



Toward multifactorial null models of range contraction in terrestrial vertebrates

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

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

Null models are representations based on the simplest and most general mechanisms, and deliberately focus on a few key factors or processes to provide a baseline for comparison

with empirical observations or with more complex models (Gotelli 2001). The simplicity of null models can be useful for species for which little information exists, as well as in theoretical studies (Hanski 1998, Hanski and Ovaskainen 2000). Generalized patterns of distribution range contraction have been described in the literature using three different null models: demographic, contagion, and refuge. These models describe contraction based on distinct mechanisms derived from theoretical principles in ecology, biogeography, and conservation biology (Hanski 1998, Hemerik et al. 2006); and have been used in empirical studies as baselines to determine the role of additional factors or to broadly describe observed contraction patterns (Parmesan 1996, Thomas et al. 2004, Franco et al. 2006, Yackulic et al. 2011, Pomara et al. 2014, Turvey et al. 2015).

The demographic null model derives from basic population dynamic principles, and from the ecological assumption which postulate that environmental conditions and resources at the center of a distribution range are more suitable than at the border, resulting in higher population growth rates and thus, higher abundance in central areas (Lawton 1993, Brown 1995). Because extinction is directly determined by

population abundance (Brown 1971, Jones and Diamond 1976, Pimm et al. 1988, David et al. 2003), when the drivers of extinction (threats) are ubiquitous, central areas would have lower extinction/extirpation risk (MacArthur and Wilson 1967). Assuming threats are indeed ubiquitous, this null model then predicts that populations would be first extirpated along the historical border (where density is lower) and would continue toward the center, where the last (most dense) population would be found (Fig. 1). The contagion null model, on the other hand, assumes that the threats have clinal distribution, with threats spreading across the landscape with distinct directionality, like a contagious disease (Lawton 1993, Channell and Lomolino 2000a, b). Based on this clinal threat pattern, the contagion null model predicts that populations would be first extirpated in the historical border closest to the extinction driver's origin, and then as the threat spreads across the range, the central areas would become extirpated until only the historical border located farthest from the initial point remains (Fig. 1). Finally, the refuge model assumes that more humanized land uses are associated with higher risk of extinction (Ceballos and Ehrlich 2002, Laliberte and Ripple 2004, Schipper et al. 2008, Hoffmann et al. 2010, Fisher 2011, Yackulic et al. 2011, Pomara et al. 2014, Li et al. 2015), and predicts that

populations would be first extirpated in areas that are more modified and heavily used by humans. According to this model, the last population will be located in the least used area, which represents a final refuge for the species (Fig. 1).

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

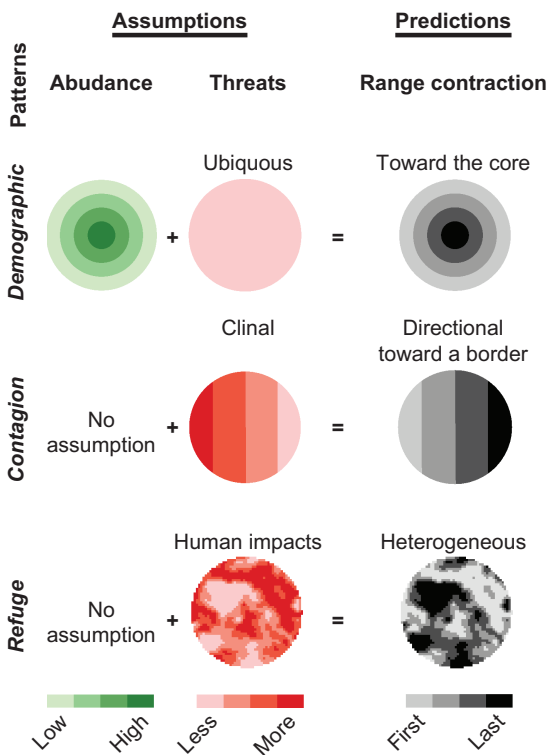


Figure 1. Assumptions and predicted range contraction patterns for each of the three null models. The demographic null model assumes higher density in the center of the range and a ubiquitous threat pattern. As a result, contractions are predicted to occur toward the core in multiple directions. The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

