - J. Biogeogr. 27: 169-179.

451 Clavero, M. et al. 2009. Prominent role of invasive species in avian biodiversity loss. -
452 Biol. Conserv. 142: 2043–2049.

453 David, H. R. et al. 2003. Estimates of minimum viable population sizes for vertebrates
454 and factors influencing those estimates. - Biol. Conserv. 113: 2334.

455 Davis, A. J. et al. 1998. Making mistakes when predicting shifts in species range in
456 response to global warming. - Nature 391: 783-786.

457 Fisher, D. O. 2011. Trajectories from extinction: where are missing mammals
458 rediscovered? - Global Ecol. Biogeogr. 20: 415-425.

459 Franco, A. M. A. et al. 2006. Impacts of climate warming and habitat loss on extinctions
460 at species' low-latitude range boundaries. - Global Change Biol. 12: 1545-1553.

461 Gaston, K. J. 2003. The Structure and Dynamics of Geographic Ranges. - Oxford
462 University Press, Oxford.

463 Gellrich, M. et al. 2007. Agricultural land abandonment and natural forest re-growth in
464 the Swiss mountains: A spatially explicit economic analysis. - *Agric., Ecosyst. Environ.*
465 118: 93-108.

466 Gilroy, J. J. et al. 2014. Effect of scale on trait predictors of species responses to
467 agriculture. - *Conserv. Biol.*

468 González-Suárez, M. et al. 2013. Which intrinsic traits predict vulnerability to
469 extinction depends on the actual threatening processes. - *Ecosphere* 4 (6): 76.

470 González-Suárez, M. and Revilla, E. 2014. Generalized drivers in the Mammalian
471 endangerment process. - *PloS ONE* 9: e90292.

472 Gotelli, N. J. 2001. Research frontiers in null model analysis. - *Global Ecol. Biogeogr.*
473 10: 337-343.

474 Hanski, I. 1998. Metapopulation dynamics. - *Nature* 396: 41-49.

475 Hanski, I. and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented
476 landscape. - *Nature* 404: 755-758.

477 Hayward, M. W. 2011. Using the IUCN Red List to determine effective conservation
478 strategies. - *Biodivers. Conserv.* 20: 2563–2573.

479 Hemerik, L. et al. 2006. The eclipse of species ranges. - *Acta Biotheor.* 54: 255-266.

480 Hoffmann, M. et al. 2010. The Impact of Conservation on the Status of the World's
481 Vertebrates. - *Science* 330: 1503-1509.

482 International Union for Conservation of Nature 2010. IUCN red list of threaten species
483 Version 2010.4. <http://www.iucnredlist.org/> (accessed February 08, 2010).

484 Jones, H. L. and Diamond, J. M. 1976. Short-time-base studies of turnover in breeding
485 bird populations on the California Channel Islands. - *Condor*

486 Laliberte, A. S. and Ripple, W. J. 2004. Range contractions of North American
487 carnivores and ungulates. - *Bioscience* 54: 123-138.

488 Lawton, J. H. 1993. Range, population abundance and conservation. - Trends Ecol.
489 Evol.

490 Li, X. et al. 2015. Human impact and climate cooling caused range contraction of large
491 mammals in China over the past two millennia. - Ecography 38: 74–82.

492 MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography. -
493 Princeton University Press, Princeton, N.J.

494 MacDonald, D. et al. 2000. Agricultural abandonment in mountain areas of Europe:
495 Environmental consequences and policy response. - J. Environ. Manage. 59: 47-69.

496 Maclean, I. et al. 2011. Predicting changes in the abundance of African wetland birds by
497 incorporating abundance– occupancy relationships into habitat association models. -
498 Divers. Distrib. 17: 480-490.

499 Maklakov, A. A. et al. 2011. Brains and the city: big-brained passerine birds succeed in
500 urban environments. - Biol. Lett. 7: 730–732.

501 Mottet, A. et al. 2006. Agricultural land-use change and its drivers in mountain
502 landscapes: A case study in the Pyrenees. - Agric., Ecosyst. Environ. 114: 296-310.

