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

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ABSTRACT

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

Keywords: conservation, extinction, fragmentation, range, vertebrates

INTRODUCTION

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

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

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

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

At the local/population scale, other spatial configuration aspects have been shown to influence extinction risk and population trends (Bascompte and Solé 1998, Crooks et al. 2017, David Tilman and Kareiva 1997, Hanski 1999, Levins 1969, MacArthur and Wilson 1967, Pfeifer et al. 2017). Landscapes are heterogeneous spaces with varying degrees of habitat suitability (Forman 1995, Forman and Godron 1986). Habitat suitability also varies within occupied fragments between the border, where is usually lower, and the core areas, where tends to be higher (Bascompte and Solé 1995). Therefore, for a given area the shape of the fragment is important. Fragments with a greater ratio of border to core tend to have lower habitat suitability and thus, less carrying capacity, than more compact or circular fragments. The viability of spatially structured populations is also influenced by the degree of fragmentation, i.e., the size and number of fragments, of the available habitat (Gyllenberg and Hanski 1992, Hanski and Gyllenberg 1997, Hanski and Gyllenberg 1993). Heterogeneity in fragment size may also influence vulnerability. When heterogeneity is large, with one fragment much larger than the rest, vulnerability is mostly determined by the probability of extinction of this largest fragment, and larger fragments are less likely to become extinct (Hanski et al. 1996). However, if threatening impacts concentrate on that larger patch the risk could be greater with high heterogeneity than if similarly sized fragments (exposed to different risks) existed.

Complete species' ranges also show diverse spatial configurations, e.g. multiple fragments of varying sizes, located at different distances, and with diverse shapes that differ in their border to area ratios (Brown 1995, Channell and Lomolino 2000a, b, Gaston 1990, Gaston 1994, Gaston 2003, Gaston 2008, 2009, Lawton 1993). Some of this variation reflects differences in geographic conditions and species' traits (dispersal abilities or habitat specialization). Additionally, variation in spatial configuration can reflect effects of human impacts, such as changes in land use or climate change, which can cause local extinctions leading to area loss, changes in shape and fragmentation, and altered patterns of dispersal and colonization (Albrecht et al. 2017, Turvey et al. 2015). Arguably, ignoring variation in the spatial configuration of species' ranges could lead to over- or under-estimation of conservation status and thus, less effective use of conservation resources. Previous studies have assessed the effects of different spatial metrics on conservation status (Cardillo et al. 2008, Joppa et al. 2016, Keith et al. 2018, Murray et al. 2017), but we lack a comprehensive evaluation covering different taxa and testing multiple descriptors.

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

METHODS

Data

Species maps were downloaded from the International Union for Conservation of Nature (IUCN 2015) for all available species of amphibians, non-marine birds, and terrestrial mammals. Reptile and fish data are only available for particular clades (assessments are ongoing) and thus, these vertebrate groups were not considered for this general study. IUCN spatial maps are not perfect representations of each species distribution but are the best possible map assessors can make considering the available information (IUCN 2018). These maps are depicted as polygons, and each polygon has information about several attributes including presence, origin, and seasonality (IUCN 2018). Ideally, polygons for these maps should be drawn by assessors using occurrence data, but the methods and the quality and quantity of the occurrence data can vary across assessment. Using occurrence data a species EOO can be directly calculated linking locations by a minimum convex polygon, and AOO can be estimated by the overlap of species occurrences with a grid with a standard cell size (Lee et al 2019). However, the IUCN provides only the polygons defined by the assessor, not the occurrence data. Given this limitation we estimated range size here using the approach taken by most previous studies (Cardillo et al. 2008, Purvis et al. 2000): adding the area of polygons classified as native or reintroduced in origin, with extant or probably extant presence, and seasonality values of resident, breeding season, or non-breeding season for birds, and all seasonality values for amphibians and mammals (IUCN 2018; Table A1). This estimate approximates AOO in many cases, but could be larger (approaching EOO) for species in which species maps were defined with poor quality data or making broad assumptions about occupancy. We projected the selected polygons using the Winkel tripel projection, which aims to minimize the three kinds of distortions: area, direction and distance and with the Cylindrical equal area projection which maintain the area.

From each of the projected maps we used ArcMap 9.3 (ESRI 2008) to measure geometries and R 3.1.2 (R Development Core Team 2017) to process the information, we calculated four variables: range size (*Area*), fragment shape (*Circularity*), number of fragments (*N_frag*), and fragment size heterogeneity (*Heterogeneity*; definitions in Fig. 1). To minimize the error in our variables due to distortions from projections, we used Cylindrical equal area to calculate *Area*, *N_frag* and *Heterogeneity*, and Winkel tripel to calculate *Circularity*. To better evaluate the role of fragmentation we limited our analyses to ranges with >1 distinct fragments (the minimum required to estimate *Heterogeneity*; Table A1). We tested the correlation among variables for each class and type analysis using Spearman correlation (Tables A2 and A3). In addition, because we expected spatial descriptors could be affected by *Area* (e.g., heterogeneity may be more likely in widely distributed species) we also explored how *Circularity*, *N_frag* and *Heterogeneity* vary with *Area* with correlation plots (Fig. A1) and fitting generalized linear mixed models for each variable (Table A4) with *Area* as the predictor and including taxonomic information (order, family, and genus) as random factors to control for evolutionary non-independence of the observations following González-Suárez and Revilla (2013), using the function lmer from the “lme4” package (Bolker 2018) in R.