Methods

Spatial distribution data

We used global distribution data of 386 terrestrial vertebrates (International Union for Conservation of Nature 2010) with known range contraction (i.e. a distribution with extirpated areas, where the species was present in the past but is no longer found, and current areas, where the species is currently present, and following the notation of the International Union for Conservation of Nature 2010; detailed information is provided in Supplementary material Appendix 1). Since most species distributions are fragmented and have complex shapes, our analyses were conducted at two different scales. At the range scale, we used data from the complete historical distribution range of each species ($n = 374$), which often included multiple fragments separated by unoccupied areas. At the fragment scale, we used data from all individual fragments with observed contraction ($n = 273$). See Supplementary material Appendix 1–2 for additional information in data preparation. Supplementary material Appendix 2, Table A3 and A4 and Fig. A1 provide descriptive summaries of these data including total area in km^2 and percentage of contraction (calculated as the percentage of the historical range area classified as extirpated) for complete ranges and individuals fragments. For complete ranges we also summarize the number of fragments present in the historical, extirpated, and current ranges, as well as the percentage of extirpated fragments (percentage of historical fragments classified as extirpated). Spatial data were

projected into an equal area projection (cylindrical equal area) and rasterized.

Analyses

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

Indexes

The demographic and contagion null models both associate the probability of extirpation with an area's relative position within a range (Fig. 1). Therefore, we defined a position index based on relative distance to the border. We use the border instead of the center because identifying meaningful centers is complicated in complexly shaped and fragmented distributions (Sagarin et al. 2006). For each distribution range and

fragment analyzed, we first estimated the geodetic distance from each grid cell to the closest historical border cell (Fig. 2, and Supplementary material Appendix 2). A geodetic distance is the distance between two unprojected points on the spheroid of the Earth (using the spheroid World Geodetic System 1984, WGS84). Distances were standardized dividing species' values by the maximum distance observed for the range (at range scale) or fragment (at fragment scale) to facilitate comparison among species with different distribution ranges. Using these distance values from each cell to the nearest border, we then calculated the variable *Border* as the arithmetic mean distance to the border from all cells within one area, with *Border_ext* representing extirpated areas and *Border_curr* current areas. Using these values we defined the *Centrality Index* = $Border_ext / Border_curr$ for each range and fragment. The demographic null model predicts *Centrality Index* < 1 (extirpated areas are closer to the border), whereas the contagion model predicts *Centrality Index* < 1 only for initial stages of contraction (approximately < 50% of the historical range extirpated), and *Centrality Index* > 1 for contractions > 50%. Therefore, both the contagion and demographic null models predict the same values of