503 Newbold, T. et al. 2014. Functional traits, land-use change and the structure of present
504 and future bird communities in tropical forests. - Global Ecol. Biogeogr. 23: 1073-1084.

505 Oak Ridge National Laboratory Distributed Active Archive Center 2010. MODIS
506 (MCD12Q1) Land Cover Product <http://webmap.ornl.gov> ORNL DAAC, Oak Ridge,
507 Tennessee, USA. Accessed September, 2013.

508 Parmesan, C. 1996. Climate and species' range. - Nature 382: 765-766.

509 Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change
510 impacts across natural systems. - Nature 421: 37-42.

511 Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the
512 distribution of species: are bioclimate envelope models useful? - *Global Ecol. Biogeogr.*
513 12: 361-371.

514 Pekin, B. K. and Pijanowski, B. C. 2012. Global land use intensity and the
515 endangerment status of mammal species. - *Divers. Distrib.* 18: 909-918.

516 Peters, H. et al. 2014. Identifying species at extinction risk using global models of
517 anthropogenic impact. - *Global Change Biol.* doi: 10.1111/gcb.12749.

518 Pimm, S. L. et al. 1988. ON THE RISK OF EXTINCTION. - *Am. Nat.* 132: 757-785.

519 Plieninger, T. et al. 2006. Traditional land-use and nature conservation in European
520 rural landscapes. - *Environ. Sci. Policy* 9: 317-321.

521 Pomara, L. Y. et al. 2014. Demographic consequences of climate change and land cover
522 help explain a history of extirpations and range contraction in a declining snake species.
523 - *Global Change Biol.* 20: 2087–2099.

524 R Development Core Team 2013. R: A language and environment for statistical
525 computing. R Foundation for Statistical Computing, Vienna, Austria.

526 Safi, K. and Pettorelli, N. 2010. Phylogenetic, spatial and environmental components of
527 extinction risk in carnivores. - *Global Ecol. Biogeogr.* 19: 352-362.

528 Sagarin, R. D. and Gaines, S. D. 2002. The 'abundant centre' distribution: to what extent
529 is it a biogeographical rule? - *Ecol. Lett.* 5: 137-147.

530 Sagarin, R. D. et al. 2006. Moving beyond assumptions to understand abundance
531 distributions across the ranges of species. - *Trends Ecol. Evol.* 21: 524-530.

532 Schipper, J. et al. 2008. The status of the world's land and marine mammals: diversity,
533 threat, and knowledge. - *Science* 322: 225-230.

534 Selwood, K. E. et al. 2014. The effects of climate change and land-use change on
535 demographic rates and population viability. - *Biol. Rev. Camb. Philos. Soc.* doi:
536 10.1111/brv.12136.

537 Stanton, J. C. et al. 2014. Warning times for species extinctions due to climate change. -
538 *Global Change Biol.* doi: 10.1111/gcb.12721.

539 Strijker, D. 2005. Marginal lands in Europe—causes of decline. - *Basic Appl. Ecol.* 6:
540 99-106.

541 Thomas, C. et al. 2006. Range retractions and extinction in the face of climate warming.
542 - *Trends Ecol. Evol.* 21: 415-416.

543 Thomas, C. D. et al. 2004. Extinction risk from climate change. - *Nature* 427: 145-148.

544 Thomas, C. D. et al. 2008. Where within a geographical range do species survive best?
545 A matter of scale. - *Insect Conserv. Divers.* 1: 2-8.

546 Thomas, C. D. et al. 2011. A framework for assessing threats and benefits to species
547 responding to climate change. - *Methods Ecol. Evol.* 2: 125-142.

548 Turvey, S. T. et al. 2015. Historical data as a baseline for conservation: reconstructing
549 long-term faunal extinction dynamics in Late Imperial–modern China. - *Proc. R. Soc. B*

550 Whittaker, R., J. et al. 2001. Scale and species richness: towards a general, hierarchical
551 theory of species diversity. - *J. Biogeogr.* 28: 453-470.

552 Wilson, R. J. et al. 2004. Spatial patterns in species distributions reveal biodiversity
553 change. - *Nature* 432: 393-396.

554 Yackulic, C. B. et al. 2011. Anthropogenic and environmental drivers of modern range
555 loss in large mammals. - *Proc. Natl. Acad. Sci. USA* 108: 4024-4029.