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

Analyses

To avoid circularity in our analyses of extinction risk (based on Red List Status) caused by using predictors that had been used to define the response, we excluded species classified as threatened based on criteria B and/or D (small geographic range or area of occupancy and possibly fragmented and few locations, respectively; Table A1). We defined generalized linear mixed regression multinomial models that aimed to predict conservation status (modelled as Red List Status ordinal categories or Population Trend ordinal categories) as a function of *Area*, *Circularity*, *N_frag*, and *Heterogeneity*. Because our objective was to assess if additional descriptors of spatial configuration may affect the conservation status, we look if these descriptors resulted in improved models, using as our null model a regression including *Area* as the single predictor. Increasingly complex models that incorporated the other variables describing shape and/or fragmentation (Table 1) were compared to this null model using an information theoretic approach based on AICc (Burnham and Anderson 2002). Because we hypothesized that spatial configuration may have different effects depending on the range size, and because we found correlations between *Area* and the other variables (Table A4), we also defined models including interaction terms between *Area* and shape (*Circularity*) and/or fragmentation (*N_frag* and *Heterogeneity*). Inferences were based on the best supported model, defined as the one with the lowest AICc. If there were several supported models (models within two AICc units of the best model) these were considered and discussed. Because models included interaction terms we could not use model averaging techniques (Burnham and Anderson 2002). We fitted separate models for each taxonomic class because of their distinct characteristics in dispersal and life-history.

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

RESULTS

The final database for extinction risk analysis (based on Red List status) included data for 11,052 species (55% of the recognized diversity of the three taxonomic classes considered) representing 1,482 amphibians, 7,147 birds, and 2,423 mammals (23%, 69% and 46% of each group's diversity respectively. For a summary by Red List Status category see Table A6). The database available to predict Population Trend included 10,495 species (47% of the recognized diversity) representing 1,676 amphibians, 6,979 birds, and 1,840 mammals (26%, 67% and 35% of each group's diversity respectively. For a summary by trend category see Table A7). Initial descriptive analyses of these data showed that species with higher risk of extinction and decreasing population trend generally had smaller ranges, with more circular shapes and possibly fewer, more evenly-sized fragments (Figs. A2 and A3). We found *Area* was associated with all other descriptors of spatial configuration (Table A4, Fig. A1) with smaller range sizes associated with higher values of *Circularity*, lower values of *Heterogeneity*, and fewer fragments (*N_frag*).

Spatial Configuration and Extinction Risk

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

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

Spatial Configuration and Population trend

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

DISCUSSION

The spatial configuration of terrestrial vertebrate ranges varies by orders of magnitude in total area of occupancy and in the number, size and shape of their fragments. This heterogeneity is caused by natural and anthropogenic processes that define range boundaries and that vary in space and time (Gaston 2003, Lucas et al. 2016). This complexity is often considered when studying local extinction processes (Pfeifer et al. 2017), and it is acknowledged in the global assessments of the IUCN (IUCN 2012, 2015). However, it has been largely overlooked in comparative studies of species' extinction risk (Arbetman et al. 2017, Cardillo et al. 2008). As previously reported, the best descriptor of conservation status is the area of the range, likely due to its direct association with total population size: all else been equal, larger ranges should have lower risks (Bielby et al. 2008, Davidson et al. 2009, Giam et al. 2011, Harris and Pimm 2008, Joppa et al. 2016, Keith et al. 2018). In addition, the better conservation status of large range areas could be associated to a buffer effect against stochastic impacts. It is less probable that a big range would be entirely affected by a stochastic impact, while a catastrophe could affect a whole small range (Bland et al. 2016, Murray et al. 2017).

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

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

Range shape and conservation status

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

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

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

Moreover, there are situations in which extinction risk may not increase with the number of fragments. If the primarily causes of extinction are environmental stochastic processes, even large populations are vulnerable to extinction, e.g. in the spread of invasive species there is a positive spatial autocorrelation (Veran et al. 2016), thus multiple fragments (subject to independent environmental processes), could act as a buffer against perturbations (Gilarranz et al. 2017), reducing the overall risk (Quinn and Hastings 1987). This buffer effect mechanism could be explaining why for amphibians, a class where the risk of extinction in many species is associated to a contagious disease (Hoffmann et al. 2010, O'Hanlon et al. 2018, Stuart et al. 2004), more fragmented ranges are associated with less risk of extinction.

Populations with a fragmented range but with most area located in a single fragment (continent-island system) would have a substantially lower extinction probability when compared with populations with a more homogeneous distribution of fragment areas (Hanski et al. 1996, Thomas and Kunin 1999, Wiegand et al. 2005). If the population is divided into multiple fragments the heterogeneity of the network can reduce risk favoring rescue effects (Gilarranz and Bascompte 2012, Hanski et al. 1996). If we consider that connectivity of a fragment is positively correlated with its size, a range with high heterogeneity in its area would have a high heterogeneity in its connectivity and less risk of extinction. How the range area was distributed among the existing fragments was also a relevant descriptor of conservation status with an effect that often depended on the total area of the range. As expected, for big range sizes, high heterogeneity was generally associated with lower extinction risk, as the overall species extinction risk is directly linked to the risk of the largest fragment, and because large continuous fragments suffer less edge effects (Murray et al. 2017). As the size of the largest fragment is the main limiting factor, species with small ranges cannot show a large effect of the heterogeneity of fragment size. Indeed, heterogeneity and number of fragments increased with range area. In birds, the effect was most noticeable in species with ranges with many fragments for which the potential for higher heterogeneity is greater. On the other hand, increased extinction risk in ranges with more homogeneously-sized fragments may be a consequence of the dynamics of range contraction and expansion. Range contraction may lead to range collapse and a high fragmentation at the end of the process (Riordan et al. 2016, Rodríguez and Delibes 1992, 2002, 2003). During contraction, fragments may split into smaller fragments, thus reducing maximum fragment size. However, minimum fragment size is constrained by the minimum size that can support a population in the short term. Therefore, the final stages of range contraction may lead to more homogeneously-sized areas (Rodríguez and Delibes 2003).