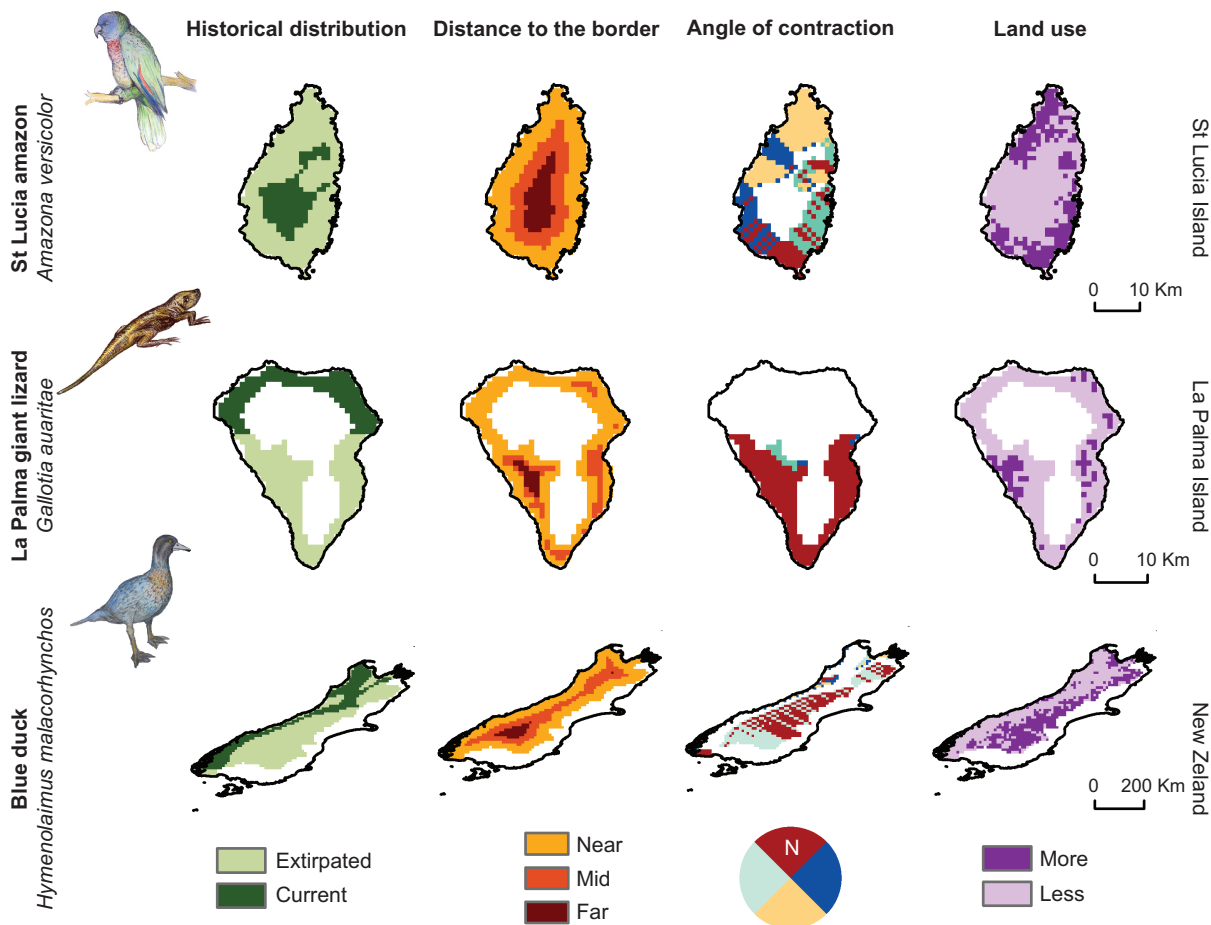


Figure 2. Examples of the three variables defined to represent the key predictors of the three null models. Distance to the border (*Border*): average distance to border from each cell; *Angle of contraction*: geodetic angle of contraction (from each extirpated cell to the closest current cell); and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

Centrality Index in early stages of contraction but different values in later stages. The refuge null model makes no general prediction for the *Centrality Index* (Fig. 1).

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

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

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

Prior to visualizing the empirical data the behavior of the *Centrality* and *Directionality* indexes was evaluated using simulated scenarios. We sketched three example distribution range areas (Supplementary material Appendix 2, Fig. A3) for which we simulated two patterns: range contraction towards the center (demographic model), and clinal range contraction (contagion model). For irregularly shaped distributions we explored two different directions of contraction because distinct clines could influence results. The indexes were then validated exploring the behavior of values calculated at seven stages along the contraction process in these simulated scenarios (Supplementary material Appendix 2, Fig. A3).

Regression analyses

We defined regression models to estimate the probability of extirpation of an area based on two of the previously defined variables (*Border* and *Land use*) and the percentage of contraction (*Contraction*). For this approach we excluded distributions (ranges and fragments) with < 10% or > 90% contraction (Supplementary material Appendix 1, Table A1 and A2) because at early and late stages of contraction stochastic noise may confound existing patterns (Yackulic et al. 2011). Under the demographic model, the probability of extirpation should continuously decrease with the distance to the border independently of the percentage of contraction. Thus, the probability of extirpation of an area could be simply defined by the variable *Border* (*Mod_Demographic*, Table 1). A key prediction of the contagion null model is that there is directionality in contraction, but the angle of contraction is a relative concept that compares extirpated and current areas and thus, cannot be estimated for completely extirpated or current areas. Instead, we

Table 1. Results from the regression analyses based on regression models (GLMM) to evaluate the three main null models of range contraction (demographic, contagion and refuge) and two combined models that incorporate multiple processes. *Combined_1* proposes that the probability of 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 (variable *Border*). *Combined_2* proposes that the probability of extirpation depends on *Land use* and the interaction of *Border* and *Contraction* (reflecting the expectation that as range contraction progresses the risk associated with being near the border changes). All models were fitted at two scales: complete historical range and historical fragment. We report model coefficients (best estimates and their SE), AIC, Δ AIC (difference 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 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</i> × <i>Contraction</i>	AIC	Δ AIC	Δ AIC _{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