556 Zar, J. H. 1999. *Biostatistical analysis*, 4/e. - Pearson Education India.

557

558 **SUPPLEMENTARY MATERIAL**

- 559 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).
- 560 Appendices 1-2.

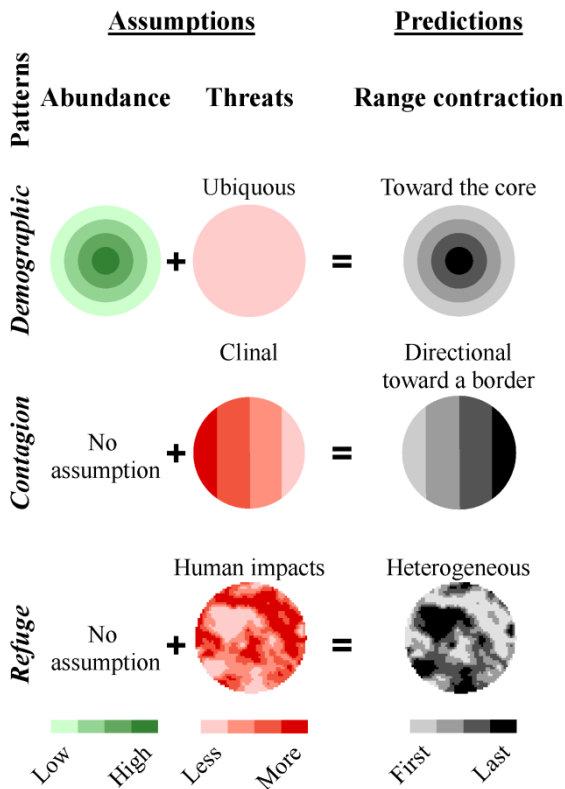
561 **TABLES**

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, Δ AIC (difference
568 in AIC with the best model comparing all five models), and Δ AIC_{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>	ΔAIC	ΔAIC_{sm}
Range scale (N=457, 229 species)							
<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
Fragment scale (N=362, 142 species)							
<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