Future directions

We found clear patterns of association between extinction risk and the spatial configuration of species' ranges. These effects can be interpreted as emergent properties of population dynamics at smaller spatial scales. In principle, they can be used to complement the role of range size in categorizing risk of extinction. Current data availability, quality and practice call for some caution in doing so (Hurlbert and Jetz 2007, Maréchaux et al. 2017). The spatial configuration of ranges is very sensitive to the method employed to define it. A range delineated by experts, using minimum convex polygon or a kernel method on the same dataset would look very different (Joppa et al. 2016). The large biases in sampling effort across the globe, with large areas with few data available also precludes obtaining good quality ranges (González-Suárez et al. 2012). We need more systematically and transparently built ranges that can offer better information over time, including patterns of range expansion and contraction. Current efforts compiling information at large scales and in big numbers, often with the aid of citizen science, could help in improving the quality of the ranges. Improved ranges would allow future work considering how species' traits, distinct threatening processes, and local environmental conditions may affect range dynamics and extinction risk. To advance from correlations between spatial pattern of ranges and risk of extinction/population trend to mechanisms, we need long-term data reflecting temporal variation in distribution ranges with different levels and combination of impacts. Looking to the past biodiversity responses to climate and human impacts will importantly help to fill this gap (Fordham et al. 2016, Nogués-Bravo et al. 2018).

Conclusions

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

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SUPPLEMENTARY MATERIAL

Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1.

TABLES

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

Model	**ΔAICc (AICc)**					
	Red List Status			**Population Trend**		
	Amphibians (n=1,482)	**Birds (n=7,147)**	**Mammals (n=2,423)**	**Amphibians (n= 1,676)**	**Birds (n=6,979)**	**Mammals (n=1,840)**
Size						
Area (Null model)	30.13	55.50	12.81	34.13	101.13	15.80
Size and Shape (*Circularity*)						
Area+Circularity	15.17	54.42	13.55	15.07	92.41	7.09
*Area*Circularity*	**10.37**	**25.32**	15.22	**1.69**	**33.61**	**4.19**
Size and Fragmentation						
Area+N_frag	26.48	57.33	14.35	24.42	103.12	15.58
*Area*N_frag*	27.94	58.57	15.27	26.44	94.98	15.74
Area+Het	31.69	45.32	10.84	35.65	68.83	14.73
*Area*Het*	18.51	25.90	**0.21**	34.71	61.87	10.87

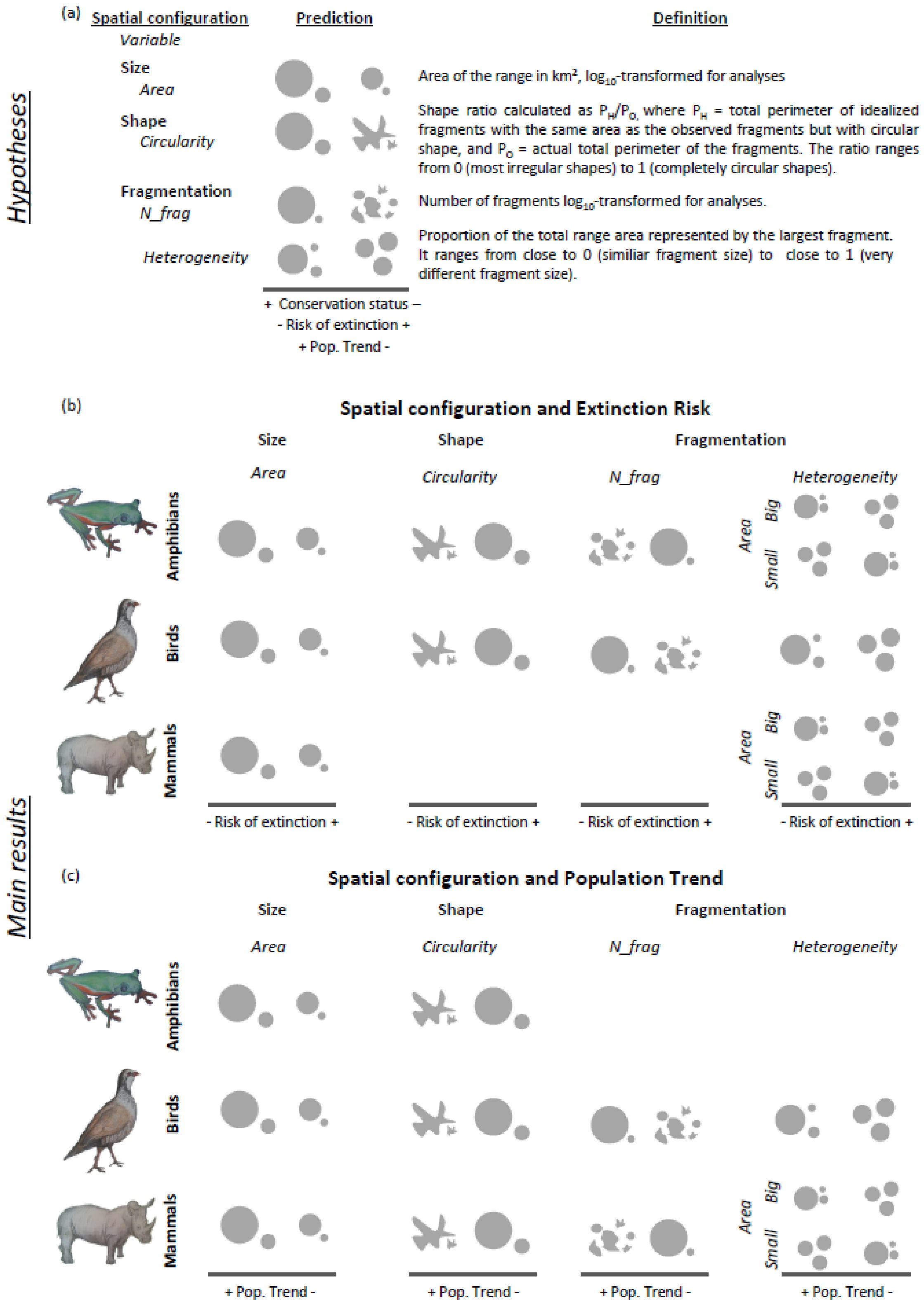
Area*Het+ Area*N_frag	**11.91**	28.39	**0.00**	**21.54**	57.00	**6.43**
Area*Het+ Area*N_frag+ Het*N_frag	13.14	**20.55**	**1.44**	22.69	**50.55**	5.84
Size, Fragmentation and Shape						
Area* Circularity+Area*Het+Area*N_frag	**0.00**	–	–	**0.00**	–	**0.00**
Area*Circularity+Area*Het+Area*N_frag+N_frag*Het	–	**0.00**	–	–	**0.00**	–