*p < 0.05; [†]p < 0.10

evaluated another prediction of this null model, namely that the effect of distance to the border on the probability of extirpation depends on the percentage of contraction. We modeled this prediction using an interaction term between the variables *Border* and *Contraction* (*Mod_Contagion*, Table 1). Finally, under the refuge null model, the probability of extirpation should simply depend on the human land use intensity, which is represented by the variable *Land use* (*Mod_Refuge*, Table 1). For each of the analysis scales (range and fragment) we fitted generalized linear mixed regression models (GLMM) with family binomial and a logit link using the function `glmer` from the `lme4` package in R (R Development Core Team). All models included taxonomic class, order, family, and genus as random factors to control for evolutionary non-independence of the observations. We compared models using an information theoretic approach based on Akaike information criterion, AIC (Burnham and Anderson 2002).

Finally, we explored the possibility that the multiple processes postulated by these null models may occur simultaneously. We fitted two additional models that combine predictions from compatible null models. *Combined_1* modelled the probability of extirpation considering both *Land use* and *Border*, *Combined_2* included *Land use* and allowed for the interaction of *Border* with *Contraction* (Table 1).

Results

We analyzed spatial data for 386 species (374 species at range scale and 213 at fragment scale) which represent ~ 1.6% of the terrestrial vertebrates listed by the IUCN. The studied distribution ranges and fragments have widely variable areas, with an observed mean percentage of contraction of 41% for complete ranges and 51% for fragments (Supplementary material Appendix 2, Table A3 and A4 and Fig. A1). Distribution ranges are often fragmented with a mean of 6.7 fragments per historical range.

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

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

Results from the regression analyses at both scales also failed to clearly identify a single best null model. At the

range scale, both the refuge (*Mod_Refuge*) and the contagion (*Mod_Contagion*) null models received support; whereas at the fragment scale the only supported model was *Mod_Refuge* (Table 1). Although overall the refuge null model received greater support compared to other null models, results at both range and fragment scales revealed that either of the combined models represents a great improvement (based on AIC) over models based on the unifactorial null models (Table 1). At least for the available data, multiple processes appear to best explain the general patterns of contraction among terrestrial vertebrates.

At the range scale *Combined_2* was the only supported model (Table 1), which describes the probability of extirpation as positively correlated with human use (*Land use*) and identifies a contraction-dependent effect of distance to the border. In particular, at early stages of contraction (up to ~ 60% contraction, obtained when the $\partial\text{Probability of Extirpation}/\partial\text{Border}$ is equal to zero) areas near the border are more likely to be extirpated whereas at later stages the pattern is reversed (Fig. 4a). At the fragment scale, both combined models were supported (being within 2 AIC units of each other, Table 1) and show a positive association between the probability of extirpation and *Land use*, with the best supported model, *Combined_2*, additionally supports an interaction between *Border* with *Contraction* with extirpation being generally more likely near the border, but with a weakening effect as contraction advances. In this model, extirpation only becomes more likely near the center outside the range of data values used to fit the model (approximately > 98% contraction, obtained when the $\partial\text{Probability of Extirpation}/\partial\text{Border}$ is equal to zero). Data used to fit the models exclude fragments with < 10% or > 90% contraction). The simpler supported model (*Combined_1*) does not include an interaction term and suggests that extirpation is consistently more likely near the border (Fig. 4b, c). Thus, at the fragment scale, and considering both supported models we interpret the results as that in the early stages of contraction areas close to the border have higher probability of extirpation than central areas. However, this difference between border and central areas may weaken as contraction progresses. Separate analyses for data rasterized at different resolutions offered results consistent with these analyses (Supplementary material Appendix 2, Table A9).