570 *P < 0.05; †P < 0.10

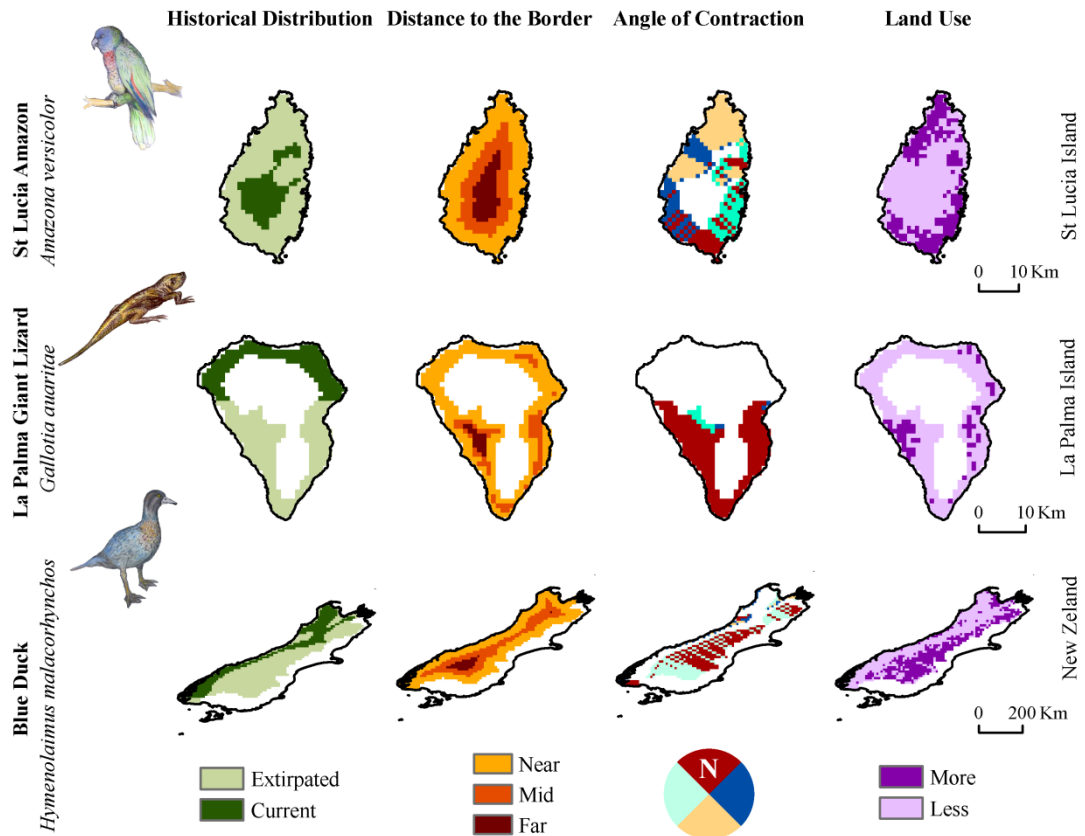
571 **FIGURES**



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.