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

Variables	**T-values (coefficient/SE) Red List Status**			**T-values (coefficient/SE) Population Trend**		
	Amphibians (n= 1,482)	**Birds (n=7,147)**	**Mammals (n=2,423)**	**Amphibians (n= 1,676)**	**Birds (n=6,979)**	**Mammals (n=1,840)**
Area	-0.43	-6.745	-3.44	-7.39	-5.84	-2.36
Circularity	0.28	-4.21	-	-2.16	-6.08	-1.17
Heterogeneity	2.49	2.24	3.09	-	0.08	0.80
N_frag	-1.45	0.30	-	-	1.06	-2.23
Area* _Circularity_	0.66	4.69	-	3.94	6.91	1.86
Area* *N_frag*	0.93	1.65	-	-	0.94	2.00

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

FIGURE LEGENDS



Area of the range in km², $\log_{10}$-transformed for analyses

Shape ratio calculated as P_H/P_O, where P_H = total perimeter of idealized fragments with the same area as the observed fragments but with circular shape, and P_O = actual total perimeter of the fragments. The ratio ranges from 0 (most irregular shapes) to 1 (completely circular shapes).

Number of fragments $\log_{10}$-transformed for analyses.

Proportion of the total range area represented by the largest fragment. It ranges from close to 0 (similiar fragment size) to close to 1 (very different fragment size).

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

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

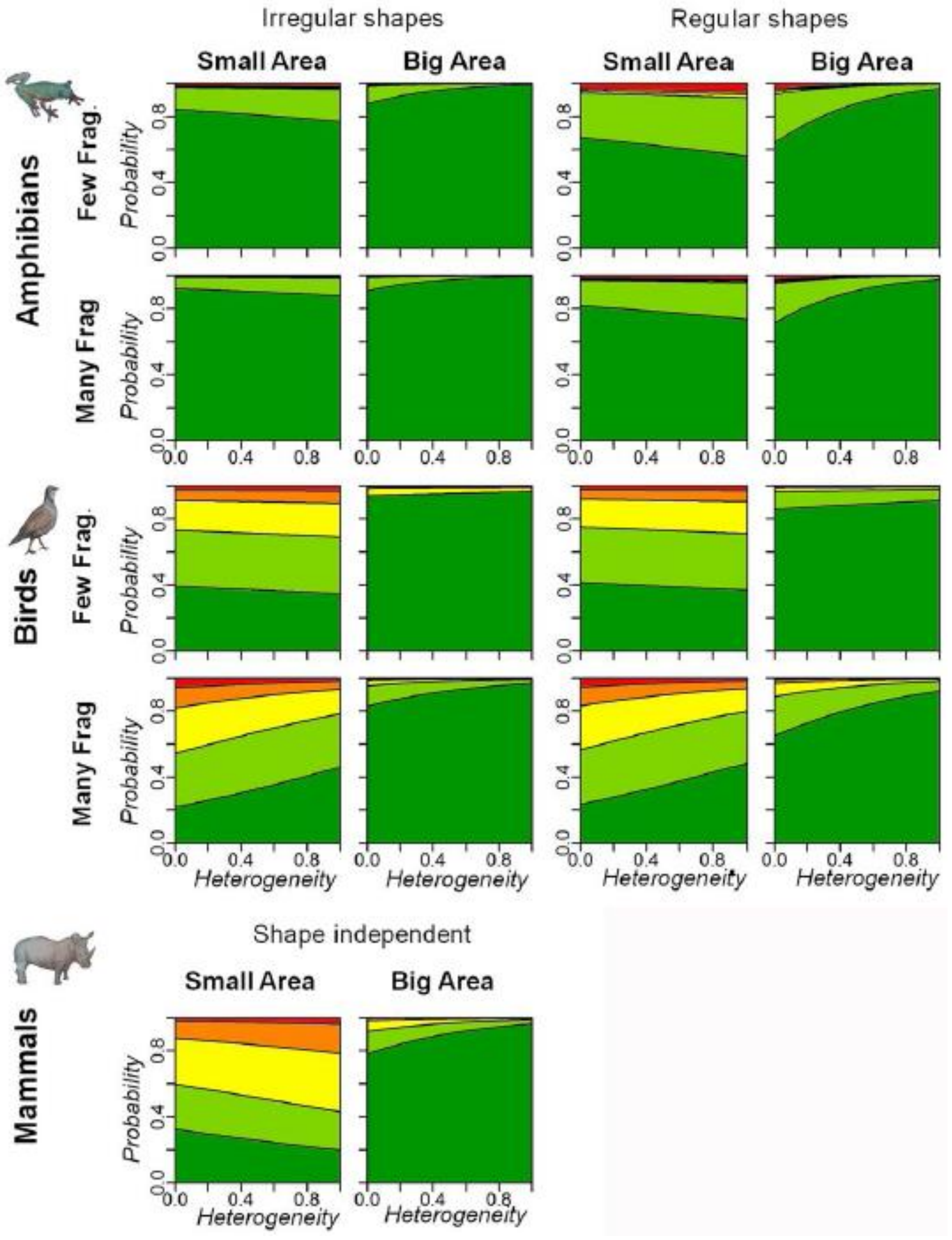


Figure 2. Predicted marginal probabilities for each Red List Status (Table A6), with dark green for Least Concern (LC), light green for Near Threatened (NT), yellow for Vulnerable (VU), orange for Endangered (EN) and red for Critically Endangered species (CR), based on the best models for each class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