Discussion

The three main null models of range contraction proposed to date make diverse predictions derived from their theoretical underpinnings. Our evaluation using global spatial data for terrestrial vertebrates reveals that none of these null models is sufficiently general to describe contraction range patterns. Even though in the majority of species extirpated areas are more likely to be heavily humanized, as predicted by the refuge null model, we also find support for models that incorporate two distinct mechanisms that likely act together. In addition, the relative position within a range also appears to influence extirpation probability (independently of human use). For many of the studied species, extirpation is more likely near the border during early stages of contraction

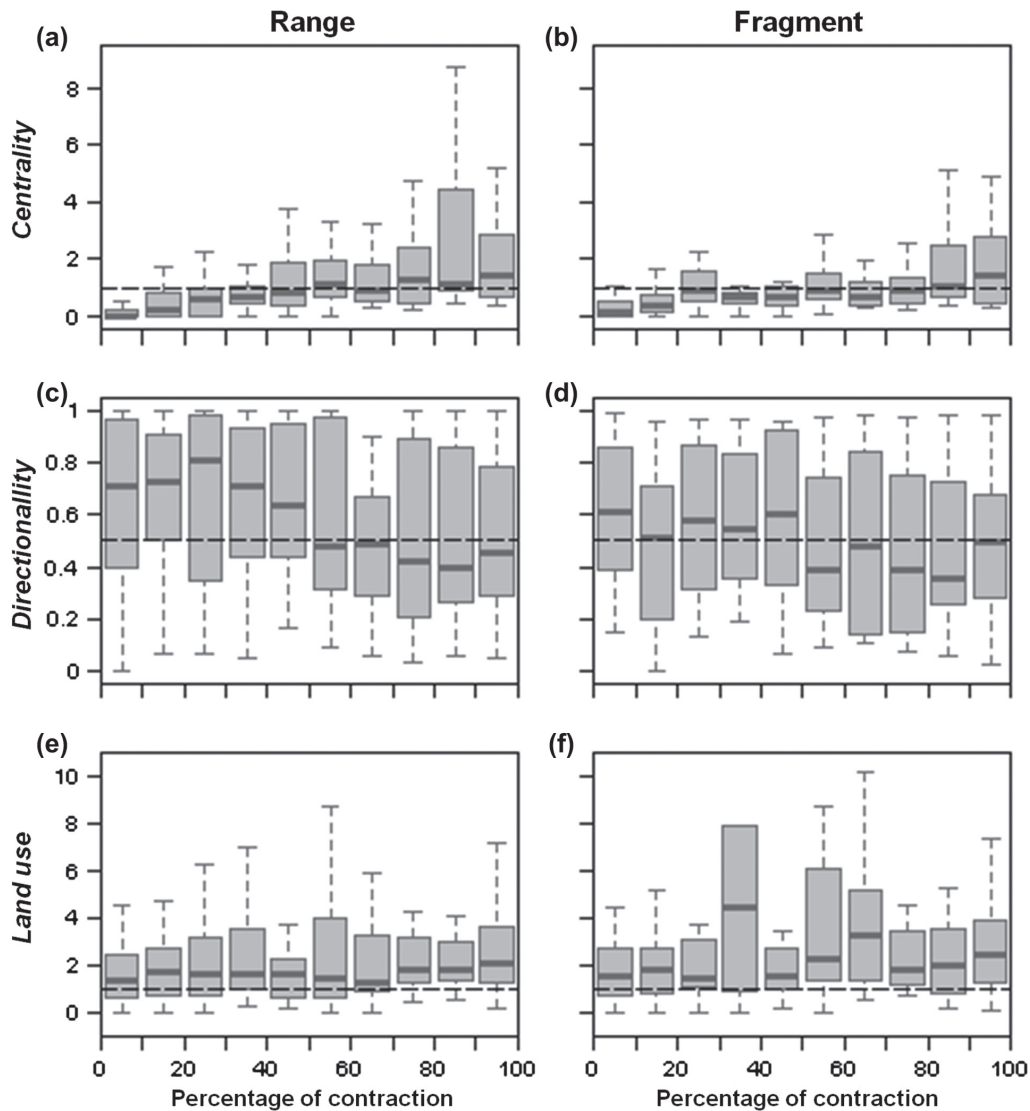


Figure 3. The distribution of three indices at the range (a, c, e) and fragment scale (b, d, f). For initial stages of contraction (< 50% contraction) both demographic and contagion null model predict *Centrality Index* < 1. For higher stages of contraction (> 50% contraction) *Centrality Index* < 1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

but during the final stages of contraction extirpation becomes more likely in central areas, as proposed by the contagion null model. Yet, we also find support for the demographic model which postulates that the probability of extirpation is always higher near the border. Future research focused on the final stages of contraction would be necessary to disentangle these patterns. Nevertheless, our results show that contraction is better described by multi-process models that consider both human impacts and relative position, than by the three originally-proposed null models.