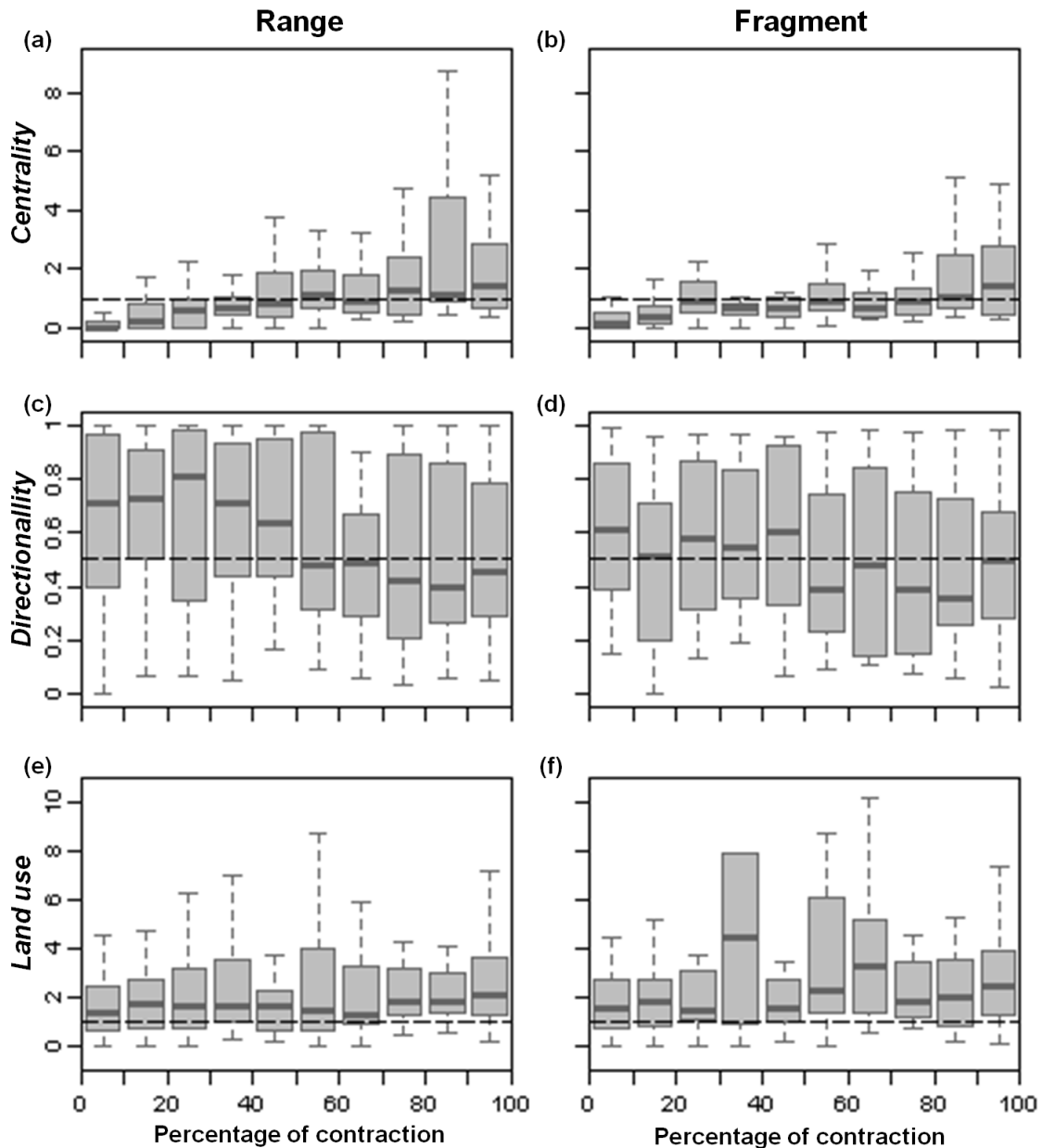
581



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

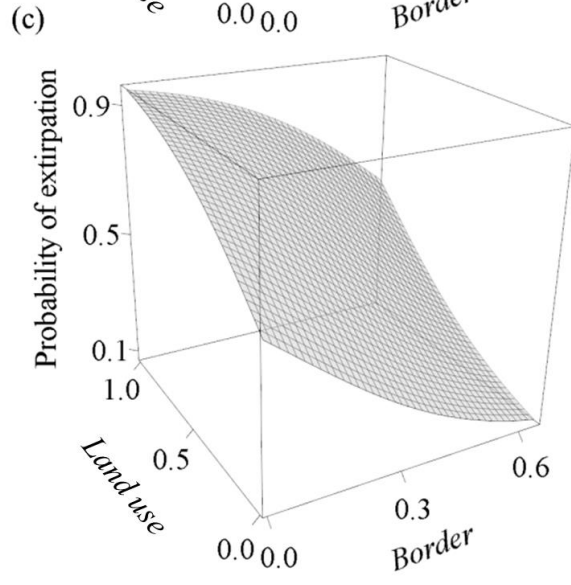
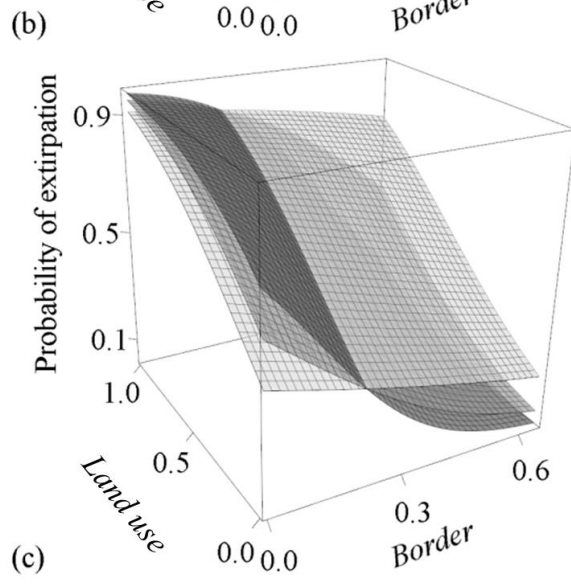
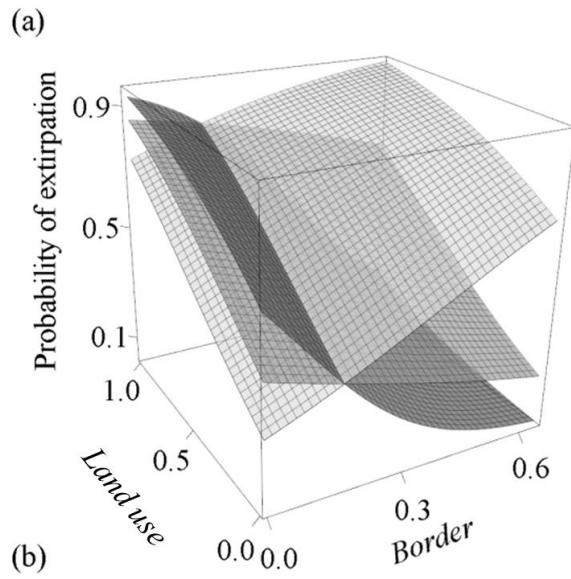


595

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



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.