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

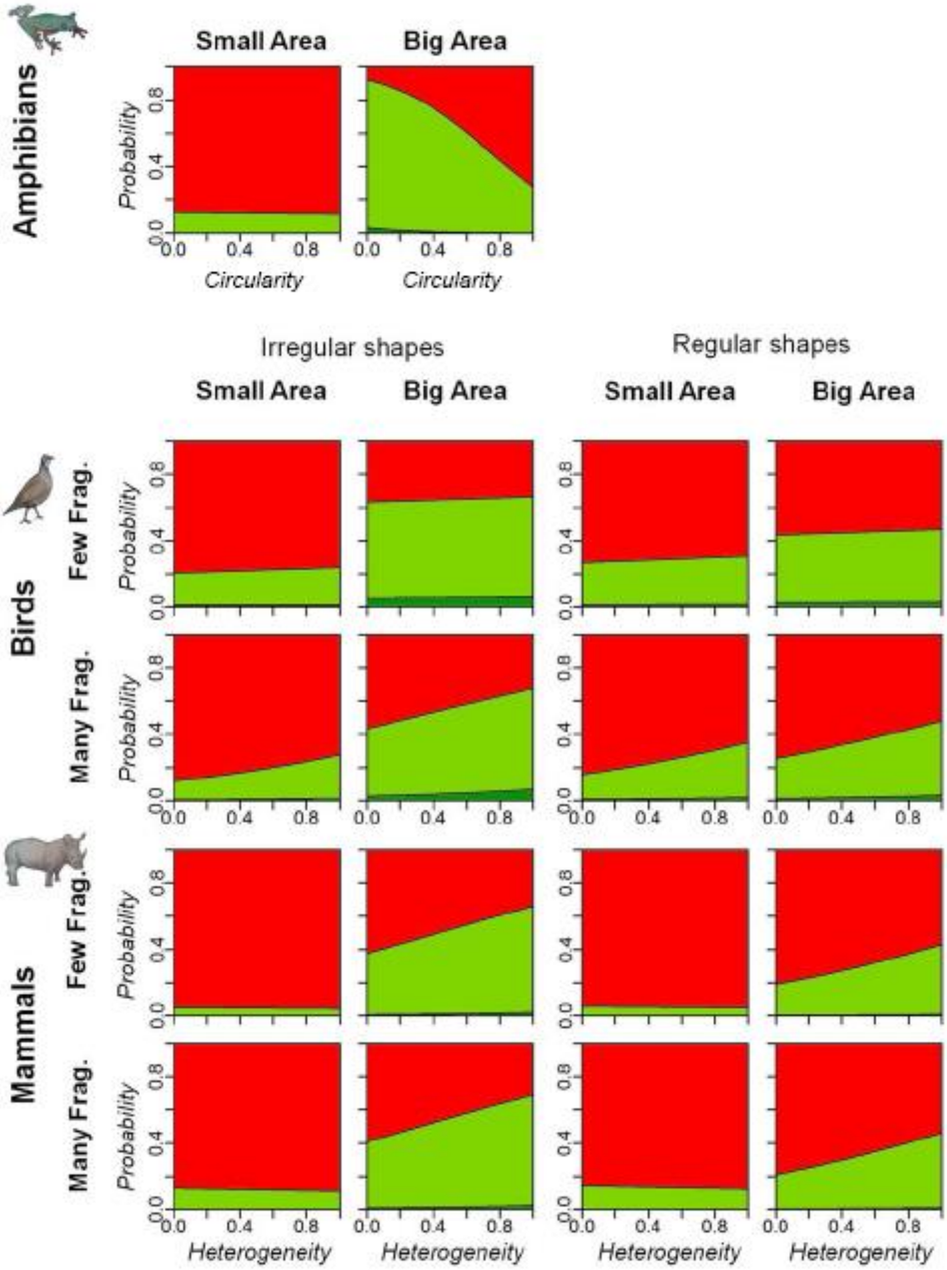


Figure 3. Predicted marginal probabilities for each category of Population Trend (Table A7), with dark green for Increasing, light green for Stable, and red for Decreasing trends, based on the best models with descriptors of spatial configuration for each class (coefficients in table 2). Note that in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

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

Supplementary material

Appendix 1.