Contraction and human land use

We find that human use is probably the best single predictor of extirpation probability, as previously suggested by Yackulic

et al. (2011). The key role of human land use changes in species extinction has been proposed by previous studies that identified habitat loss due to human land use as the main threat for diverse vertebrate groups (Schipper et al. 2008, Hayward 2011, Pekin and Pijanowski 2012, González-Suárez and Revilla 2014). In our study, we find that indeed greater extirpation risk is generally associated with more humanized areas. However, a correlation between human use and extirpation does not imply a direct causal relationship. Other factors, such as the presence of invasive species or climate change, could be spatially correlated with human uses leading to similar patterns of contraction (Franco et al. 2006, Thomas et al. 2006). The potential role of these other factors could be explored considering our new proposed baseline that accounts for relative position and human impacts.

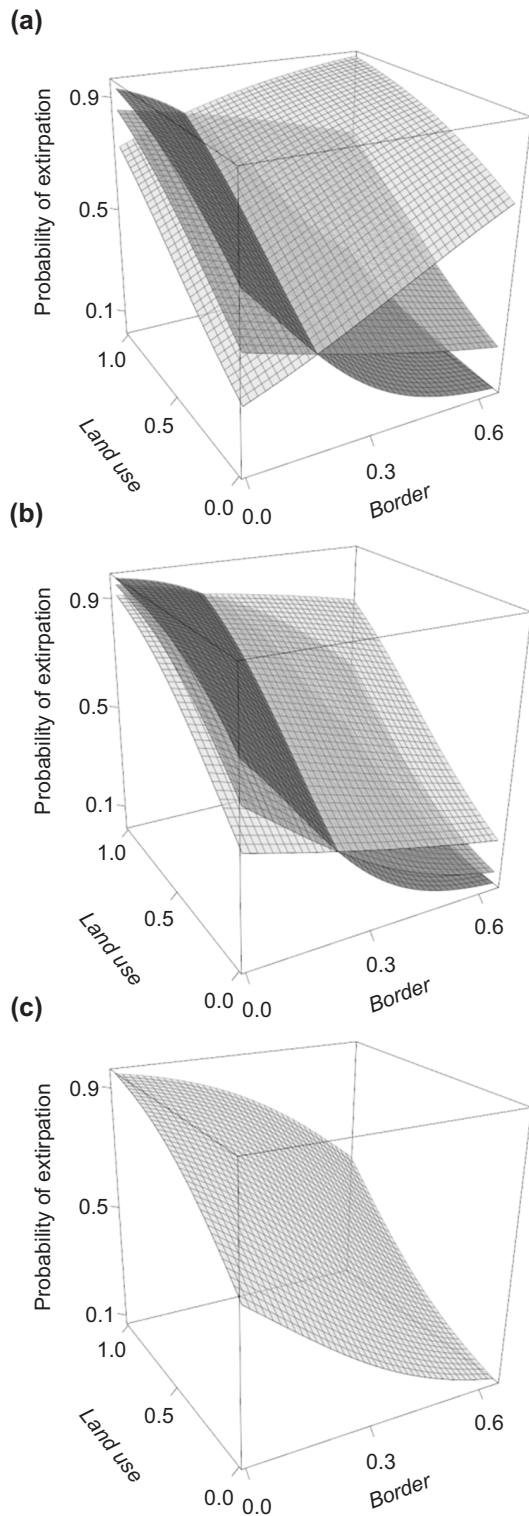


Figure 4. Predictions of the supported regression models explaining probability of extirpation of an area as a function of its distance to the historical border (*Border*) and its human land use (*Land use*) with a possible interaction of *Land use* and the percentage of contraction (*Contraction*). At the range scale, panel (a), model *Combined_2* (including the interaction) was the single supported model (Table 1). At the fragment scale both model *Combined_2* (b) and model *Combined_1* (c, no interaction) were supported. To visualize the effect of the interaction between *Border* and *Contraction* (a, b), we represent predictions at three levels of contraction: 20% in darker grey, 50% in medium dark grey, and 80% in light grey.