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

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

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

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

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

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

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

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

* $p < 0.05$

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

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

* percentile 5

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

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

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

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

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

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

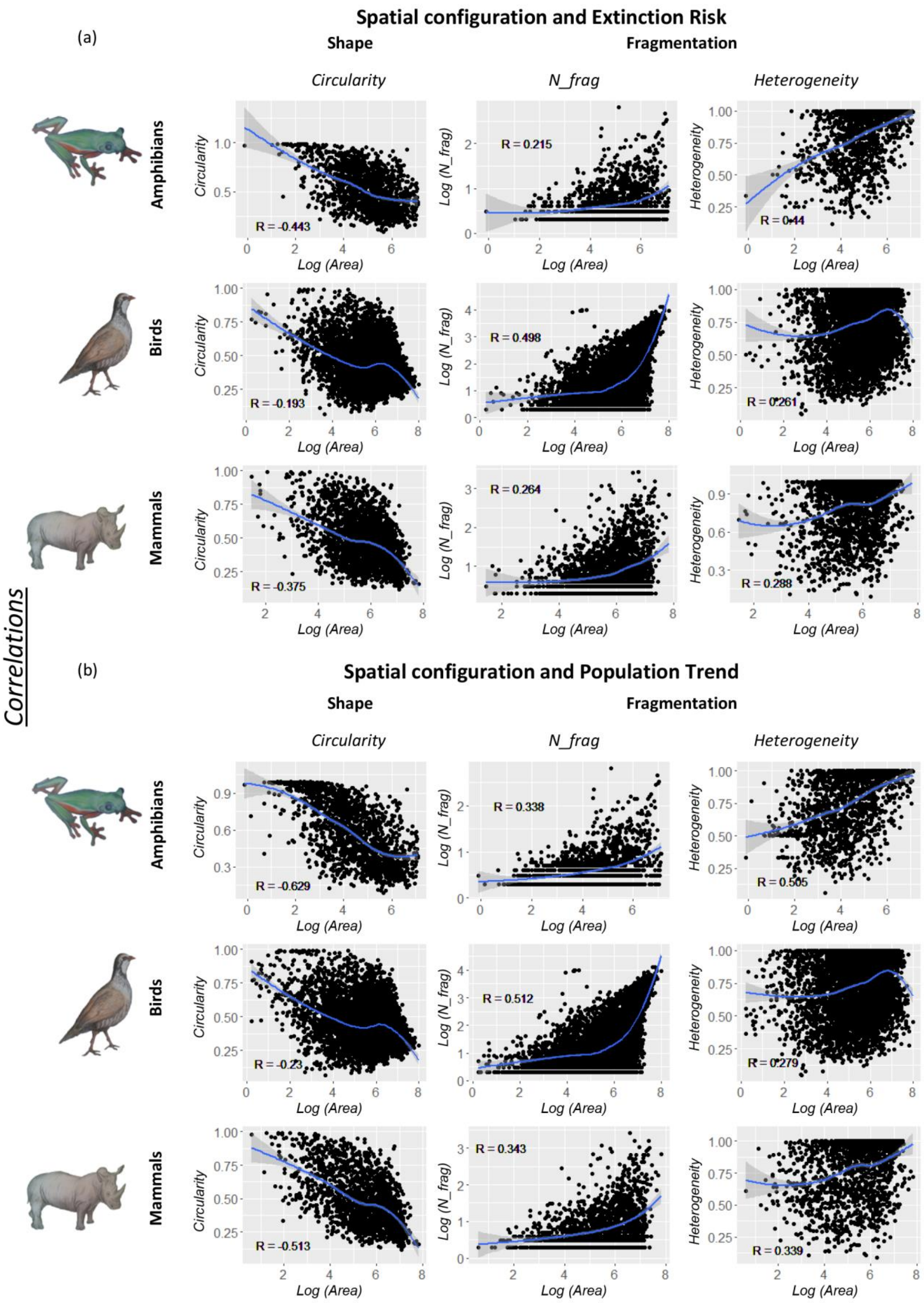


Figure A1. Correlation among the variable *Area* and the other variables used in the analysis (*Circularity*, *N_frag*, *Ratio*) for the data used in the analysis of spatial configuration and extinction risk (a) and the data used in the analysis of spatial configuration and population trend (b).

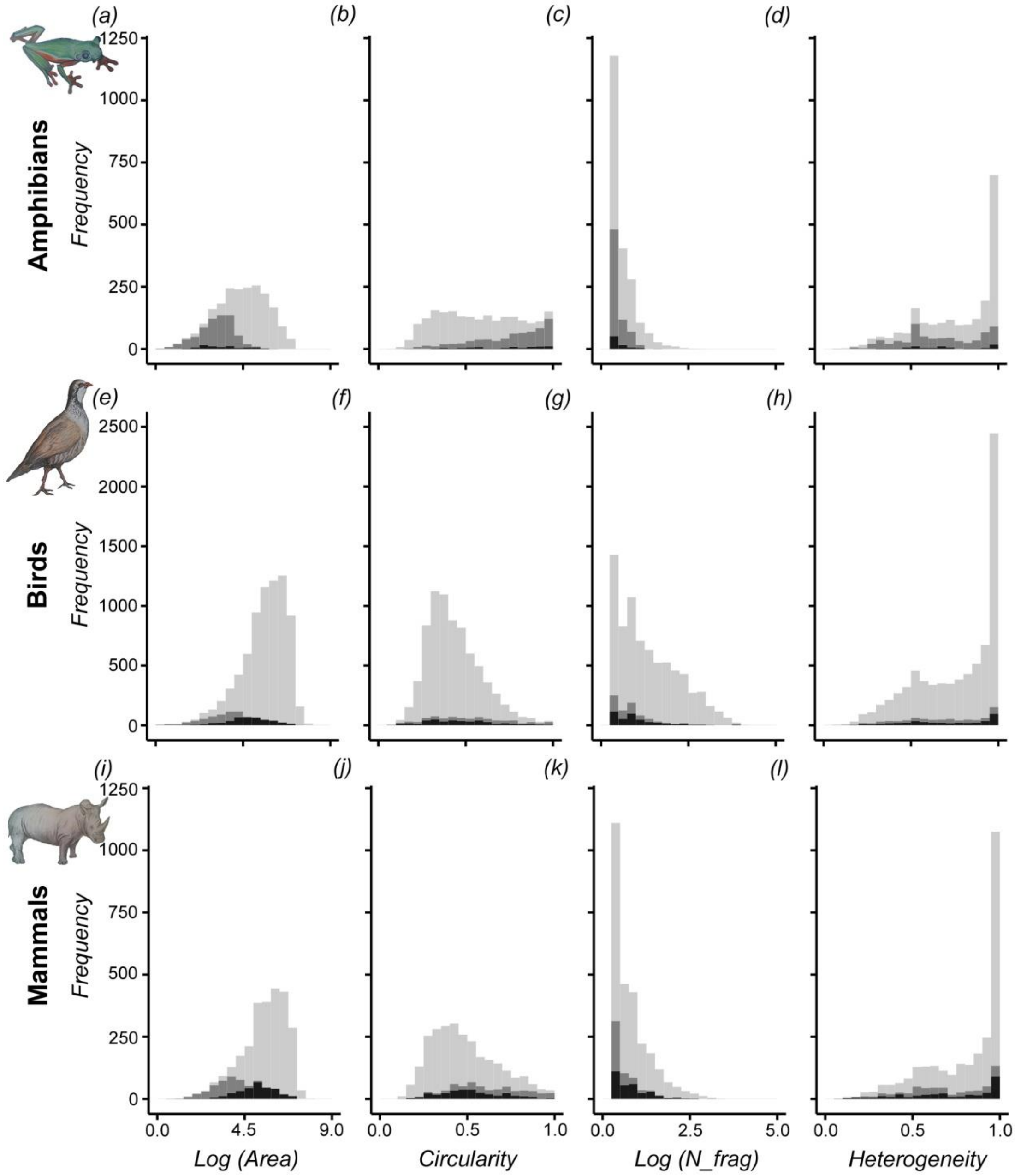


Figure A2. Frequency distributions for the variables *Area*, *Circularity*, *N_frag* and *Heterogeneity* for multi-fragment ranges of amphibians, panels a, b, c, d respectively, mammals, panels e, f, g, h respectively, and birds, panels i, j, k, l respectively. Non-threatened species (Least Concern and Near Threatened Status) are in light grey (1,403 species of amphibians, 6,718 species of birds and 2,110 species of mammals which were included in our regression analyses), threatened (Vulnerable, Threatened and Critically Endangered) species classified based on criterion B and D (608 species of amphibians, 382 species of birds and 291 species of mammals which were not included in our regression analyses) are in medium grey, and all other threatened species (79 species of amphibians, 429 species of birds and 313 species of mammals which were included in our regression analyses, table S2) are in dark grey.

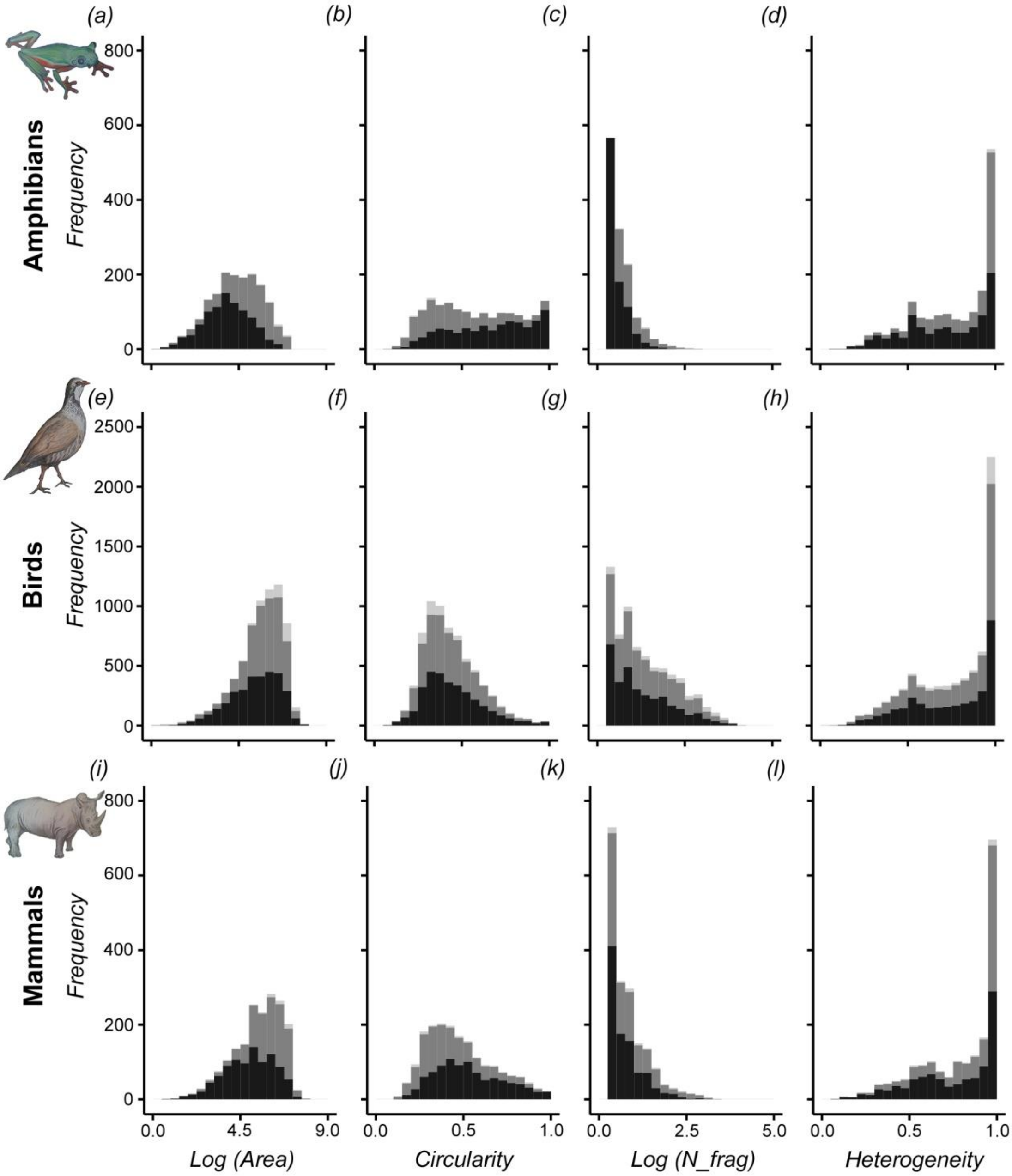


Figure A3. Frequency distributions for the variables *Area*, *Circularity*, *N_frag* and *Heterogeneity* for multi-fragment ranges of amphibians, panels a, b, c, d respectively, mammals, panels e, f, g, h respectively, and birds, panels i, j, k, l respectively. Species within increasing Population Trend are in light grey (19 species of amphibians, 472 species of birds and 49 species of mammals; generally few species and thus, sometimes not clearly visible), stable Population Trend are in medium grey (726 species of amphibians, 3,312 species of birds and 830 species of mammals), and decreasing Population Trend are in dark grey (931 species of amphibians, 3195 species of birds and 961 species of mammals which were included in our regression analyses, table S3).