Although extirpations are generally more common in humanized areas, some species persist within these regions. Distinct patterns may be due to intrinsic responses; some species are less sensitive to human impacts than others (Maklakov et al. 2011), and some even benefit from humanized conditions (Maclean et al. 2011). Additionally, extirpation may be determined by other drivers of extinction with different spatial configurations (Thomas et al. 2006, Clavero et al. 2009, González-Suárez et al. 2013, González-Suárez and Revilla 2014). A caveat of our approach is that our data reflect only current human land uses, which may not correspond to the past uses potentially responsible for observed extirpations (Plieninger et al. 2006, Carvalheiro et al. 2013). It is not clear to us, however, how this could bias our results since we analyzed a large number of species at a global scale, and the progress of land use changes has been heterogeneous across the world. While land uses often intensify with time, the rates of intensification vary by area, and may affect species differently (Bregman et al. 2014, Gilroy et al. 2014). For example, in some areas of Europe and North America there has been a reversal toward more natural uses as agricultural land has been abandoned, but this reversal has not occurred in other areas (MacDonald et al. 2000, Strijker 2005, Mottet et al. 2006, Gellrich et al. 2007). Future studies would be necessary to address the temporal aspect of land use changes; however, human activities and land use are still likely to be key factors driving range contraction. In fact, they may well play an even more important and complex role than identified here, e.g. areas with intense agricultural uses have a greater impact than agri-environmental management areas (Franco et al. 2006, Carvalheiro et al. 2013).

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

In addition to the importance of human land use, our analyses show that the relative position of an area also influences its probability of extirpation (Lawton 1993, Brown 1995, Channell and Lomolino 2000a, b). At the range scale our results indicate that the probability of extirpation near the border (or the center) depends on the contraction stage. This pattern can be caused by directional threats as proposed by Channell and Lomolino (2000a, b). For example, climate change can create latitudinal and altitudinal clines (Parmesan 1996, Parmesan and Yohe 2003). However, there are alternative mechanisms that can also lead to this observed pattern. Climatic and biotic factors generally define range limits (Araújo and Rozenfeld 2014), but some boundaries are due to abrupt ecosystem changes or physical barriers, such as mountain chains or the transition from land to ocean. In these cases, border areas may actually represent optimal habitat and thus, be the most populated (Caughley et al. 1988, Sagarin and Gaines 2002, Gaston 2003). When optimal habitat occurs in a range border, a directional pattern of contraction could simply occur due to intrinsic population dynamics, as less dense populations are more likely to go extinct.

At the fragment scale we found support for two apparently contrasting models. The simplest model predicts that the probability of extirpation is always higher near the border, while the best model suggests that the probability

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

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

A new baseline to understand range contraction: multifactorial null models

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

Understanding range contraction is important for conservation and management, particularly if we hope to accurately predict future range changes and assess the effects of new threats (Thomas et al. 2004, 2011, Newbold et al. 2014, Peters et al. 2014, Selwood et al. 2014, Stanton et al. 2014). Our global study based on data from four different groups of vertebrates reveals the need to develop more realistic null models to use as baselines. Without departing from the objective of simplicity, we propose to combine simple key elements already identified as relevant to define new multi-process null models of range contraction. We realize that

data at this scale could have their own limitations, but we feel that these models can offer a more realistic baseline to evaluate the role of additional factors, such as the effect of different types of range borders, the role of environmental conditions, additional human and natural threats, as well as how intrinsic species' traits influence contraction range dynamics.

Acknowledgements – We are sincerely grateful to Kevin Gaston, Thomas Wilson, Miguel Delibes, Miguel Ángel Olalla, the members of the Spatial Ecology Lab (Univ. of Queensland), the members of the Dept of Conservation Biology (EBD-CSIC) and the personal from the Geographic Information System Laboratory (LAST-EBD-CSIC) for their help with technical aspects and helpful suggestions about the manuscript. We are also in debt to Ángel Lucas for the artwork in Fig. 2. This work was funded by the Spanish Ministry of Economy and Competitiveness (CGL2009-07301/BOS and CGL2012-35931/BOS co-funded by FEDER, and the FPI grant BES-2010-034151), by the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 235897, and by a Juan de la Cierva post-doctoral fellowship (JCI-2011-09158). We also acknowledge funding from the Spanish Severo Ochoa Program (SEV-2012-0262).

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Supplementary material (Appendix ECOG-01819 at <www.ecography.org/appendix/ecog-01819>). Appendix 1–2.