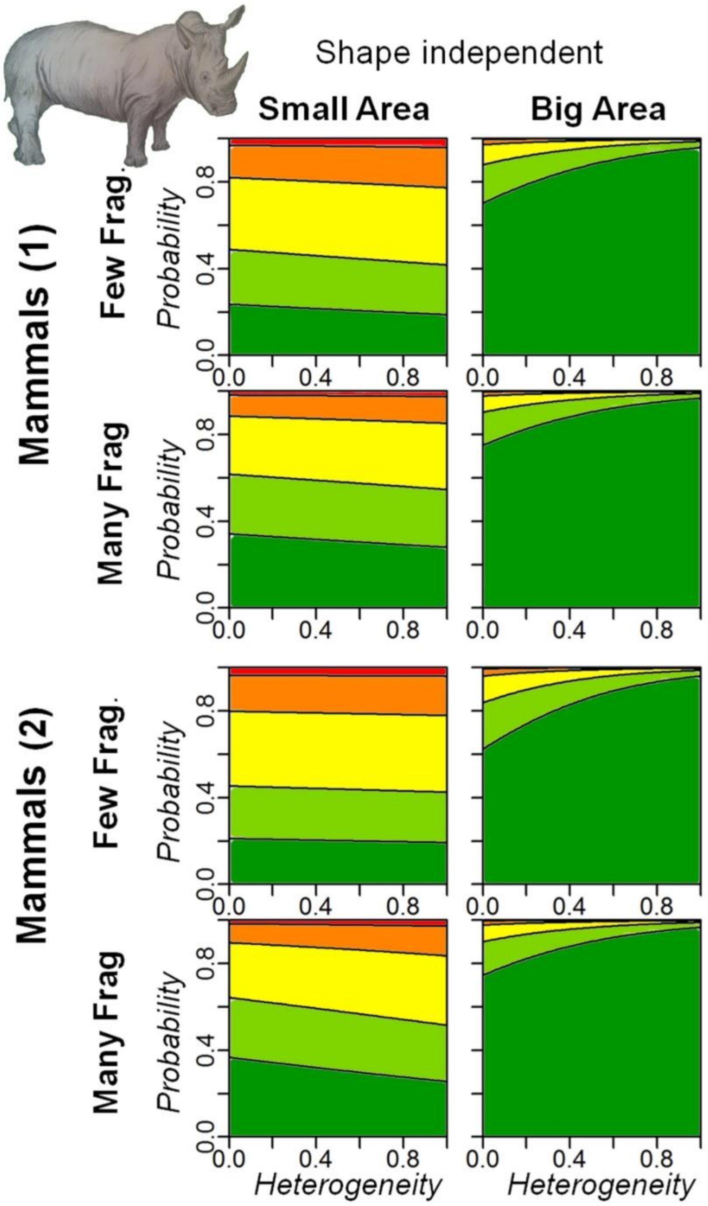


Figure A4. Predicted marginal probabilities for each Red List Status (Table S2), with dark green for Least Concern (LC), light green for Near Threatened (NT), yellow for Vulnerable (VU), orange for Endangered (EN) and red for Critically Endangered species (CR), based on the two best alternative models,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

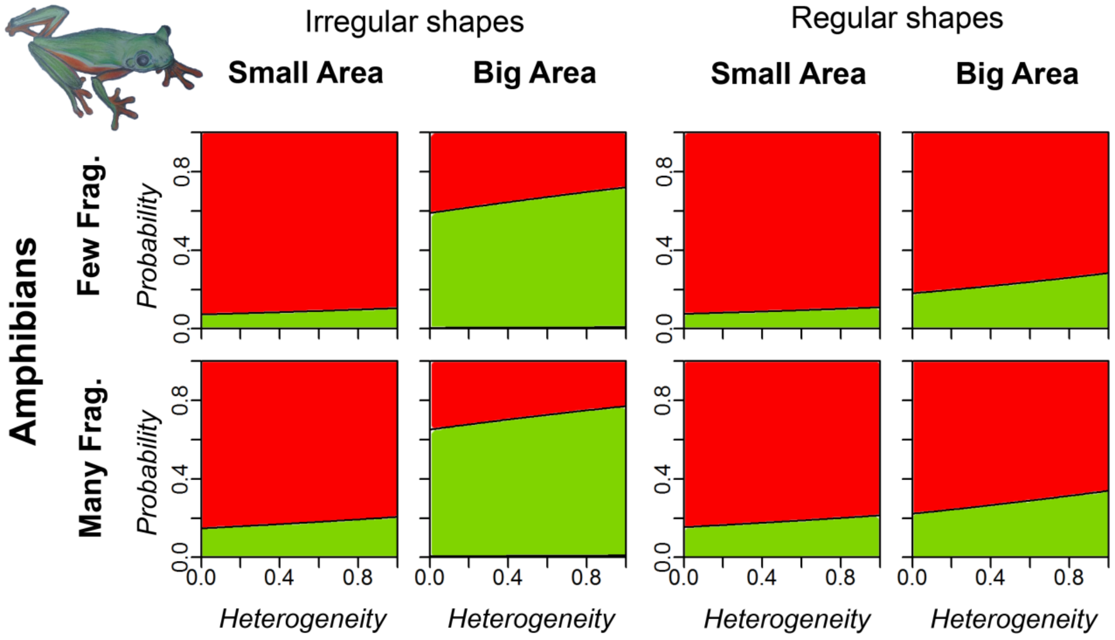


Figure A5. Predicted marginal probabilities for each category of Population Trend (Table S3), with dark green for Increasing, light green for Stable, and red for Decreasing trends, based on the best alternative model, for amphibian class (Tables 1 and A6). Note that in some plots the predicted probably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